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Peter G. Beninger *Editor*

Mudflat Ecology

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Mudflat Ecology

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Photo PG Beninger

Mud is Beauty in the making,

Mud is melody awaking…

Mud is mankind in the moulding,

Heaven's mystery unfolding…

- Robert William Service

For three wonderful women who have enriched my life immensely: my wife Li Jin, and our daughters Amelia and Cordelia.

For my brother Ian, without whom none of this would have been possible.

Foreword

By any measure, and despite visual appearances, mudflats constitute a highly diverse scientific subject, posing a great challenge for the student or researcher of this ecosystem. Embedded within this disciplinary diversity is the extraordinary biological diversity of mudflats, once again belying their visual appearance. Mudflats have existed since the oldest sediments were formed, and hosted Earth's earliest life, unambiguously already evolved in 3.48-billion-year-old rocks. Let me add that they are one of Earth's largest ecosystems, lining thousands of miles of our worldwide coastlines. From this point of view, it is astonishing that scientific exploration, while proficient in heading to remote areas such as Mars, seemingly is still in its infancy when it comes to the understanding of the mucky and wet mudflats so close to us.

Perhaps it is indeed the seemingly inhospitable nature of mudflats that has kept research efforts at bay? Or perhaps, since mainstream research in the ocean and Earth sciences focuses on topics of either the marine or the terrestrial realm, the very hybrid character of mudflats, bridging the terrestrial and marine environments, has created a subconscious 'confusion barrier'? Funding agencies, methodological approaches, and terminology commonly serve only one or the other environment, so it requires those with a strong heart to overcome at times significant disciplinary barriers. And then there is the intrinsic problem that ecosystem research faces by definition: tracking an ecosystem's individual components is a slippery endeavour, because they constantly interact and affect each other.

This well-composed book discusses the fundamental ecology of mudflats, as well as the human impact of the Anthropocene on this environment. Human impact includes the introduction of invasive species, the harvesting of natural and cultured populations by the growing human population, and the overprint of the natural setting by these and other human activities. While effects on macroscopic organisms such as birds may be easier to document, the complexity of the immensely fine network between microorganisms, and their effect on physical and chemical properties of the sediment and water, is beyond our comprehension at this time. In order to analyse a complex ecosystem such as mudflats, it is imperative that scientists of various disciplines work together. This inspirational volume will greatly contribute to this discussion and assist the student/scientist drawn to interdisciplinary research in acquiring the indispensable overview of the many facets of mudflat ecosystems, the status quo of research, and the most interesting challenges for the future.

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Nora Noffke

Preface

Historically, our efforts to understand the natural world have been the most fruitful when we proceeded to carve it up into cognitively manageable units—whether geological epochs, locations in the periodic table of the elements, taxonomic categories, or whole fields of study. Over the course of its history, the field of marine biology has itself progressively subdivided with the growth of its knowledge base; today, it is no more surprising to find coral reef or deep-sea ecologists than it is to find forest or grassland ecologists in the terrestrial system.

Perhaps due to its particular 'charisma', the mudflat habitat has not yet been ennobled by a study field label. Yet although it shares some features with the soft-substrate sublittoral environment, the mudflat is nonetheless a distinct habitat, with specific and ecologically far-reaching particularities. Previously scattered throughout the marine biology literature, the multiple facets of mudflat ecology are brought together for the first time in this work; we thereby hope to establish mudflat ecology as a true, diverse, yet intrinsically and necessarily coherent, field of study.

We are fortunate that such talented researchers as those assembled here have made their contributions to this work. Some of them will be very familiar to those who follow the literature, while others may be less well known, and this is because they may be younger scientists replete with promise. We are also indebted to their equally talented peers who have agreed to review chapters within their specialties:

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Chapter 1
Introduction: Mudflat Basics

Peter G. Beninger and David M. Paterson

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Abstract The study of mudflats should logically start with the type of intertidal depositional shore we consider to be true mudflats, and then an overview of their global distribution. Their dominant feature being mud, we then consider the etymology and cognitive associations of the word 'mud', the basics of sediment composition and its living matrix, and the concept of mudflats as systems of superposed emergent properties. Equipped with these basics, we may then proceed to a proper geological consideration of mudflats, our next chapter.

1 Mudflat Distribution

Intertidal depositional shores composed of fine sediments are a familiar environment to most marine biologists. The most commonly recognised parts of such coasts consist of either salt marshes (temperate zones) or mangrove systems (tropical zones). Indeed, mangrove systems occupy approximately 170,000 km^2, or 75% of

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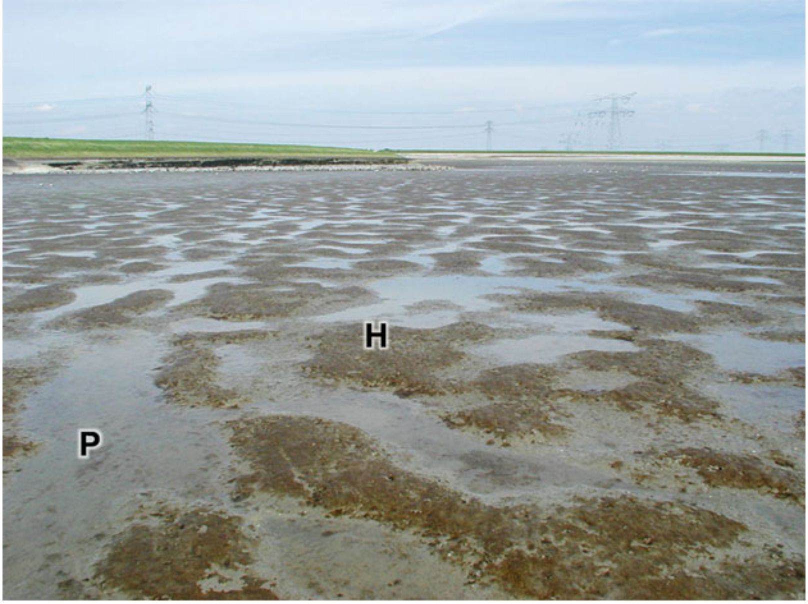

Fig. 1.1 A mudflat in the Netherlands, showing low-grade topography, with alternating pools (P) and hummocks (H). Microphytobenthos (light brown pigmentation) is evident on the crests of the hummocks. Photo J. van der Koppel.

all tropical coastline (Flemming 2002). In contrast to these extensively-vegetated habitats, true intertidal mudflats are vegetationally depauperate, and also generally lacking in visible macrofauna, such that the term 'mudflat' is very apt to describe their appearance: muddy, with very little three-dimensional complexity (Fig. 1.1). Although intertidal mudflats are commonly understood to be 'distributed widely along the world's coastlines' (Gao 2009), estimations of the total area occupied by these environments are conspicuously lacking. A remarkable, although incomplete, survey of the world's mudflats identified 350 major sites, with 79 greater than 5 kha (Deppe 1999). Of these, 19 were from 5–20 kha, 28 from 20–80 kha, and 26 were larger than 80 kha. Most (84%) mudflats were situated in protected topographical formations such as estuaries, bays, and behind barrier islands. The two largest and well-known examples are the Yellow Sea and the Wadden Sea mudflats (Fig. 1.2). An unknown number of mudflats remain undocumented in poorly-mapped regions of the globe (Deppe 1999).

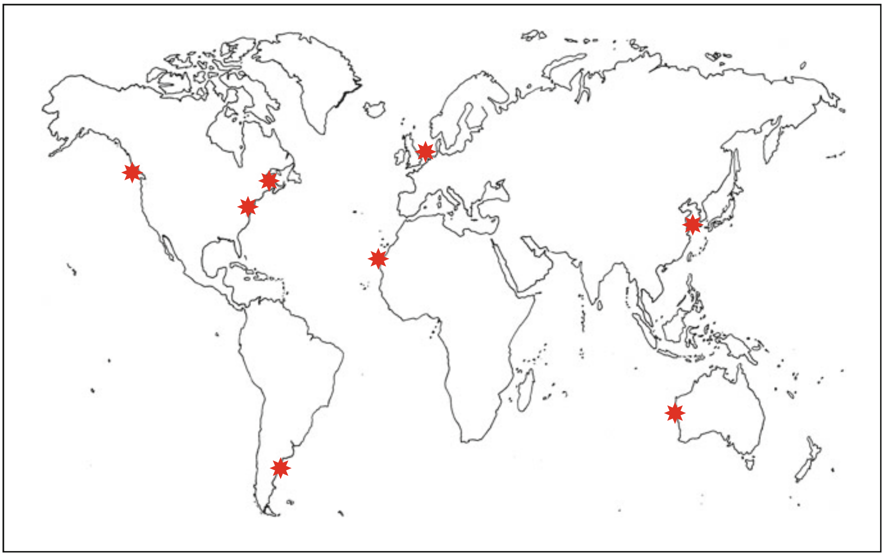

Fig. 1.2 Locations of some notable mudflats mentioned in the present volume. From west to east: Roberts Bank, Canada; Chesapeake Bay, USA; Bahía Blanca Estuary, Argentina; and Bay of Fundy, Canada; Banc d'Arguin, Mauritania; Wadden Sea, Netherlands; Shark Bay, Australia; Jiangsu (Yellow Sea), China. Original artwork, PG Beninger.

2 What Is Mud? Etymology and Cognitive Associations

At the outset, it is useful to define the term 'mud'. The full-size, multi-volume Oxford Dictionary devotes over 20 columns of very fine print to the word 'mud', its derivatives, and its etymological history. What emerges from this exposition is, first, that mud is a mixture of rock particles and water, varying in consistency from a semi-liquid to a plastic solid (much of the present volume will show how mudflat 'mud' is much more complex than this simple definition), and second, that the description as 'mud' or 'muddy' is a "loaded" term at several levels, persistently incorporating connotations of uncleanliness. It conveys a state lacking clarity, indeed, of almost complete opacity, and this may even be brought about intentionally ('muddying the waters'). It is used to describe confused thought ('muddled thinking'; 'clear as mud'). It has been used repeatedly to denote the worst of anything ('Scum of the mud of hell!', 'the mud of all races'). It characterizes an uninteresting person ('a stick in the mud'). It symbolizes spreading insults ('a mud slinger'). It describes a state of utter abjection ('your name is mud'). It is used to refer to the drug opium, due to its mud-like appearance (Simpson and Weiner 1989).

Amid all these negative associations with mud, there are some more positive ones. The Douay-Rheims version of the Bible translates Genesis 2: 7 as '. . .the Lord God formed man of the *slime* of the earth' (rather than the 'dust' in other versions).

Fig. 1.3 Making measurements and obtaining samples from extensive areas of mudflat can be logistically challenging, potentially dangerous, and exhausting. (NERC CBESS Project, Image E. Paterson).

Certainty can be declared 'as sure as mud'. And the popular toast 'here's mud in your eye' probably refers to the New Testament Siloam episode, where a man's sight was restored when Jesus put mud over his eyes (John 9: 7). However, even the knowledge that mud was the probable cradle of life (Cairns-Smith 1965; Ponnamperuma et al. 1982; Cairns-Smith and Hartman 1986; Sami and Tewari 2009; Noffke et al. 2013; Yang et al. 2013) has had comparatively little popular echo. Similarly, the probable role of mudflats in prehistoric human sedentarization (as sources of relatively easily-captured animal food) is largely unrecognized, despite the fact that they probably led to the establishment of the first settlements, and ultimately to the cities of today (the 'coastal zone' has a population density three times that of inland areas) (Jackson et al. 2001; Crossland et al. 2005). These examples illustrate our complex cognitive relationship with the term 'mud', and, together with the difficult working conditions imposed by mud (Fig. 1.3), may explain why mudflat ecology has not previously been widely considered a *bona fide* field of study.

Table 1.1 Mud-sediment grain sizes and corresponding sediment type

Grain size (μm)	*Φ* Value	Wentworth size class (Wentworth 1922)
6.25 to 3.1	4–5	Coarse silt
3.1 to 1.56	5–6	Medium silt
1.56–0.78	6–7	Fine silt
0.78–0.39	7–8	Very fine silt
<0.39		Clay

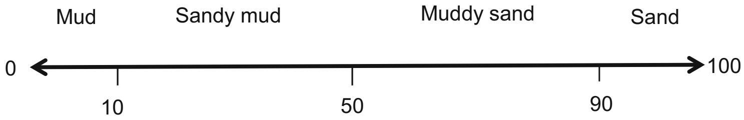

Fig. 1.4 Classification of sediments according to percent sand content (after Folk et al. 1970, modified and re-drawn, PG Beninger).

3 What Is Mud? Sediment Composition

Although a thorough treatment of mudflat geology is provided in Chap. 2, a brief definition of the terms of reference is warranted here. First of all, mud is chiefly *siliclastic*, i.e. composed of silicate particles eroded from rocks. Geologists classify sediments using the numerically-convenient phi size scale (Krumbein and Pettijohn 1938), based on the log ratio of grain size to a reference grain size (1 mm): $\Phi = \mathrm{Log}_2\ D/D_0$, where Φ is the phi-scale value, D is the grain size, and D_0 is the reference size (1 mm). Use of this numerically-convenient scale explains why the grain size class boundaries consist of non-rounded millimetric measurements; thus, mud-containing sediments are defined as non-indurated moist sediments with grain sizes <0.063 mm (very fine sand). At the finest extreme, the silt-clay boundary is fixed at 3.9 μm (Table 1.1).

Mudflats contain various proportions of these grain size classes, in addition to various proportions of larger-grained sand, and corresponding to the familiar classification of mud, sandy mud, muddy sand, and sand (Folk et al. 1970; Fig. 1.4).

4 What Is Mud? The Living Matrix

Microbes have been colonizing muddy sediments for billions of years (Noffke et al. 2013), and their activities have greatly contributed to the physical, chemical, geological, and biological properties of this substratum. The terminology used to refer to the living mud matrix is more precise in the geological literature, and more ‘loose’ in the biological, and especially the ecological, literature. As most of the following chapters will make reference to this matrix, it is necessary to define a set of descriptive terms at the outset:

Fig. 1.5 An empty cockle shell (*Cerastoderma edule*), deposited on the surface of an intertidal mudflat (Dee Estuary, UK) which has the brown coloration of a transient epibenthic biofilm (Photo D.M. Paterson).

Biofilm A population of microorganisms, typically at a solid-liquid interface, surrounded by a matrix of extracellular polymeric substance (EPS = mucopolysaccharides). At the microscopic level, biofilms may form around individual sediment particles; on mudflats, we (rather loosely) refer to the macroscopic patches of microbes and EPS on top of sediments as 'biofilm', when in fact we mean either 'transient epibenthic biofilm' or 'epibenthic microbial mat', or both (see below). While many workers generally understand 'biofilm' as microscopic and 'mats' as macroscopic, many others understand it as a catch-all term (whose convenience is matched by its ambiguity).

Transient Epibenthic Biofilm Characteristic of muddy habitats, epipelic (see below) microbes often migrate to the sediment surface during periods of daylight low tides and form visible patches (biofilms) on the sediment surface (Fig. 1.5). These patches disappear just before the return of the tide, (although they probably leave behind EPS and other microbes), hence the term "transient" (Consalvey et al. 2004).

Epibenthic Microbial Mat This EPS-rich mat develops within the first millimeters of muddy to sandy sediments in the lower supratidal zone, just above the upper intertidal zone. This zone can be quite large, given the low grade of the mudflat slope, especially on macrotidal flats (Noffke 2010). The epibenthic microbial mat separates the sediment from the water column when immerged, and from the atmosphere when emerged. When subjected to currents, sediment biostabilization is up to 12 times higher compared to that of equivalent barren sediment (Noffke and Krumbein 1999; Noffke 2010); this property will be seen to be crucial to the formation and function of geomorphological features on mudflats (Chap. 9). Epibenthic microbial mats form over several months and are functionally and structurally different from transient epibenthic biofilms, in that they are supratidal, anchored to the sediment, persist between strong tides, and are of a thicker and more coherent structure. If never eroded by strong storms, they can occur at the same location for many years (Noffke 2010).

Endobenthic Microbial Mat This type of mat develops in the upper few mm of the more sandy [*sensu* Folk et al. (1970) 'sandy mud'] sediment of the upper intertidal

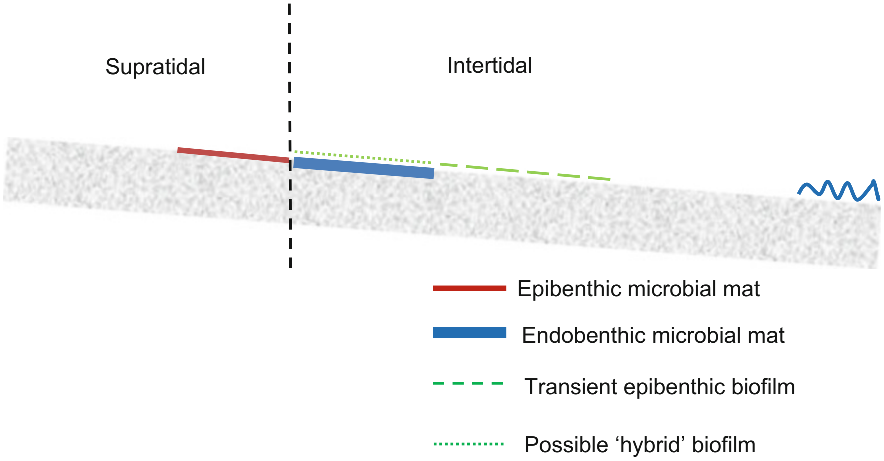

Fig. 1.6 Profile of a mudflat at low tide, showing locations where different microbial mats and biofilms develop. Original artwork, PG Beninger.

zone, and contains comparatively much less EPS than does the epibenthic microbial mat. Sediment biostabilization is about five times that of barren sediment (Noffke and Krumbein 1999). These mats can form within several hours (Noffke 2010). Their relation to the transient epibenthic biofilm is not yet clear; some of the same organisms may colonize both structures. In contrast to the transient epibenthic biofilm, the endobenthic microbial mat is not characterized by vertical migration.

Many mudflat ecologists do not indicate what type of biofilm or mat they report; any pigmented, superficially-visible patch is often simply termed a ‘biofilm’.

Microphytobenthos (MBP) MBP designates the photosynthetic eukaryotic and prokaryotic (mainly diatoms and cyanobacteria) microorganisms that grow within and upon the upper several millimeters of the sediment bed. They are major components of microbial mats and transient biofilms.

Epipelic The term ‘epipelic’ denotes any organism living on top or migrating through the surface layers of muddy sediment, e.g. epipelic diatoms.

Endopsammic The term ‘endopsammic’ denotes any organism living within sandy sediment.

The zones wherein may be found the epibenthic and endobenthic microbial mats, as well as the transient epibenthic biofilms, are shown in Fig. 1.6.

5 Mudflats as Systems of Superposed Emergent Properties

As geologists themselves emphasize, mudflats are much more than just mud! In the following chapters, we will see that, beginning with the lowest level of organization (the physical, geological, and chemical), increasing levels of organization emerge from this mud, along with increasingly intricate properties. Mudflats harbour prolific unicellular assemblages which profoundly influence their physical, geological, chemical, and biological features, including the redox reactions driving the system energetics. Although we might expect the sedimentary mosaic of electrochemical gradients to be conducive to the metazoan chemosymbioses which are so characteristic of other mud-dominant marine habitats, such symbioses are found mainly among the meiofauna, and are intriguingly rare in the macrofauna. In the upper sedimentary layers, however, complex biofilms containing unicellular microphytobenthic organisms assemble and set the stage for geomorphological and ecological self-organization, which in turn largely determines the feeding and spatial distributions of both endobenthic and epibenthic invertebrates. These spatially-organized organisms may then influence vertebrate feeding distributions. All of these organisms harbour and transmit parasites, an important yet often overlooked component of trophic webs on mudflats. The combination of these living and nonliving features promote ecological engineering and the provision of ecological services. Mudflat geological and biological complexity affects the dynamics of colonization and invasion, as well as the multiple interactions with migratory shorebirds, which export mudflat production over thousands of kilometers. Spatially-organized living resources are exploited on mudflats through fishing and aquaculture. These themes are set out and explored in the chapters of the present work. Although certain study techniques are specific to each of these dimensions of mudflat ecology, some quantitative techniques and approaches are necessary and common to most of them; these are presented in the final chapter.

It is hoped that in bringing together the various disciplines which have been applied to the study of mudflats for decades, the present volume will provide the foundation for an integrated perspective of this important, yet understudied, environment.

References

Cairns-Smith AG (1965) The origin of life and the nature of the primitive gene. J Theor Biol 10:53–88

Cairns-Smith AG, Hartman H (1986) Clay minerals and the origin of life. Cambridge University Press, Cambridge

Consalvey M, Paterson DM, Underwood GJC (2004) The ups and downs of life in a benthic biofilm: migration of benthic diatoms. Diatom Res 19:181–202

Crossland CJ, Baird D, Ducrotoy JP, Lindeboom H (2005) The coastal zone – a domain of global interactions, Chap 1. In: Crossland CJ, Kremer HH, Lindeboom HJ, Marshall Crossland JI, Le Tissier MDA (eds) Coastal fluxes in the anthropocene. Springer, Berlin, pp 1–38

Deppe F (1999) Intertidal mudflats worldwide. Common Wadden Sea Secretariat. http://www.waddensea-secretariat.org/sites/default/files/downloads/mudflats-worldwide-2000.pdf, 99p

Gao S (2009) Geomorphology and sedimentology of tidal flats, Chap 10. In: Perillo GME, Wolanski E, Cahoon DR, Brinson MM (eds) Coastal wetlands: an integrated ecosystem approach. Elsevier, Amsterdam, pp 295–343

Flemming BW (2002) Geographic distribution of muddy coasts. In: Healy T, Wang Y, Healy JA (eds) Muddy coasts of the world: processes, deposits, and function, Proceedings in marine science, vol 4, pp 99–201

Folk RL, Andrews PB, Lewis DW (1970) Detrital sedimentary rock classification and nomenclature for use in New Zealand. NZ J Geol Geophys 13:937–968

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638

Krumbein WC, Pettijohn FJ (1938) Manual of sedimentary petrography. D. Appleton-Century, New York

Noffke N (2010) Microbial mats in sandy deposits from the Archean Era to today. Springer, Heidelberg, 193p

Noffke N, Christian D, Wacey D, Hazen RM (2013) Microbially induced sedimentary structures recording a complex microbial ecosystem in the 3.5 Ga Dresser formation, Pilbara, Western Australia. Astrobiology 13:1–22

Noffke N, Krumbein WE (1999) A quantitative approach to sedimentary surface structures contoured by the interplay of microbial colonization and physical dynamics. Sedimentology 46:417–426

Ponnamperuma C, Shimoyama A, Friebele E (1982) Clay and the origin of life. Orig Life Evol Biosph 12:9–40

Sami F, Tewari BB (2009) Interaction of amino acids with clay minerals and their relevance to chemical evolution and the origins of life. Orig Life Evol Biosph 39:348–349

Simpson JA, Weiner ESC (1989) The Oxford English dictionary, vol X, 2nd edn. Oxford University Press, Oxford, pp 52–59

Wentworth CK (1922) A scale of grade and class terms for clastic sediments. J Geol 30:377–392

Yang D, Peng S, Hartman MR, Gupton-Campolongo T, Rice EJ, Chang AK, Gu Z, Lu GQ (Max), Luo D (2013) Enhanced transcription and translation in clay hydrogel and implications for early life evolution. Sci Rep 3: https://doi.org/10.1038/srep03165

Chapter 2
Geological, Physical and Chemical Foundations

Jerónimo Pan, Paula D. Pratolongo, and Diana G. Cuadrado

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Abstract Modern tidal flats are coastal geomorphological features with a recent geologic history (Holocene period, 10,000 YBP) that are found globally, under different climatic, hydrodynamic and sedimentological regimes. They are primarily characterized by fine-grained sedimentary deposits (silt and clay) that present unique physical and chemical properties, in comparison to other sediment types. The input of sediments to mudflats can be either riverine, from offshore, and/or from the erosion of coastal sedimentary deposits. Tides and tidal currents are the dominant hydrodynamic forces shaping mudflats, with wave action playing a secondary role. The occurrence of intermittent or temporary flooding and the presence of variable redox (oxidation-reduction) conditions are typical features of mudflat sediments. The temporally and spatially variable changes from aerobic, oxidized states of mudflat sediment and porewater to anaerobic, reduced states drive particular redox reactions that govern the characteristic chemical processes and biogeochemical functioning that distinguish mudflats from other coastal settings. Mudflat sediments are not inert; the high surface area:volume ratio of fine-grained sediment particles offers a vast and structurally-complex landscape for colonization by microbes that rely on surface-adhesion processes. Photosynthetic microalgae belonging to several taxonomic groups (collectively known as microphytobenthos MPB) are the dominant microorganisms growing in association with sedimentary particles, and forming a biofilm layer on top. In addition to physical forces, living benthic communities modify sediment properties as part of their normal physiology (micro- and macro-biota) and feeding, movement, and burrowing activity (meio- and macrofauna), especially in relation to stabilization and destabilization processes. These may ultimately have marked effects on sediment stability and geomorphology. The interplay between such biological processes and sediments in mudflats is currently an active field of research.

1 Geological Foundations

1.1 Mudflat Formation: Their Evolution in Geologic Time and Space

Modern mudflats, along with many other coastal geomorphological features, became well established during the mid-Holocene, with the rate of sediment supply and changes in sea level becoming the most important factors contributing to the formation of mudflats. Geologically-stable coasts accumulate erosional sediments on the continental margin, thus leading to the formation of sandy or muddy shores (Bertness 1999). The formation of soft-sediment habitats and the long-term fate of mudflats are dictated by the interplay of sediment supply and transport processes.

The Scientific Committee on Ocean Research (SCOR) established Working Group 106 to assess the impacts of relative sea-level change on muddy coasts, convening for the first time in China in 1995, and then in Germany in 1997. The task required a better understanding of the physical and biological processes acting in the formation of muddy coasts, something that, in comparison to sandy coasts, was poorly understood at the time. The Working Group first established a clear definition of *muddy coasts* as "*a sedimentary-morphodynamic type characterized primarily by fine-grained sedimentary deposits—predominantly silts and clays—within a coastal sedimentary environment. Such deposits tend to form rather flat surfaces, and are often, but not exclusively, associated with broad tidal flats*" (Wang and Healy 2002). Mud is further defined as a mixture of mainly fine-grained clay- and silt-sized sediments (and sometimes a minor sand fraction), organic matter and porewater. Such deposits typically display cohesive properties derived from water tension and the charged surfaces of clay minerals, enhanced by the chemical properties of the organic matter, that together dominate the overall rheological behavior of the mudflat. Mudflats also generally contain enough fine sediment that permeability is low and prevents draining at low tide, keeping the deposits perpetually saturated even when aerially exposed.

1.2 Sediment Classification and Characteristics

As mentioned previously (Chap. 1), the term "mud" or "fine grain" collectively refers to inorganic sediment <62.5 μm [4 phi, in Folk's (1968) sedimentological classification], that comprise mineral material in the silt (62.5–3.9 μm) and clay (3.9–0.5 μm) size-ranges. Clay minerals are ubiquitous components of marine sediments, produced by chemical weathering of terrestrial rocks and the authigenic reactions that occur in seawater. Clays are aluminosilicates (i.e. constituted primarily by oxygen and hydroxyl-bound aluminum and silicon), with the most abundant mineral forms being illite, kaolinite, smectite and chlorite. One feature shared by all clay minerals is the tetrahedral (Si) and octahedral (Al) crystalline structure of their base units that self-arrange in sheets or layers, so as to form a platy, or sheet-like, structure (Grim 1968) (Fig. 2.1). Most clay minerals comprise double-sheets (combined tetrahedral-octahedral-tetrahedral layers) that are bound together by various cations (e.g. Na^+, K^+ Ca^{2+}, Mg^{2+}, etc.) that themselves can exist in differing states of hydration or coordination. Differences in these cationic binding layers are what largely distinguish the different clay minerals and their physicochemical behavior. Weathering and varying environmental conditions can also drive the diagenetic alteration of clays between the different clay-mineral types, and even the intermediate states such as the regularly occurring mixed-layer illite-smectite (Libes 1992). The variability, alteration, and reactivity of clay minerals all exert a strong influence on the chemical and physical behavior of mudflat settings.

Mud has different and significant properties in comparison to other sediments. In addition to its cohesiveness, other important rheological properties include its viscoelastic behavior that is defined by mud's strain-dependent change between a particle-supported solid and a highly viscous, non-Newtonian fluid (Metha 2002). Furthermore, when mud is comprised of significant proportions of small clays (<2 μm), electrochemical processes become important and particles bind together, forming an adhesive floc. Due to their net negative surface charge, clay minerals

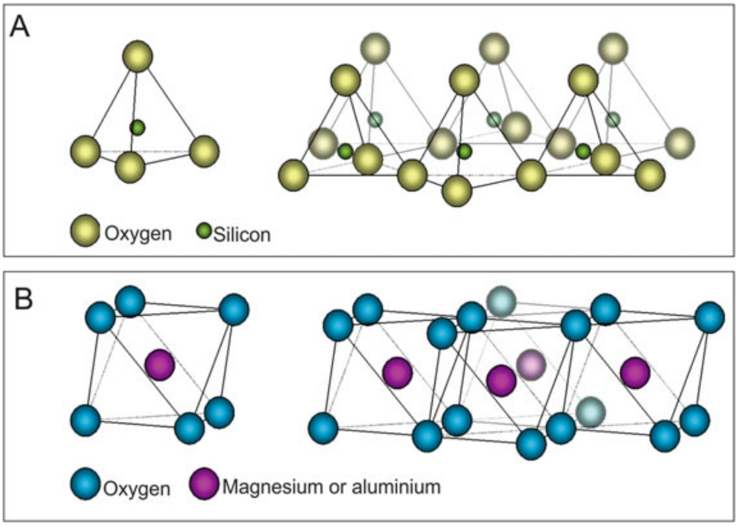

Fig. 2.1 Schematic molecular structural units of clay minerals, and their arrangement into (**a**) tetrahedral and (**b**) octahedral crystalline models.

adsorb cations and organic matter, which, upon settling, are carried to sedimentary deposits (Libes 1992). The adsorption of compounds such as pollutants, pesticides and heavy metals leads to the accumulation of these in sediments, which is particularly intense in some human-impacted coastal areas.

1.3 Sediment Supply

The supply of fine-grained sediments is one of the most important factors behind the formation of mudflats. Sediment can be eroded or accumulated by a number of physical processes, and muddy deposits persist where the provision of fine sediment exceeds the rate of removal by hydrodynamic processes. The source of sediments may either be riverine, from offshore, and/or the erosion of coastal sedimentary deposits. A coastal sedimentary environment is subject to erosion, transport and deposition processes due to coastal and estuarine mechanisms. High concentrations of fine-grained suspended loads carried by rivers contribute to the formation of muddy deposits at the river mouth and adjacent coast, such as the Amazon River where the suspended sediment discharge influences the geomorphology and sediment dynamics over a 1500 km-long stretch of coast along northeastern South America (Lisboa Cohen et al. 2012; Anthony et al. 2013). Similar delivery and transport of river-derived fine-grained sediments support the tide-dominated region in the Bengal Delta formed by three great rivers (Ganges, Brahmaputra, and Meghna). Shifting of the river mouths eastward over the late Holocene has diminished the direct supply of river-borne sediment in the distal portions of the delta, but tidal processes and

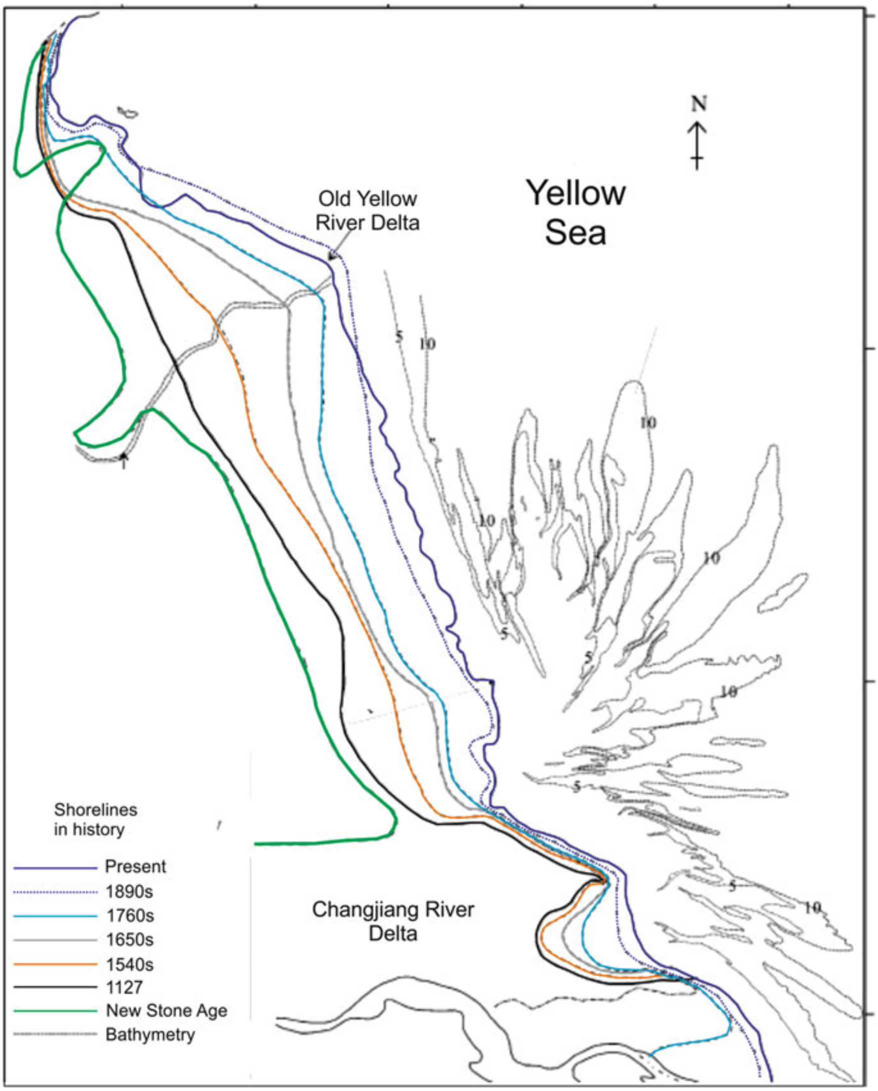

Fig. 2.2 Coastal plain of Jiangsu province, eastern China (modified from Gao 2009). The historical progradation of the shoreline from the New Stone Age (*ca.* 10,000 BC) to the present is shown.

alongshore currents have continued to sustain the coast through onshore transport of mud onto intertidal mangrove flats (Rogers and Goodbred 2014). Conversely, changes in sediment supply can have important consequences in coastal geomorphology; for example, the sediment discharge from the Yellow River in China formed large mudflats until 1855, after which its course was shifted and the shoreline retreated as a response to the reduced supply of particulate material (Gao and Zhu 1988) (Fig. 2.2).

1.4 Geographical Distribution

Mudflats are found globally, under different climatic, hydrodynamic and sedimentological regimes. A detailed distribution of fine cohesive sediment deposits around the world was compiled in Flemming (2002) and mapped at a 1:100,000 scale. A characteristic shared by all mudflats is the extremely low slope of the aggraded terrain, producing a tidal intrusion of as much as several km, and often being backed by low-lying saltmarsh or mangrove areas.

The Atlantic coast of North America is dominated in part by barrier islands associated with sheltered muddy backbarrier lagoons and large estuaries such as Chesapeake Bay, Delaware Bay, Long Island Sound, Narragansett Bay, and the Bay of Fundy, ranging from micro- to macrotidal regimes (Fig. 2.3a). Muddy deposits are present in sheltered embayments of many estuaries in northwestern Europe, including the British Isles, France, and the Netherlands (Flemming 2002; Carling et al. 2009). In the Wadden Sea the mudflats are sheltered by a chain of barrier islands, and the sediment source is mainly provided by the North Sea rather than river input (Pejrup et al. 1997) (Fig. 2.3b). On the Chinese coast (Fig. 2.3c), the Yellow River has the largest suspended sediment load in the world, forming extensive mudflats (Wang 1983), with Jiangsu province having the widest and most concentrated mudflats on Earth (Yao 2013; Zhang et al. 2016). A multi-decadal satellite-imagery reconstruction of mudflat accretion in Jiangsu province not only documented the seaward expansion of the coastline due to a combination of natural siltation and human activities, but also the significant changes in coastal land-use that took place over a ~20 year period (Yao 2013). As is typical of tropical regions, the Ganges-Brahmaputra-Meghna Delta on the Bengal Basin harbors the Sundarbans (Fig. 2.3d), the largest area of mangroves in the world, shared by India and Bangladesh (Wilson and Goodbred 2015). In the macrotidal coast of northern and northwestern Australia, large tidal flows entrain considerable volumes of mud which are carried in suspension to sediment-retaining mangroves (Wolanski 2006).

Methodological Approaches for Sediment Grain-Size Analysis

Traditionally, the methods for estimating the distribution of sediment grain sizes from a sample were sieve analysis and sedimentation analysis. The first method used different sieves on samples composed of particles with intermediate diameters (63 μm to 16 mm; i.e. fine sand to fine gravel) in order to separate them, based on their size (Ingram 1971) (Fig. 2.4a, b). Sedimentation analysis was based on Stoke’s law of settling velocities (Galehouse 1971), and has been widely used for samples with particles in the 0.5–50 μm diameter range (i.e. clay and silt). The so-called “pipette” analysis, the most widely used of sedimentation techniques, basically consists of letting sedimentary particles with differential settling velocities settle in a graduated cylinder, and then sampling the different fractions with pipettes at specific settling times (known for each fraction in a

(continued)

suspension medium) (Fig. 2.4c). These sub-samples then are resuspended into graduated cylinders with a liquid medium of known density, and the pipetting process is reiterated. Thus, the different sediment fractions are separated by the sequential time-specific pipetting and resuspension; the proportions of the different size-fractions are then estimated by weighing. Although these traditional techniques require a considerable amount of time and effort, the training is relatively simple and the specific laboratory equipment is inexpensive.

Since the 1970s, a variety of automated devices based on the principle of measuring the angular distribution of forward-scattered light have been developed and popularized for the estimation of particle grain-size distributions. In the UK, Malvern Instruments developed one such automated particle-counter based on the principle that particles of a given size diffract light through a given angle, the angle increasing with decreasing size (McCave et al. 1986) (Fig. 2.4d). A narrow beam of monochromatic light from a laser is passed through a suspension and the diffracted light is focused onto a detector that senses the angular distribution of scattered light energy. Particles in suspension are made to pass through a laminar flow. Laser-diffraction-size analysis not only gives particle counts, but also size distributions with more accurate, efficient, and reproducible results than the traditional pipette and sieve analyses, especially for the clay fraction (Konert and Vandenberghe 1997), which represents the major advantage of this method. Besides laser diffraction, there are other technical approaches to automated particle counting that, analogously to the sedimentation analysis, start from a suspension of particles and measure the absorption of either X-radiation by settling particles (e.g. the X-ray sedigraph—Micromeritics Instrument Corporation, USA); or changes in the electrical resistance caused by particles passing through a microchannel (e.g. the Coulter counter—Beckman Coulter Inc., USA). Given that automated counters yield a tremendous amount of data from a single sample, versatile and user-friendly computer programs capable of processing this information and providing graphical outputs are routinely used, such as Gradistat (Blott and Pye 2001). Automated particle-counting techniques require a certain level of specific training, and familiarity of the operator with the equipment and the principles behind it.

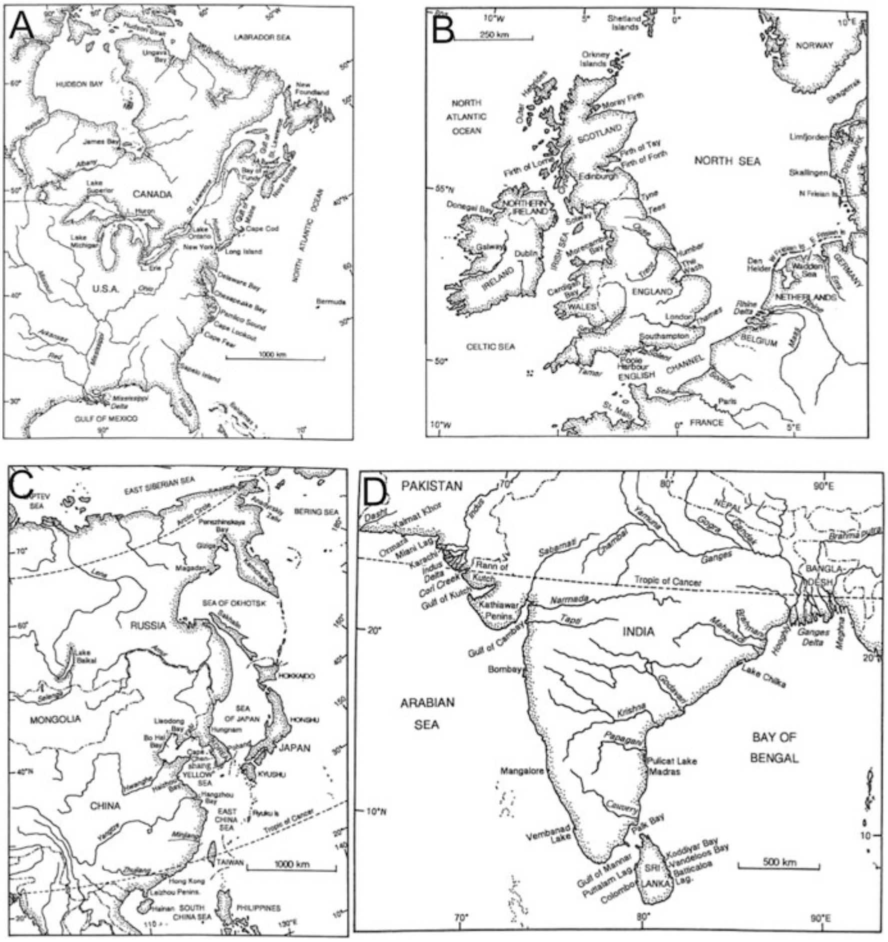

Fig. 2.3 Examples of world coastlines where significant continental sediment input has created extensive mudflats (modified from Flemming 2002). (**a**) Atlantic coast of North America dominated in part by barrier islands associated with sheltered muddy coasts, and large estuaries. (**b**) Mudflats are formed on sheltered embayments across many northwestern European estuaries. (**c**) The Yellow River has the largest suspended sediment load, creating the widest mudflats on Earth in Jiangsu province (China). (**d**) The Ganges-Brahmaputra-Meghna Delta on the Bengal Basin harbors the Sundarbans mudflats.

Fig. 2.4 Equipment for the estimation of sediment grain-size distributions. (**a**) Sieves of different mesh sizes are routinely used in the sieving method. (**b**) Stacked sieves and vibrating siever. (**c**) Fine sediment fraction resuspended in distilled water at room temperature, and settling in graduated cylinders, as used in pipette analysis. (**d**) An automated particle-size counter (Malvern Mastersizer 2000), which measures particle size distributions based on laser diffraction.

2 Physical Processes

2.1 Tidal Range

Studies by Kirby (1992, 2000) and Dyer (1998), attempted to gain an empirical understanding of the external forces shaping mudflat morphology; until then, the study of mudflats had been overlooked in comparison to sandy beaches. Various field programs have been carried out since, such as the INTRMUD Project (Morphological Development of Intertidal Mudflats), which studied the physical, biological and morphological characteristics of individual mudflats across 18 northwest European

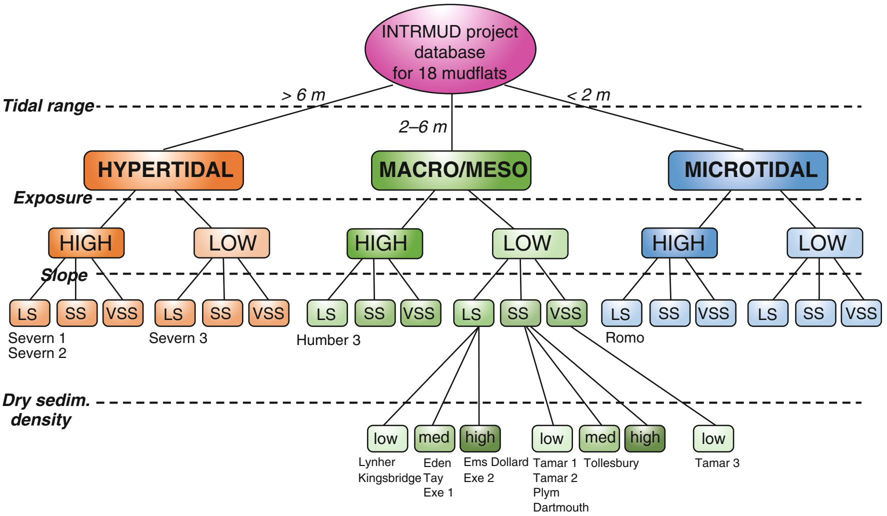

Fig. 2.5 Classification scheme for 18 North-west European mudflats, based on tidal range, wave exposure, mudflat slope [LS: low slope (<0.04); SS: steep slope (>0.04); VSS: very steep slope (~0.16)], and density of dry sediments (kg m^{-3}); examples of systems upon which the classification was constructed are included (modified from Dyer et al. 2000).

estuaries (see *Continental Shelf Research* Special Volume 20, 2000). This comprehensive study helped identify the variables that exert the largest influence in mudflat development and evolution. Dyer et al. (2000) classified parameters from independent variables, which is a challenge for those working in mudflats, since many variables are interdependent. They identified tidal range, exposure to waves and slope as the most important external driving variables (Fig. 2.5). Wave exposure was a resultant of the relationship between the orientation of the flat relative to the prevailing wind and maximum fetch, and the slope was calculated as the mean tidal range/mean flat width. The effect of the slope depends on the tidal range and width of the mudflat, considering 1:750 as a boundary between flat and steep mudflats.

On the other hand, Flemming (2012; Fig. 2.6) updated the original scheme proposed by Hayes (1979) of global distribution of tidal shores based on tidal range, as microtidal <1.0 m; lower mesotidal 1.0–2.0 m; upper mesotidal 2.0–3.5 m; lower macrotidal 3.5–5.0 m; and upper macrotidal >5.0 m; and the areas where back-barrier tidal mudflats are developed. As there is a positive correlation between intertidal mudflat extent and tidal range (Wang and Healy 2002), in microtidal areas, mudflats may form in sheltered embayments where wave action is of secondary importance in comparison to tidal currents. In high-energy, tidally-dominated settings, the deposition of fine-grained sediments onto mudflats can occur in a well-mixed estuary with low river discharge and strong tidal currents, where shoreline erosion and seabed erosion or resuspension provide muddy sediments to form mudflats (Shchepetkina et al. 2016). Archer (2013) gives other examples of mudflats in hypertidal coastal settings in North- and South America, and Europe.

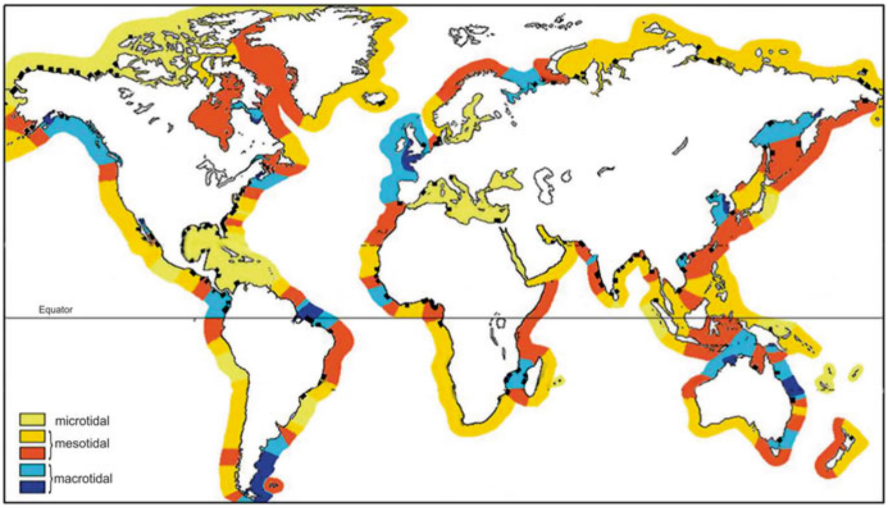

Fig. 2.6 Global tidal range distribution pattern (colors) and coastal barriers backed by mudflats or lagoons (black dots; modified from Flemming 2012).

The suspended river load can be alternately deposited and entrained on each tidal cycle. Deloffre et al. (2006) studied physical benthic-pelagic coupling and sedimentation processes on tidal flats along the Seine, a macrotidal estuary in France. A long-term (22 months) study of high frequency (1 measurement $\cdot$ 10 min^{-1}) and high resolution (0.6 mm) altimeter data, showed that during the largest spring tides (tidal range >7.1 m), sedimentation on the mudflat was predominantly controlled by vertical transfer of fine particles (<63 μm) from the turbidity maximum to the bed. Deposition of suspended particulate matter during high tide was favored by low current velocities at the mudflat bed (<0.4 m s^{-1}). Conversely, during periods of wave activity and periods of increased river discharge, the mudflat surface experienced erosion, also characterized by a vertical transfer of fine-grained material, from the mudflat bed back into the turbidity maximum. On average, 25–40% of the maximum mass of suspended particulate matter held within the turbidity maximum is temporarily deposited on the mudflat.

Wolanski et al. (1988) developed a model to explain the lutocline that separates a clear upper layer from an extremely turbid bottom layer during ebb tide in the South Alligator River (Northern Territory, Australia). In this model, sediment is entrained from the bottom and mixed vertically upward by eddy diffusion, but sediment-induced buoyancy effects inhibit vertical mixing, thus forming the two layers of comparable thickness.

The interface at which fresh- and saltwater enter into contact, such as the heads of estuaries, experiences significant changes in water biogeochemistry, over short horizontal scales, due to the high ionic strength of seawater (Libes 1992). In such areas, flocculation of suspended particles and dissolved organic matter (DOM) and colloids may represent a significant input of both inorganic and organic particles, from the water column to bottom sediments. Although organic compounds constitute a relatively small reservoir in the ocean, they play a central role in marine biogeochemical cycles; except for humic acids, all of these naturally-occurring compounds are synthesized by marine organisms (Libes 1992). Flocs are formed by a combination of two groups of processes, those bringing particles together, and those keeping them together. The first group is related to the flow conditions in the water, the coagulation of bacteria and plankton onto surfaces and each other (Libes 1992), and to organisms that clog particles into faeces or pseudofaeces or otherwise bind them in mucus. The second is related to the formation of sticky organic matter by a variety of organisms (phytoplankton, bacteria; Eisma 1986) to produce *bioflocculation* (Manning et al. 2010). Verney et al. (2009) presented experimental evidence that flocculation is mainly influenced by the constituents of suspended sediments and on the content and concentration of particulate organic matter (POM) rather than salinity changes. These authors found that diatom blooms in estuaries strongly enhanced flocculation speed and, to a lesser extent, efficiency.

Two main types of flocs have been described; *microflocs* with a diameter up to 125 μm, and *macroflocs* with a maximum size of 3–4 mm (Eisma 1986). The microflocs, together with single mineral particles, are the basic building units of macroflocs. Macroflocs are fragile, and formed in the water under conditions of viscous flow. Some flocs remain suspended in seawater, whereas others continue to aggregate until they become dense enough to sink, adsorbing metals during their transit through the water column (Libes 1992). Wells and Shanks (1987) studied flocs (therein termed “marine snow”) in a shallow coastal environment, and concluded that it is geologically significant due to its high settling rates (in the order of 50 to 200 m per day), and responsible for much of the vertical mass flux to coastal and estuarine fluid mud deposits. Flocs may thus represent a significant input of small sediment particles, organic matter and metals, from the water column to the sediments. The rate of vertical floc transport and incorporation into sediments depends upon several factors. The basic problem in floc settling relates to the variable degree of flocculation that makes settling velocity, size and density non-constant (Manning et al. 2010); the variation in settling velocity is the result of turbulence-induced aggregation and floc breakup processes (Winterwerp 2002).

In the Severn estuary in the UK, a secondary consequence of flocculation is the formation of mud : sand mixtures in turbid suspensions (Manning et al. 2010). The Severn Estuary contains both muddy and sandy sediments and they are often considered individually. However, mud and sand in estuaries can be deposited either as alternating layers or mixtures; the interaction of mud: sand mixtures can significantly affect the deposition, erodibility and transport characteristics within an estuarine system, far beyond their individual behaviors.

2.2 Wave Action

With the exception of those mudflats sheltered within estuarine environments, most mudflats are influenced by the action of waves that can mobilize and transport sediments, most significantly during storms (Le Hir et al. 2000).

Under normal conditions, the waves that arrive on the mudflat are attenuated by bed friction, and non-breaking waves lose 93–96% of their energy across shallow mudflat environments (Komar 1998). Regardless of the energy dissipation, wind waves in shallow water can resuspend fine sediment and transport it shoreward by tidal action. While sand particles settle at faster rates and travel shorter distances, muds are often maintained in suspension much longer and thus travel longer distances. Pereira et al. (2011) studied the episodic attenuation of the surface wave spectra due to the presence of fluid muds along the fine-grained sandy beach of Cassino (Brazil), and were able to describe how fluid mud overlays the sandy bottom episodically. On the other hand, during exceptional events such as storms, the wave disruption can produce a net difference in mud and sand transport. For instance, for the Louisiana coast, Draut et al. (2005) found that under certain conditions (i.e. abundant supply of fine-grained fluvial sediment and wave-induced resuspension that maintains an unconsolidated sea floor; dominant onshore wind direction during energetic conditions; and low tidal range), mudflat accretion can occur during energetic atmospheric activity episodes. Yang et al. (2015) developed an integrated model for the simulation of cohesive sediment transport during storm events where winds, currents, and waves play an important role in wave-induced shear stress.

The shear rate created by wave loading over a mud layer is highly phase-dependent (in turn, this is explained by the rheological properties of mud); thus a mud layer produces wave attenuation (Hsu et al. 2013b). Applying this principle to the field, it has been shown for the South American coast between the Amazon and the Orinoco river mouths that the interaction of muddy banks with waves results in complex and fluctuating shorelines (Anthony et al. 2010). Bank zones are protected from offshore wave attack as a result of wave-energy dampening by a fluidized mud layer that absorbs wave energy, and as a consequence, significant (albeit temporary) coastal accretion accompanied by rapid mangrove colonization is possible.

Wells (1983) compared intertidal and subtidal fluid muds in low-, moderate-, and high-tide-range environments, and found similarities in process-response behavior despite the wide range in tidal energy. The main findings in this study were the extreme wave attenuation produced by mudflats, and the rapid migration of soft muds. Muds are made "soft" by a wave-mediated process of fluidization. Small waves play a significant part in mud fluidization (Wells 1983), but tidal mixing may also be important in some estuaries [as discussed in the previous section, regarding the Wolanski et al. (1988) study].

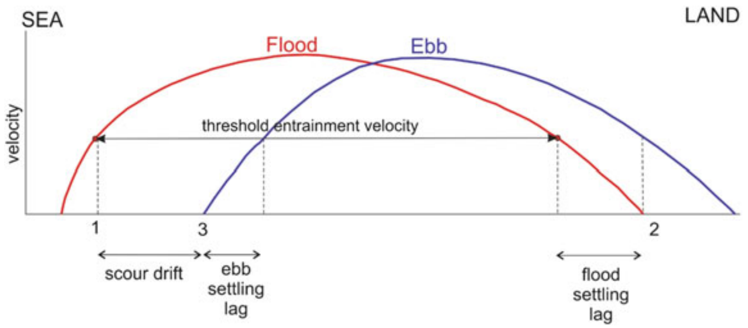

Fig. 2.7 Postma (1961) schematic diagram for net landward particle transport (modified by Carter 2013). A particle at point 1 is entrained into suspension and remains in suspension as long as it is over the threshold entrainment velocity. Thereafter it settles resting in point 2 after a flood settling lag. The particle then becomes re-entrained on the ebb tide settling out at point 3 after an ebb settling lag. The distance between point 1 and 3 represents the net landward movement over a tidal cycle.

2.3 Sediment Transport

The process of sediment transport comprises three stages, erosion (i.e. initiation of sediment motion), transport and deposition. While the non-cohesive sediment is transported as bedload (i.e. rolling or sliding along the sediment bed), the fine cohesive sediments and sand-sized particles are transported mainly as a suspended load (i.e. sediment uplifted in the water column by the flow), and are deposited under calm conditions during slack tides (i.e. net tide velocity = 0 m s^{-1}). A detailed explanation of sediment transport principles can be found in Wang (2012).

The greatest amount of sediment transport takes place in the intertidal zone, where the level of the water coincides with the stronger tides in the middle of the tidal cycle. Mudflat accretion occurs due to an onshore transport of fine material. As previously mentioned, this sediment is transported largely in suspension, and a lag effect is associated with the time required for the suspended sediment to adjust to changes in fluid velocity (Pritchard and Hogg 2003). This “scour lag” is based on the model proposed by Postma (1961) to explain the accumulation of fine sediment landward, where a hydrodynamic asymmetry is present, and takes into consideration the slow settling velocity of fine sediments. Basically, this model considers the lag that a suspended particle takes to be deposited (after the current velocity is below the threshold velocity for deposition) while it is carried landward by the flood tide for some distance (Fig. 2.7). Then, the particle is re-entrained when the threshold ebb tide velocity is reached. The mechanism is accentuated if the threshold velocity for the erosion of sediment is higher than the threshold velocity for deposition. Recent contributions on this topic have attempted to quantify the relative importance of mud properties and hydrodynamics (Roberts et al. 2000; Pritchard 2005; Chernetsky et al. 2010; Hsu et al. 2013a; van Maren and Winterwerp 2013).

While fine sediments are primarily deposited during slack (high and low) tides, coarse sediment particles (typically sand) can be deposited during ebb and flood tides or during strong storm events. This mechanism results in a lamination which is a diagnostic feature of tidal influence in the geologic record. This lamination may be promoted and maintained by biostabilization (see also Chaps. 3, 4, 5, 8, and 10). The resulting alternation of sand and mud forms the tidal bedding, i.e. a sequence of sediments produced by the above-mentioned cyclic conditions (Davies 2012).

The net sediment budget is often reflected in mudflat morphology by the occurrence of erosion or deposition patterns that generate either a convex-upward shape of the shore profile (indicating a stable state), or a concave-upward profile associated with wave action that causes erosion and a coarsening of the underlying sediment (Metha 2002). In the case of a concave profile, the maximum slope is often located towards the upper mudflat and frequently a small ridge occurs (Fig. 2.8a), as a consequence of wave erosion at high tide during storm episodes, in conjunction with the formation of a saltmarsh (Kirby 2000). Deposition rates on tidal flats are greatest for concave profiles (van Maren and Winterwerp 2013). In contrast, in a convex upward profile, the maximum slope is closer to the low water level and sediment transport is dominated by tidal currents (Fig. 2.8b). The convex curvature in an accreting bed profile attenuates wave-induced shear stress. Often, mudflats may evidence erosion and deposition throughout their extension, and both types of profiles can be observed simultaneously on different parts of the flat (Wang 1983), such as in the inner zone of the Bahía Blanca Estuary (Argentina) depicted in Fig. 2.8.

Accretion-dominated muddy coasts occur when sediment supply exceeds the rate of erosion and the destabilizing forces are smaller than sediment-stabilizing hydraulic forcing (Kirby 2002). However, an exception to this has been described for the Louisiana coast (USA—Draut et al. 2005), also discussed in the previous section. An anomalous case of mudflat accretion was detected in the study of a 17-year meteorological record; while the area experiences widespread land loss due to rapid relative sea-level rise, the abundant supply of fine-grained fluvial sediment combined with a dominant onshore wind direction during energetic atmospheric activity (i.e. winter cold fronts and tropical-depression storms) produce mudflat accretion with a low tidal range in this system.

Given the multiple and shifting processes that govern sediment transport in mudflats, the evolution of modern mudflats can sometimes be difficult to reconstruct, although there exist good methodological approaches, such as the study of the record of sea-level fluctuations left in transgressive deposition and regressive events. Chang et al. (2006) studied sediment cores from the East Frisian Wadden Sea (Germany), and interpreted sea regressions through indicators such as the presence of peat; in this way, they were able to reconstruct the evolution of what originated as a back-barrier tidal basin.

Fig. 2.8 Evidence of erosion and deposition throughout the extension of a mudflat; inner zone of the Bahía Blanca Estuary. (**a**) A convex-upward shape profile can be discerned at ebb tide. A narrow tidal channel (with water) and creeks incise the mudflat, while the upper mudflats favor the settling of cordgrass (note different coloration) forming a salt marsh interspersed among unvegetated mudflats. The city of Bahía Blanca can be seen in the background. (**b**) Small ridge (~1 m-high) in the upper mudflat formed by wave erosion during storm events caused when strong winds (in coincidence with wave fetch or blowing at a small angle with the coast) accumulate seawater in the inner estuary.

3 Chemical Processes

3.1 The Electrochemical Environment

The occurrence of intermittent or temporary flooding and the presence of anoxic conditions are typical features of mudflat sediments. The change from an aerobic and oxidized state to an anaerobic and reduced state generates particular redox reactions that govern many of the chemical processes occurring in mudflats, and controls, to a large degree, their biological functions (Mitsch and Gosselink 2000; see also Chaps. 3 and 7).

Redox reactions transfer electrons among atoms and many of these reactions in mudflats are based on organic decomposition. The loss of electrons from an atom is known as oxidation, while the gain of electrons by an atom is called reduction. Each complete redox reaction contains an oxidation and a reduction component called *half-reactions*. One important result of the oxidation and reduction processes is the frequent phase changes of the atoms in the sediment, such as causing solid minerals to dissolve and re-precipitate or dissolved ions to become gases. The basic oxidation half-reactions in mudflats are promoted by the chemical products of microorganism respiration. Oxidation occurs when organic tissues are decomposed by heterotrophic microorganisms, mainly bacteria. When tissues are oxidized, the released electrons are used in reducing reactions (Vepraskas and Faulkner 2001). The special case of organic decomposition will be considered in detail in Sect. 3.2.

The substances reduced in redox reactions are called electron acceptors, and oxygen is the primary electron acceptor in aerobic sediments. However, when oxygen is not present, anaerobic bacteria use alternative electron acceptors to continue their respiration. These alternative electron acceptors are used in a thermodynamically determined order or “thermodynamic sorting” (Richards 1965). In order of favorability, nitrate is utilized first, followed by manganese, iron, sulfate, and finally CO_2. It should be noted that different microbial species reduce each of the electron acceptors in a sequence known as a redox cascade. If nitrate, sulfate, and organic matter are present in anoxic sediments, a group of specialized bacteria (denitrifiers) will reduce all the available nitrate, and then sulfate reducers begin sulfate reduction (Fenchel and Jørgensen 1977; Reddy and DeLaune 2008).

On mudflats, the tidal regime results in alternating flooding and drying events, which have a determinant influence on the biogeochemical functioning of mudflats, leading to a highly variable temporal dynamics in the redox status of sediments. Extensive anoxic areas commonly develop below the surface because of reduced oxygen availability. The transition from predominantly oxidizing to reducing conditions is commonly termed the redox potential discontinuity (RPD) layer (Fenchel and Riedl 1970; Sturdivant et al. 2012). Under anoxic conditions, ferric iron and sulfate are reduced by microbial activity and the accumulation of reduced compounds produces a grey/green or black layer below the surface (Bloomfield 1952; Valdemarsen et al. 2009) that can be easily differentiated from the oxygenated orange-brown layer above it. This transition is often used as a relative measure of oxygen penetration into the sediment (e.g. Sundby et al. 1986; Moodley et al. 1998; Diaz and Trefry 2006). The depth of the RPD can vary extensively in time and space and is influenced by physical and biological factors like temperature, sediment particle size, hydrodynamic conditions, organic content, bacterial activity, and the presence of burrowing animals. Finer sediment particles and higher organic content, subject to warm conditions, promote microbial activity and proliferation. In such conditions, there is an increased anaerobic degradation, and the anoxic zone may extend almost to the sediment surface. Faunal irrigation and bioturbation, on the other hand, allow oxygenated water to penetrate deeper into the sediment, creating a three-dimensional mosaic of redox conditions (Kristensen 2000; Solan and Kennedy 2002; Hunting and Kampfraath 2013).

3.2 Sources of Organic Matter and Biogeochemical Cycles

The fixation of atmospheric carbon through photosynthesis is the major source of carbon to most terrestrial and aquatic ecosystems, and light penetration is sufficient in intertidal mudflats to allow photosynthesis and net primary production of organic carbon by benthic microalgae belonging to several taxonomic groups, and collectively known as microphytobenthos (MPB; MacIntyre et al. 1996). However, most of the organic matter in mudflats comes from allochthonous sources, through sedimentation from the water column (Mann 2009). Depending on the environmental parameters, different sources of organic matter may be dominant, e.g. sedimentation of phytoplankton, continental inputs from rivers, detritus of salt marsh macrophytes, or POM transported by tides. Invertebrate deposit feeders play a significant role in the processing of the organic matter settling on the mudflat surface. In the process of bioturbation, deposit feeders such as polychaete worms, crabs, and mollusks can mix sediments to a depth of several centimeters, burying organic matter below the upper well-aerated layer, into the deeper anaerobic sediments (Rosenberg et al. 2008; see also Chaps. 5, 6, and 10).

From an ecosystem perspective, a major function of mudflats is the regeneration of nutrients through the complete decomposition of organic matter from different sources (Sundbäck et al. 2003) into soluble forms of nitrogen, phosphorous and carbon. In the aerobic layer, organic matter is rapidly colonized by aerobic bacteria, and the end products of aerobic decomposition are CO_2 and inorganic nutrients like ammonium and phosphate, which are released back to the water column. Degradation of organically combined nitrogen involves two important biological transformations: ammonification (Fig. 2.9b), that oxidizes organic nitrogen to ammonium under either aerobic or anaerobic conditions; and nitrification, which transforms ammonium to nitrate under aerobic conditions (ZoBell and Feltham 1942; Owens et al. 1979; Reddy and DeLaune 2008). Nitrification is a two-step oxidation reaction that involves two different groups of bacteria: first the oxidation of ammonium to nitrite, and second the oxidation of nitrite to nitrate (Fig. 2.9c).

In anaerobic conditions, different groups of bacteria use alternative electron acceptors to decompose organic matter and generate energy. The most important groups are fermenters, nitrate reducers, sulfate reducers, and methanogens. In fermentation, water-soluble substances are degraded to low-molecular-weight organic compounds like lactate, acetate, propionate, or alcohol. Fermenting bacteria are mostly obligate anaerobes, and can derive a relatively small amount of energy through partial oxidation of organic substrates using specific organic compounds present in the bacterial cell as electron acceptors (Molongoski and Klug 1976).

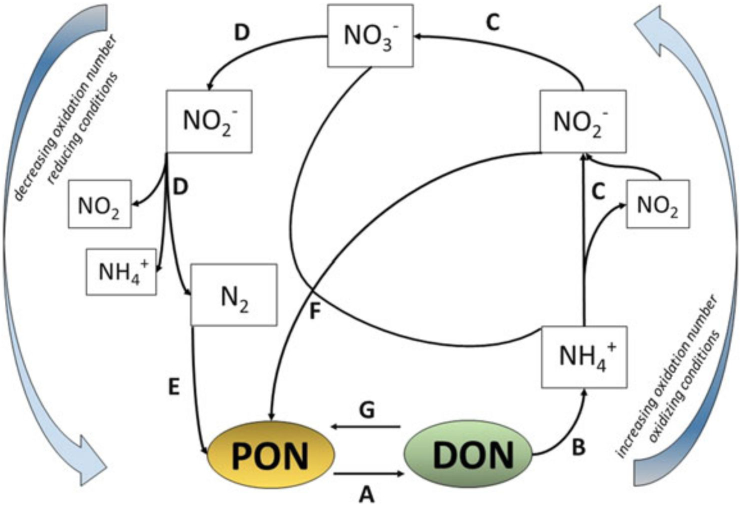

Fig. 2.9 Schematic representation of the biogeochemical nitrogen cycle. Relevant processes: (A) remineralization; (B) ammonification; (C) nitrification; (D) DNRA (dissimilatory nitrate reduction to ammonia); (E) nitrogen fixation; (F) assimilatory nitrogen reduction; (G) assimilation of DON. *DON* dissolved organic nitrogen, *PON* particulate organic nitrogen (modified from Libes 1992).

Nitrate reducers are the microbial group involved in N cycling. Denitrification and dissimilatory nitrate reduction to ammonia (DNRA; Fig. 2.9d) are two very important processes of microbially-facilitated nitrate reduction that occur under low oxygen concentrations (Tiedje et al. 1982). Denitrifiers are mainly facultative aerobic bacteria that oxidize organic compounds, including the end products of fermentation, by reducing nitrate to gaseous N_2. This reaction occurs under moderately reduced conditions, in the absence of oxygen (Ljungdahl and Eriksson 1985). On mudflats, the coupling of aerobic and anaerobic processes is enhanced (as shown in Fig. 2.9), and much of the nitrate formed during nitrification under aerobic conditions is rapidly consumed by denitrifiers in adjacent anaerobic micro-environments.

Dissimilatory reduction of nitrate to ammonia is performed by obligate and facultative anaerobes (Tiedje 1988). While denitrification removes N_2 from the system as a gaseous product, thereby reducing the potential for eutrophication, DNRA recycles nitrate into ammonium, retaining nitrogen within the mudflat. Intertidal sediments are hotspots of DNRA, and recent studies suggest that tidal pumping may sustain this nitrate-reducing pathway (Zheng et al. 2016).

Nitrogen reduction under anoxic conditions can also occur through anaerobic ammonium oxidation (*anammox*), a process that was not identified until 1995 (Mulder et al. 1995). In the presence of nitrite, the anammox process also produces N_2, by using nitrite as an electron acceptor to oxidize ammonium (Keunen 2008). Anammox makes a great contribution to N_2 formation in the continental shelf (Thamdrup and Dalsgaard 2002). In intertidal environments, a coupling between nitrification and anammox has been proposed; similarly to nitrification-denitrification coupling, anammox would be enhanced by high rates of nitrification in aerobic zones and accumulation of nitrate, which can diffuse into anaerobic zones. If denitrification is nitrate-saturated, some of the formed nitrite may support the anammox process (Dalsgaard et al. 2005). Intertidal sediments with an aerobic-anaerobic interface and redox oscillations provide an interesting system for the estimation of anammox rates, and for the evaluation of a possible coupling between nitrification and denitrification, as well as with anammox (Oliveira Fernandes et al. 2016).

Sulfate-reducing bacteria are obligate anaerobes that reduce the terminal electron acceptor sulfate to sulfides during the degradation of organic compounds (Muyzer and Stams 2008). Sulfur cycling largely regulates many microbial communities and redox reactions, and sulfate reducers have been extensively studied in mudflats and salt marshes. Thermodynamically, sulfate is a much less favorable electron acceptor than nitrate, manganese and iron oxides, but sulfates are widely available in the marine environment. Sulfur cycling processes are similar to those of nitrogen. In dissimilative sulfate reductions, obligate anaerobes reduce sulfate to sulfide to obtain energy. In assimilative sulfate reduction, sulfate is reduced to organic sulfhydryl groups by organisms that assimilate sulfate and sulfide for the synthesis of cellular constituents. In desulfuration, organic-bound sulfur is desulfurated, producing hydrogen sulfide gas. Hydrogen sulfide can be oxidized to elemental sulfur by sulfide oxidation, a process carried out by photosynthetic green and purple bacteria and some chemolithotrophs. Sulfur oxidizers produce sulfate by oxidizing sulfur, and elemental sulfur may be reduced to hydrogen sulfide through dissimilatory sulfur reduction (Reddy and DeLaune 2008).

In aerobic environments, most of the energy trapped in organic matter is released during decay. In anaerobic decomposition, on the contrary, a comparatively low amount of energy is released, and most of the remaining energy is conserved in high-energy reduced sulfur compounds such as soluble sulfides, iron monosulfides, pyrite, elemental sulfur, thiosulfate, and polythionite. When these reduced inorganic compounds are subsequently reoxidized, the energy is released. Thus, sulfur is a key element in the recycling of the energy in anaerobic environments, and accounts for a significant portion of the total respiration in intertidal sediments (Hansen 1994).

Dimethylsulfoniopropionate (DMSP) is a sulfur compound produced in great amounts by certain species of marine algae through osmoregulation. When released into the marine environment as dissolved DMSP, it is readily degraded to dimethylsulfide (DMS) by chemoheterotrophic bacteria, serving as a link between primary production and microbial food webs (Kiene 1990). The biogeochemical significance of these compounds was first suggested in 1972, when global DMS emissions from coastal waters and mudflats were found to be significant, and considered a key step in the global sulfur cycle (Lovelock et al. 1972).

Methanogenesis is the dominant process in organic matter degradation in anaerobic sediments with low levels of sulfate. The organisms capable of producing methane (Archaea) use carbon as the terminal electron acceptor in respiration (Figure 2.10c evidences methanogens in mudflat sediments). There is competition for electron donors between methanogens and sulfate reducers, and sulfate reduction

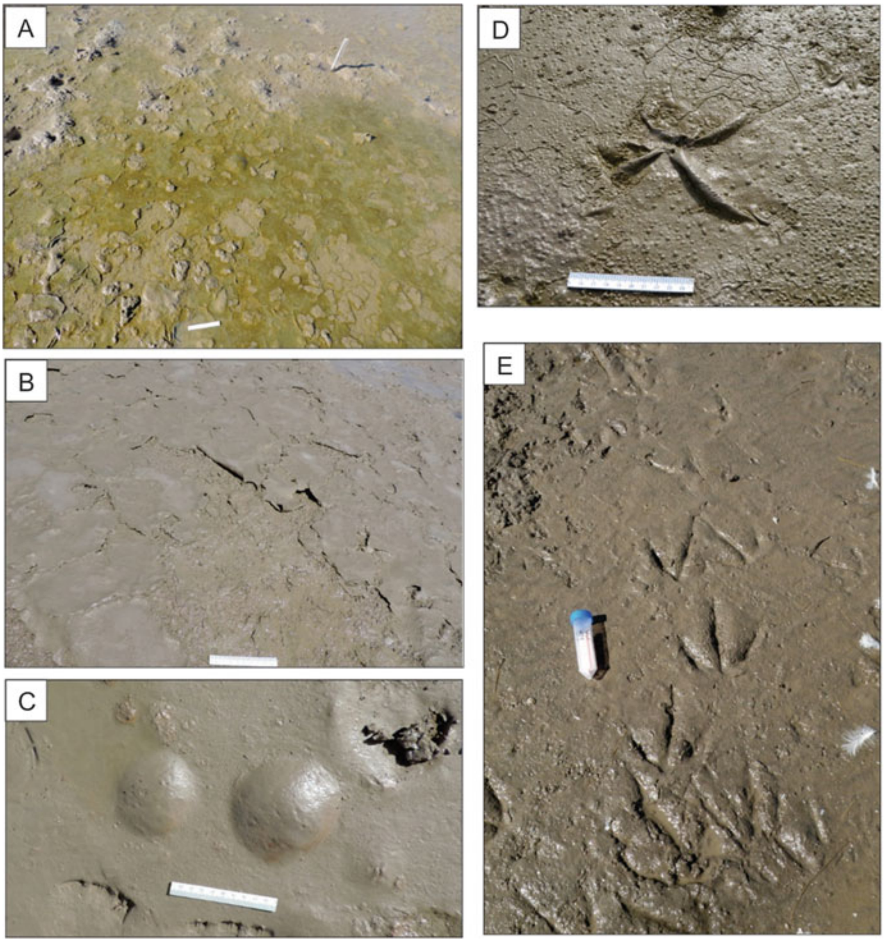

Fig. 2.10 Biologically-colonized surface sediments in mudflats of the Bahía Blanca Estuary. (**a**) Diatom-containing biofilms confer a characteristic golden-brown coloration; note interspersed microbial-mat chips. (**b**) Torn microbial mats covering muddy sediments, evidencing physical deformation as a product of wave shear stress; some of them have been flipped-over by wave action. (**c**) Gas domes (putatively, methane), indicative of microbial metabolic activity in underlying sediments. (**d**) A collapsed gas dome; there are also numerous gas bubbles trapped under the microbial mat. (**e**) Bird footprint preservation in biostabilized muddy sediments due to the presence of microbial mats. Field scales = 10.0 cm; except tube in (**e**) = 11.5 cm.

results in the liberation of more energy than methanogenesis. Therefore, in the anaerobic layer of mudflats and salt marshes, sulfate reduction is considered the most important process in organic matter remineralization (Llobet-Brossa et al. 2002), and methanogenesis becomes the dominant oxidation process when sulfate is depleted.

Biogeochemical cycles in marine sediments have been mostly studied in surface sediments, but processes occurring in deeper layers are gaining increasing attention. The sulfate-methane transition zone, commonly located at depths from 1 to 100's of meters below the sediment surface, is the region where sulfate is almost depleted and methane concentration starts to increase dramatically (Komada et al. 2016). The anaerobic oxidation of methane is a microbial process which may be coupled to sulfate reduction. In the sulfate-methane transition zone the maximum anaerobic methane oxidation rates coincide with local maximum rates of sulfate reduction, suggesting that anaerobic methane oxidation could be a process that effectively controls emissions of methane from many anaerobic environments into the atmosphere (Thomsen et al. 2001).

4 Interplay Between Sediments and Biological Processes in Mudflats

4.1 General Concepts

Based on an increasing body of publications and scientific meetings, the decades since the 1960s have witnessed a shift from the prevalent paradigm that physical processes alone are sufficient to interpret sedimentary dynamics, to a renewed interest in the chemical-biological processes affecting the physical behavior of cohesive sediments. It has been highlighted that sedimentology and biology interact in a complex manner with the hydrodynamic regime on temporal and spatial scales (de Brouwer et al. 2000).

Simply put, and as previously stated, *sediments are not inert*. It is estimated that shallow, marine, well-illuminated sediments have not been inert for at least 3.4 Ga! In fact, the oldest known fossils of any life form, correspond to filamentous cyanobacteria colonizing coastal sediments in the form of biofilms and microbial mats (Tice and Lowe 2004; Noffke et al. 2013a). Their modern counterparts are photosynthetic, stratified consortia of Bacteria, Archaea and eukaryonts present at sediment-water interfaces in shallow and intertidal marine sediments (Des Marais 2003).

The sedimentary habitat, with its high surface area:volume ratio of fine-grained sediment and organic matter, offers a vast and structurally-complex landscape for colonization by microbes that rely largely on surface-adhesion processes. Particularly, this is enhanced by the laminated structure of clays and the small size of mud particles. The majority of biofilm-producing microbes present a two-dimensional growth mode, in the sense that populations require surfaces to which to adhere, and later develop into biofilms (Stoodley 2016).

The microscopic unicellular eukaryotic algae and cyanobacteria that grow within the upper several millimeters of illuminated sediments in association with sedimentary particles are collectively termed *epipelic* microphytobenthos (MPB—Vos and de Wolf 1993; MacIntyre et al. 1996). Sediment grain size can determine the type of dominant MPB community that becomes established in a sediment patch; for instance, sediments with very fine silt and mud with adsorbed nutrients are colonized by diatoms (Stal 2010), readily seen as a golden-brown biofilm on the surface of sediments (Paterson and Black 1999; Fig. 2.10a). On the other hand, cyanobacteria prefer fine sandy sediment substrates (Noffke 1998; Watermann et al. 1999). Filamentous cyanobacteria and diatoms dominate most present-day mudflat microbial biomass. While the fossil record of the former dates back to the Archaean Era, diatoms date back to the Jurassic Period (185 MA); thus, it is reasonable to assume that muddy sediments have not always had the same biological associations and physical properties throughout Earth's history.

4.2 Physical Environment-Driven Interactions

MPB biofilms require calm conditions and several hours of atmospheric exposure per day in order to develop; yet, once established, they can withstand high-energy, dynamic environments (Cuadrado et al. 2013; see Chap. 8). The distribution and abundance patterns of biofilms are not spatially-uniform throughout a mudflat, but rather depend upon extrinsic physico-chemical forcings and species-specific characteristics of the microbial consortia, which is reflected at macro- (Riethmüller et al. 2000; Fidalgo e Costa et al. 2002) and microscales (Seuront and Spilmont 2002; Pan et al. 2017). As a result, within a single mudflat it is possible to observe a mosaic of different sedimentary structures that arise as a consequence of physical action (Fig. 2.9a, b), and biological activity (Fig. 2.9c–e).

On a temporal scale, the community structure of MPB is determined by seasonality of physical (e.g. temperature, light, resuspension) and chemical parameters (e.g. pore-water nutrient and oxygen concentration, pH and redox potential; Jesus et al. 2009). Accordingly, over the past 30 years, much attention has been paid to the seasonal variation in microbial communities of estuarine sediments, largely focusing on species dominance, chlorophyll *a* content, extracellular polymeric substances (EPS) production, and the correlation of all these with sediment stability (Admiraal et al. 1984; Underwood and Paterson 1993; de Jonge and Colijn 1994; Underwood 1994). In a paper that contributed to building bridges between disciplines, de Brouwer et al. (2000) investigated the importance of biological processes on the sediment characteristics and the morphology of a mudflat. They found that the seasonal development of a MPB biofilm doubled sediment stability in spring, trapping fine-grained sediment (<50 μm), and altering the overall mudflat morphology. Conversely, two independent year-round surveys of microphytobenthic biomass variations in the Bahía Blanca Estuary found that the peak in MPB biomass took place during winter, inversely to what had been described for most European mudflats (Pan et al. 2013a, b).

Tides are an important factor in coastal mudflats not only for the sediment transport and deposition mechanisms presented in Sect. 2.1, but also for modifying the immersed area and exposing the middle and high mudflat sections for several hours, and 'washing' them in each flood cycle. Nutrient exchange in mudflats occurs with each tidal cycle; tidal water from the adjacent sea diffuses into sedimentary interstices, becoming enriched in bioremineralized nutrients and metabolites from the sediment. On the other hand, Webster et al. (2002) measured gross nutrient release rates from the muddy sediments of a shallow coastal lagoon, and concluded that MPB intercept the vertical flux of re-mineralized nutrients from the sediment into the water column, and sequester them for primary production.

Tidal range is also of paramount importance in the distribution of biota, known as the *zonation pattern* of intertidal benthic mudflat species. The surface elevation of mudflat organisms within the tidal range can be related to inundation frequency and duration, oxygen availability, desiccation, and concentration of evaporated minerals. The different assemblages of benthic fauna and primary producers are distributed along the intertidal gradient in relation to their tolerance to environmental conditions and animal-sediment interactions, resulting in a zonation parallel to the shore that mirrors the varying environmental conditions from high- to low tidal level (Donadi et al. 2013) (Fig. 2.11). Progression of the tidal wave across the intertidal zone can also control local current velocities and the occurrence of erosional or depositional areas (Bassoullet et al. 2000; Glockzin and Zettler 2008).

4.3 Biota-Driven Interactions with the Physical Environment: Biostabilization

In addition to physical processes, living benthic communities are capable of significantly modifying sediment properties, especially in relation to stabilization and destabilization processes. Epipelic diatoms exhibit a remarkable motility and excrete organic compounds collectively known as extracellular polymeric substances (EPS—Decho 1990), which not only facilitate the gliding motion of individual cells through sedimentary particles but, on an ecosystem scale, contribute to the stabilization of sediments by agglutination and adhesion of particles (Stal 2010). EPS exudation in benthic diatoms occurs mostly during daytime and emersion of the sediment (Stal and de Brouwer 2005); it is a widespread feature of normal diatom physiology associated with both (vertical) migration, and “unbalanced growth”, i.e. when nitrogenous nutrients are depleted (Staats et al. 2000a, b; Stal and de Brouwer 2003; Stal 2010).

EPS are complex protein-polysaccharide molecular networks (Decho 1990). Most bacteria cells are encapsulated within EPS and attached to sediment particles (Ransom et al. 1997). Likewise, the external mucus coatings of diatoms provide protection against desiccation and also promote aggregation and colony formation. The organic EPS matrix in sediments is tightly associated with the mineral matrix and often observed between sediment grains (Wiese and Rheinheimer 1978; DeFlaun and Mayer 1983; Ransom et al. 1997), contributing to maintain the integrity of individual sedimentary particles, increase cohesion and in turn, inhibit the diffusion of molecules (Ransom et al. 1997). The percent of organic carbon made

Fig. 2.11 Zonation pattern of intertidal benthic mudflat species related to tidal range in the Bahía Blanca Estuary. (**a**) Upper intertidal colonized by crabs (*Neohelice granulata*), and supratidal patches vegetated by the pickleweed (*Sarcocornia ambigua*) which are only inundated at spring tides. The boundary between the bioturbated and the biofilm-stabilized areas coincides with the mean high water level. (**b**) Supratidal fringe zone with pickleweed patches, and desiccation cracks in microbial mat-colonized areas. Differences in sediment moisture correspond to differences in tidal flooding.

up by EPS in sediment is probably small, but the volume percentage of EPS is more significant (DeFlaun and Mayer 1983), since they exist in a highly hydrated state. EPS are surface-active compounds enriched with sulfur, carboxyl, and amino groups that give their high adsorption potential. Grain size and particle surface area are important since they determine the number of active adsorption sites and consequently the degree of interaction; an inverse relationship has been observed between EPS content and sediment grain size (de Brouwer et al. 2003; Stal 2010). Given the huge adsorptive surface area of the collective sediment grains, a large part of the loosely-bound carbohydrates are retained in the sediment (de Brouwer et al. 2000).

Through the secretion of EPS, the MPB may have pronounced effects on sediment stability and geomorphology (Stal 2010). On the one hand, colloidal carbohydrate concentrations in sediments are directly related to epipelic diatom biomass (Madsen et al. 1993), yet the sole presence of EPS in sediments is not sufficient for biostabilization. For instance, de Brouwer et al. (2005) extracted EPS from diatom cultures and tested erosion thresholds in diatom-free and diatom-colonized sediments; they found that EPS concentration *per se* did not explain the changes in erosion thresholds, suggesting that a certain arrangement and structure determined by microbially-bound EPS is paramount for biostabilization. This demonstrates once again the theme introduced at the beginning of this section; microbial consortia are complex biochemically- and biologically-diverse systems, in which the microbial constituents cooperatively exploit every niche (Noffke et al. 2013b).

In summary, modern mudflats are expanding on a global scale. Fine-grained mudflat sediments present unique physical and chemical properties, and are reworked by the dominant hydrodynamic forces of tides and tidal currents. The enormous surface area in the mudflat sediments offers a vast and structurally-complex landscape for colonization by microbes that rely on surface-adhesion processes, and ultimately have significant, landscape-scale effects on sediment stability and geomorphology.

References

Admiraal W, Peletier H, Brouwer T (1984) The seasonal succession patterns of diatom species on an intertidal mudflat: an experimental analysis. Oikos 42:30–40

Anthony EJ, Gardel A, Gratiot N, Proisy C, Allison MA, Dolique F, Fromard F (2010) The Amazon-influenced muddy coast of South America: a review of mud-bank-shoreline interactions. Earth Sci Rev 103:99–121

Anthony EJ, Gardel A, Proisy C, Fromard F, Gensac E, Peron C, Walcker R, Lesourd S (2013) The role of fluvial sediment supply and river-mouth hydrology in the dynamics of the muddy, Amazon-dominated Amapá-Guianas coast, South America: a three-point research agenda. J South Am Earth Sci 44:18–24

Archer AW (2013) World's highest tides: hypertidal coastal systems in North America, South America and Europe. Sediment Geol 284–285:1–25

Bassoullet P, Le Hir P, Gouleau D, Robert S (2000) Sediment transport on an intertidal mudflat: field investigations and estimation of fluxes within the "Baie de Marennes-Oleron" (France). Cont Shelf Res 20:1635–1653

Bertness MD (1999) The ecology of Atlantic shorelines. Sinauer, Sunderland

Bloomfield C (1952) The distribution of iron and aluminium oxides in gley soils. J Soil Sci 3:167–171

Blott SJ, Pye K (2001) Gradistat: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surf Process Landforms 26:1237–1248

Carling PA, Williams JJ, Croudace IW, Amos CL (2009) Formation of mud ridge and runnels in the intertidal zone of the Severn Estuary, UK. Cont Shelf Res 29:1913–1926

Carter RWG (2013) Coastal environments. Academic Press, London

Chang TS, Flemming BW, Tilch E, Bartholoma A, Wostmann R (2006) Late Holocene stratigraphic evolution of a back-barrier tidal basin in the East Frisian Wadden Sea, southern North Sea: transgressive deposition and its preservation potential. Facies 52:329–340

Chernetsky A, Schuttelaars HM, Talke SA (2010) The effect of tidal asymmetry and temporal settling lag on sediment trapping in tidal estuaries. Ocean Dyn 60:1219–1241

Cuadrado DG, Bournod CN, Pan J, Carmona NB (2013) Microbially-induced sedimentary structures (MISS) as record of storm action in supratidal modern estuarine setting. Sediment Geol 296:1–8

Dalsgaard T, Thamdrup B, Canfield DE (2005) Anaerobic ammonium oxidation (anammox) in the marine environment. Res Microbiol 156:457–464

Davies RA (2012) Tidal signatures and their preservation potential in stratigraphic sequences. In: Davis RA, Dalrymple RW (eds) Principles of tidal sedimentology. Springer, New York, pp 35–56

de Brouwer JFC, Bjelic S, de Deckere EMGT, Stal LJ (2000) Interplay between biology and sedimentology in a mudflat (Biezelingse Ham, Westerschelde, The Netherlands). Cont Shelf Res 20:1159–1177

de Brouwer JFC, de Deckere EMGT, Stal LJ (2003) Distribution of extracellular carbohydrates in three intertidal mudflats in Western Europe. Estuar Coast Shelf Scince 56:313–324

de Brouwer JFC, Wolfstein K, Ruddy GK, Jones TE, Stal LJ (2005) Biogenic stabilization of intertidal sediments: the importance of extracellular polymeric substances produced by benthic diatoms. Microb Ecol 49:501–512

de Jonge VN, Colijn F (1994) Dynamics of microphytobenthos biomass in the Ems estuary. Mar Ecol Prog Ser 104:185–196

Decho AW (1990) Microbial exopolymer secretions in ocean environments: their role(s) in food webs and marine processes. Oceanogr Mar Biol 28:73–153

DeFlaun MF, Mayer LM (1983) Relationships between bacteria and grain surfaces in intertidal sediments. Limnol Oceanogr 28:873–881

Deloffre J, Lafite R, Lesueur P, Verney R, Lesourd S, Cuvilliez A, Taylor J (2006) Controlling factors of rhythmic sedimentation processes on an intertidal estuarine mudflat - Role of the turbidity maximum in the macrotidal Seine estuary, France. Mar Geol 235:151–164

Des Marais DJ (2003) Biogeochemistry of hypersaline microbial mats illustrates the dynamics of modern microbial ecosystems and the early evolution of the biosphere. Biol Bull 204:160–167

Diaz RJ, Trefry JH (2006) Comparison of sediment profile image data with profiles of oxygen and Eh from sediment cores. J Mar Syst 62:164–172

Donadi S, van der Heide T, van der Zee EM, Eklöf JS, van de Koppel J, Weerman EJ, Piersma T, Olff H, Klemens Eriksson B (2013) Cross-habitat interactions among bivalve species control community structure on intertidal flats. Ecology 94:489–498

Draut AE, Kineke GC, Huh OK, Grymes JM III, Westphal KA, Moeller CC (2005) Coastal mudflat accretion under energetic conditions, Louisiana chenier-plain coast, USA. Mar Geol 214:27–47

Dyer KR (1998) The typology of intertidal mudflats. In: Black KS, Paterson DM, Cramp A (eds) Sedimentary processes in the intertidal zone. Geological Society, London, pp 11–24

Dyer KR, Christie MC, Wright EW (2000) The classification of intertidal mudflats. Cont Shelf Res 20:1039–1060

Eisma D (1986) Flocculation and de-flocculation of suspended matter in estuaries. Netherlands J Sea Res 20:183–199

Fenchel TM, Jørgensen BB (1977) Detritus food chains of aquatic ecosystems: the role of bacteria. In: Alexander M (ed) Advances in microbial ecology. Plenum Press, New York, pp 1–58

Fenchel TM, Riedl RJ (1970) The sulfide system: a new biotic community underneath the oxidized layer of marine sand bottoms. Mar Biol 7:255–268

Fidalgo e Costa P, Brotas V, Cancela da Fonseca L (2002) Physical characterization and microphytobenthos biomass of estuarine and lagoon environments of the Southwest coast of Portugal. Limnetica 21:69–79

Flemming BW (2002) Geographic distribution of muddy coasts. In: Healy T, Wang Y, Healy A (eds) Muddy coasts of the World: processes, deposits and function. Elsevier, Amsterdam, pp 99–201

Flemming BW (2012) Siliciclastic back-barrier tidal flats. In: Davis RA Jr, Dalrymple RW (eds) Principles of tidal sedimentology. Springer, New York, pp 231–267

Folk RL (1968) Petrology of sedimentary rocks. Hemphills, Austin

Galehouse JS (1971) Sedimentation analysis. In: Carver RE (ed) Procedures in sedimentary petrology. Wiley-Interscience, New York, pp 69–94

Gao S (2009) Geomorphology and sedimentology of tidal flats. In: Perillo GME, Wolanski E, Cahoon DR, Brinson MM (eds) Coastal wetlands: an integrated ecosystem approach. Elsevier, Amsterdam, pp 295–316

Gao S, Zhu DK (1988) The profile of Jiangsu's mud coast. J Nanjing Univ (Natural Science Version) 21:75–84 (in Chinese, with English abstract)

Glockzin M, Zettler ML (2008) Spatial macrozoobenthic distribution patterns in relation to major environmental factors - a case study from the Pomeranian Bay (southern Baltic Sea). J Sea Res 59:144–161

Grim RE (1968) Clay mineralogy, 2nd edn. McGraw-Hill, New York

Hansen TA (1994) Metabolism of sulfate-reducing prokaryotes. Antonie van Leeuwenhoek 66:165–185

Hayes MO (1979) Barrier island morphology as a function of tidal and wave regime. In: Leatherman SP (ed) Barrier islands. Academic Press, New York, pp 1–27

Hsu TJ, Chen SN, Ogston AS (2013a) The landward and seaward mechanisms of fine-sediment transport across intertidal flats in the shallow-water region-A numerical investigation. Cont Shelf Res 60:85–98

Hsu WY, Hwung HH, Hsu TJ, Torres-Freyermuth A, Yang RY (2013b) An experimental and numerical investigation on wave-mud interactions. J Geophys Res Oceans 118:1126–1141

Hunting ER, Kampfraath AA (2013) Contribution of bacteria to redox potential (Eh) measurements in sediments. Int J Environ Sci Technol 10:55–62

Ingram RL (1971) Sieve analysis. In: Carver RE (ed) Procedures in sedimentary petrology. Wiley-Interscience, New York, pp 47–67

Jesus B, Brotas V, Ribeiro L, Mendes CR, Cartaxana P, Paterson DM (2009) Adaptations of microphytobenthos assemblages to sediment type and tidal position. Cont Shelf Res 29:1624–1634

Keunen JG (2008) Anammox bacteria: from discovery to application. Nat Rev Microbiol 6:320–326

Kiene RP (1990) Dimethyl sulfide production from dimethylsulfoniopropionate in coastal seawater samples and bacterial cultures. Appl Environ Microbiol 56:3292–3297

Kirby R (1992) Effects of sea-level rise on muddy coastal margins. In: Prandle D (ed) Dynamics and exchanges in estuaries and the coastal zone. American Geophysical Union, Washington, pp 313–334

Kirby R (2000) Practical implications of tidal flat shape. Cont Shelf Res 20:1061–1077

Kirby R (2002) Distinguishing accretion from erosion-dominated muddy coasts. In: Healy T, Wang Y, Healy A (eds) Muddy coasts of the World: processes, deposits and function. Elsevier, Amsterdam, pp 61–81

Komada T, Burdige DJ, Li H-L, Magen C, Chanton JP, Cada AK (2016) Organic matter cycling across the sulfate-methane transition zone of the Santa Barbara Basin, California Borderland. Geochim Cosmochim Acta 176:259–278

Komar PD (1998) Beach processes and sedimentation, 2nd edn. Prentice Hall, Upper Saddle River

Konert M, Vandenberghe J (1997) Comparison of laser grain size analysis with pipette and sieve analysis: a solution for the underestimation of the clay fraction. Sedimentology 44:523–535

Kristensen E (2000) Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. Hydrobiologia 426:1–24

Le Hir P, Roberts W, Cazaillet O, Christie M, Bassoullet P, Bacher C (2000) Characterization of intertidal flat hydrodynamics. Cont Shelf Res 20:1433–1459

Libes SM (1992) An introduction to marine biogeochemistry. Wiley, New York

Lisboa Cohen MC, Ruiz Pessenda LC, Behling H, Rossetti DF, França MC, Guimarães JTF, Friaes Y, Beltrão Smith C (2012) Holocene palaeoenvironmental history of the Amazonian mangrove belt. Q Sci Rev 55:50–58

Ljungdahl LG, Eriksson K-E (1985) Ecology of microbial cellulose degradation. In: Marshall KC (ed) Advances in microbial ecology. Plenum Press, New York, pp 237–299

Llobet-Brossa E, Rabus R, Böttcher ME, Könneke M, Finke N, Schramm A, Meyer RL, Grötzschel S, Rosselló-Mora R, Amann R (2002) Community structure and activity of sulfate-reducing bacteria in an intertidal surface sediment: a multi-method approach. Aquat Microb Ecol 29:211–226

Lovelock JE, Maggs RJ, Rasmussen RA (1972) Atmospheric dimethyl sulfide and the natural sulfur cycle. Nature 237:452–453

MacIntyre HL, Geider RJ, Miller DC (1996) Microphytobenthos: the ecological role of the “secret garden” of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production. Estuaries 19:186–201

Madsen KN, Nilson P, Sundbäck K (1993) The influence of benthic microalgae on the stability of a subtidal shallow water sediment. J Exp Mar Biol Ecol 170:159–177

Mann KH (2009) Ecology of coastal waters: with implications for management, 2nd edn. Blackwell Science, Malden

Manning AJ, Langston WJ, Jonas PJC (2010) A review of sediment dynamics in the Severn Estuary: influence of flocculation. Mar Pollut Bull 61:37–51

McCave IN, Bryant RJ, Cook HF, Coughanowr CA (1986) Evaluation of a laser-diffraction-size analyzer for use with natural sediments. J Sediment Petrol 56:561–564

Metha AJ (2002) Mudshore dynamics and controls. In: Healy T, Wang Y, Healy A (eds) Muddy coasts of the World: processes, deposits and function. Elsevier, Amsterdam, pp 19–60

Mitsch WJ, Gosselink JG (2000) Wetlands, 3rd edn. Wiley, New York

Molongoski JJ, Klug MJ (1976) Characterization of anaerobic heterotrophic bacteria isolated from freshwater lake sediments. Appl Environ Microbiol 31:83–90

Moodley L, Van der Zwaan GJ, Rutten GMW, Boom RCE, Kempers AJ (1998) Subsurface activity of benthic Foraminifera in relation to porewater oxygen content: laboratory experiments. Mar Micropaleontol 34:91–106

Mulder A, van de Graaf AA, Robertson LA, Kuenen JG (1995) Anaerobic ammonium oxidation discovered in a denitrifying fluidized bed reactor. FEMS Microbiol Ecol 16:177–184

Muyzer G, Stams AJM (2008) The ecology and biotechnology of sulphate-reducing bacteria. Nat Rev Microbiol 6:441–454

Noffke N (1998) Multidirected ripple marks rising from biological and sedimentological processes in modern lower supratidal deposits (Mellum Island, southern North Sea). Geology 26:879–882

Noffke N, Christian D, Wacey D, Hazen RM (2013a) Microbially induced sedimentary structures recording an ancient ecosystem in the ca. 3.48 billion-year-old Dresser formation, Pilbara, Western Australia. Astrobiology 13:1103–1124

Noffke N, Decho AW, Stoodley P (2013b) Slime through time: the fossil record of prokaryote evolution. Palaios 28:1–5

Oliveira Fernandes S, Javanaud C, Michotey VD, Guasco S, Anschutz P, Bonin P (2016) Coupling of bacterial nitrification with denitrification and anammox supports N removal in intertidal sediments (Arcachon Bay, France). Estuar Coast Shelf Sci 179:39–50

Owens NJ, Christofi N, Stewart WD (1979) Primary production and nitrogen cycling in an estuarine environment. Cyclic phenomena in marine plants and animals. In: Proceedings of the 13th European marine biology symposium, Isle of Man, 27 Sept–4 Oct 1978

Pan J, Bournod CN, Cuadrado DG, Vitale A, Piccolo MC (2013a) Interaction between estuarine microphytobenthos and physical forcings: the role of atmospheric and sedimentary factors. Int J Geosci 4:352–361

Pan J, Bournod CN, Pizani NV, Cuadrado DG, Carmona NB (2013b) Characterization of microbial mats from a siliciclastic tidal flat (Bahía Blanca estuary, Argentina). Geomicrobiol J 30:665–674

Pan J, Cuadrado DG, Bournod CN (2017) Diatom-driven recolonization of microbial-mat dominated siliciclastic tidal flat sediments. FEMS Microbiol Ecol 93:fix111

Paterson DM, Black KS (1999) Water flow, sediment dynamics and benthic biology. Adv Ecol Res 29:155–193

Pejrup M, Larsen M, Edelvang K (1997) A fine grained sediment budget for the Sylt-Rømø tidal basin. Helgoländer Meeresuntersuchungen 51:253–268

Pereira PS, Calliari LJ, Holman R, Holland KT, Guedes RMC, Amorin CK, Cavalcanti PG (2011) Video and field observations of wave attenuation in a muddy surf zone. Mar Geol 279:210–221

Postma H (1961) Transport and accumulation of suspended matter in the Dutch Wadden Sea. Netherlands J Sea Res 1:148–190

Pritchard D (2005) Suspended sediment transport along an idealised tidal embayment: settling lag, residual transport and the interpretation of tidal signals. Ocean Dyn 55:124–136

Pritchard D, Hogg AJ (2003) Cross-shore sediment transport and the equilibrium morphology of mudflats under tidal currents. J Geophys Res 108:1–15

Ransom B, Bennett RJ, Baerwald R, Shea K (1997) TEM study of *in situ* OM on continental shelf margins: occurrence and the "monolayer" hypothesis. Mar Geol 138:1–9

Reddy KR, DeLaune RD (2008) Biogeochemistry of wetlands: science and applications. CRC, Boca Raton

Richards FA (1965) Anoxic basins and fjords. Chemical oceanography. Academic Press, London

Riethmüller R, Heineke M, Kühl H, Keuker-Rüdiger R (2000) Chlorophyll *a* concentration as an index of sediment surface stabilisation by microphytobenthos? Cont Shelf Res 20:1351–1372

Roberts W, Le Hir P, Whitehouse RJS (2000) Investigation using simple mathematical models of the effect of tidal currents and waves on the profile shape of intertidal mudflats. Cont Shelf Res 20:1079–1097

Rogers KG, Goodbred SL Jr (2014) The Sundarbans and Bengal Delta: the World's largest tidal mangrove and delta system. In: Kale VS (ed) Landscapes and landforms of India. Springer, Dordrecht, pp 181–187

Rosenberg R, Grémare A, Duchêne JC, Frank M (2008) 3D visualization and quantification of marine benthic biogenic structures and particle transport utilizing computer-aided tomography. Mar Ecol Prog Ser 363:171–182

Seuront L, Spilmont N (2002) Self-organized criticality in intertidal microphytobenthos patch patterns. Phys A 313:513–539

Shchepetkina A, Gingras MK, Zonneveld JP, Pemberton SG (2016) Sedimentary fabrics of the macrotidal, mud-dominated, inner estuary to fluvio-tidal transition zone, Petitcodiac River estuary, New Brunswick, Canada. Sediment Geol 333:147–163

Solan M, Kennedy R (2002) Observation and quantification of *in situ* animal-sediment relations using timelapse sediment profile imagery (t-SPI). Mar Ecol Prog Ser 228:179–191

Staats N, Stal LJ, de Winder B, Lr M (2000a) Oxygenic photosynthesis as driving process in exopolysaccharide production of benthic diatoms. Mar Ecol Prog Ser 193:261–269

Staats N, Stal LJ, Mur LR (2000b) Exopolysaccharide production by the epipelic diatom *Cylindrotheca closterium*: effects of nutrient conditions. J Exp Mar Biol Ecol 249:13–27

Stal LJ (2010) Microphytobenthos as a biogeomorphological force in intertidal sediment stabilization. Ecol Eng 36:236–245

Stal LJ, de Brouwer JFC (2003) Biofilm formation by benthic diatoms and their influence on the stabilization of intertidal mudflats. Berichte-Forschungszentrum Terramare 12:109–111

Stal LJ, de Brouwer JFC (2005) Diatom biofilms and the stability of intertidal mudflats. Geophys Res Abstr 7:20–28

Stoodley P (2016) Biofilms: flow disrupts communication. Nat Microbiol 1:1–2

Sturdivant SK, Díaz RJ, Cutter GR (2012) Bioturbation in a declining oxygen environment, in situ observations from Wormcam. PLoS One 7:e34539

Sundbäck K, Miles A, Hulth S, Svenson A (2003) Importance of benthic nutrient regeneration during initiation of macroalgal blooms in shallow bays. Mar Ecol Prog Ser 246:115–126

Sundby B, Anderson LG, Hall POJ, Iverfeldt A, Rutgers van der Loeff MM, Westerlund SFG (1986) The effect of oxygen on release and uptake of cobalt, manganese, iron and phosphate at the sediment-water interface. Geochim Cosmochim Acta 50:1281–1288

Thamdrup B, Dalsgaard T (2002) Production of N_2 through anaerobic ammonium oxidation coupled to nitrate reduction in marine sediments. Appl Environ Microbiol 68:1312–1318

Thomsen TR, Finster K, Ramsing NB (2001) Biogeochemical and molecular signatures of anaerobic methane oxidation in a marine sediment. Appl Environ Microbiol 67:1646–1656

Tice MM, Lowe DR (2004) Photosynthetic microbial mats in the 3,416-Myr-old ocean. Nature 431:549–552

Tiedje JM (1988) Ecology of denitrification and dissimilatory nitrate reduction to ammonia. In: Zehnder AJB (ed) Biology of anaerobic microorganisms. Wiley, New York, pp 197–244

Tiedje JM, Sexstone AJ, Myrold DD, Robinson JA (1982) Denitrification: ecological niches, competition and survival. Antonie van Leeuwenhoek 48:569–583

Underwood GJC (1994) Seasonal and spatial variation in epipelic diatom assemblages in the Severn Estuary. Diatom Res 9:451–472

Underwood GJC, Paterson DM (1993) Seasonal changes in diatom biomass, sediment stability and biogenic stabilization in the Severn Estuary. J Mar Biol Assoc UK 73:871–887

Valdemarsen T, Kristensen E, Holmer M (2009) Metabolic threshold and sulfide-buffering in diffusion controlled marine sediments impacted by continuous organic enrichment. Biogeochemistry 95:335–353

van Maren DS, Winterwerp JC (2013) The role of flow asymmetry and mud properties on tidal flat sedimentation. Cont Shelf Res 60S:71–84

Vepraskas MJ, Faulkner SP (2001) Redox chemistry of hydric soils. In: Richardson JL, Vepraskas MJ (eds) Wetland soils: genesis, hydrology, landscapes and classification. Lewis, Boca Raton, pp 85–105

Verney R, Lafite R, Brun-Cottan J-C (2009) Flocculation potential of estuarine particles: the importance of environmental factors and of the spatial and seasonal variability of suspended particulate matter. Estuar Coasts 32:678–693

Vos PC, de Wolf H (1993) Diatoms as a tool for reconstructing sedimentary environments in coastal wetlands; methodological aspects. Hydrobiologia 269(270):285–296

Wang Y (1983) The mudflat system of China. Can J Fish Aquat Sci 40(S1):160–171

Wang P (2012) Principles of sediment transport applicable in tidal environments. In: Davis RA Jr, Dalrymple RW (eds) Principles of tidal sedimentology. Springer, New York, pp 19–35

Wang Y, Healy T (2002) Definition, properties, and classification of muddy coasts. In: Healy T, Wang Y, Healy A (eds) Muddy coasts of the World: processes, deposits and function. Elsevier, Amsterdam, pp 9–18

Watermann F, Hillebrand H, Gerdes G, Krumbein WE, Sommer U (1999) Competition between benthic cyanobacteria and diatoms as influenced by different grain sizes and temperatures. Mar Ecol Prog Ser 187:77–87

Webster IT, Ford PW, Hodgson B (2002) Microphytobenthos contribution to nutrient-phytoplankton dynamics in a shallow coastal lagoon. Estuaries 25:540–551

Wells JT (1983) Dynamics of coastal fluid muds in low-, moderate-, and high-tide-range environments. Can J Fish Aquat Sci 40:130–142

Wells JT, Shanks AL (1987) Observations and geologic significance of marine snow in a shallow-water, partially enclosed marine embayment. J Geophys Res 92:13185–13190

Wiese W, Rheinheimer G (1978) Scanning electron microscopy and epifluorescence investigation of bacterial colonization of marine sand sediments. Microb Ecol 4:175–188

Wilson CA, Goodbred SL Jr (2015) Construction and maintenance of the Ganges-Brahmaputra-Meghna Delta: linking process, morphology, and stratigraphy. Annu Rev Mar Sci 7:67–88

Winterwerp JC (2002) On the flocculation and settling velocity of estuarine mud. Cont Shelf Res 22:1339–1360

Wolanski E (2006) The sediment trapping efficiency of the macro-tidal Daly Estuary, tropical Australia. Estuar Coast Shelf Sci 69:291–298

Wolanski E, Chappell J, Ridd P, Vertessy R (1988) Fluidization of mud in estuaries. J Geophys Res 93:2351–2361

Yang X, Zhang Q, Zhang J, Tan F, Wu Y, Zhang N, Yang H, Pang Q (2015) An integrated model for three-dimensional cohesive sediment transport in storm event and its application on Lianyungang Harbor, China. Ocean Dyn 65:395–417

Yao H (2013) Characterizing landuse changes in 1990-2010 in the coastal zone of Nantong, Jiangsu province, China. Ocean Coast Manage 71:108–115

Zhang Q, Gong Z, Zhang C, Townend I, Jin C, Li H (2016) Velocity and sediment surge: what do we see at times of very shallow water on intertidal mudflats? Cont Shelf Res 113:10–20

Zheng Y, Hou L, Liu M, Liu Z, Li X, Lin X, Yin G, Gao J, Yu C, Wang R, Jiang X (2016) Tidal pumping facilitates dissimilatory nitrate reduction in intertidal marshes. Sci Rep 6:21338

ZoBell CE, Feltham CB (1942) The bacterial flora of a marine mud flat as an ecological factor. Ecology 23:69–78

Chapter 3
Microbiota: The Living Foundation

Daniel J. Mayor, Barry Thornton, Holly Jenkins, and Stacey L. Felgate

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Abstract Mudflats are highly productive regions that are important to local, regional and global aspects of ecology and biogeochemistry. They sequester organic carbon, recycle nutrient elements such as nitrogen and phosphorus, release climate-active gases to the atmosphere, and provide sustenance to countless resident and migrant animals. Microorganisms that remain hidden from sight underpin all of these, and many other, crucial ecosystem functions and services. This chapter explores the roles of microorganisms in mudflat sediments, their interactions with

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the other residents, and some of the contemporary techniques used to study and quantify the ways in which they influence biogeochemical cycles.

1 Biogeochemical Significance of Mudflat Microbes

Estuaries and their associated mudflats, wetlands and marshes are gateways between the terrestrial and marine biospheres. Each year ~2 Gt of terrigenous carbon are transported through aquatic ecosystems to estuaries, where a large part of this is released to the atmosphere as CO_2 (Cole et al. 2007; Cai 2011). European estuaries are estimated to release the equivalent of 5–10% of Western Europe's anthropogenic CO_2 emissions annually (Frankignoulle et al. 1998), despite representing only a tiny fraction of the associated land coverage. Waterborne terrigenous organic matter is prone to flocculation at or close to the freshwater/saltwater interface (Sholkovitz 1976), resulting in the deposition of organic-rich material in the surrounding sediments. Mudflats are among the most productive ecosystems on Earth (Heip et al. 1995; Underwood and Kromkamp 1999) and thus the resident communities receive significant inputs of both allochthonous and autochthonous organic matter. Regardless of its source, organic matter in mudflat sediments is subject to intense biological activity and a fraction is rapidly remineralized to its inorganic constituents, resulting in the release of CO_2 and nutrient compounds containing elements such as nitrogen and phosphorus.

Benthic bacteria play a central role in the remineralization of organic matter. This 'unseen majority' (Whitman et al. 1998) provides the living foundation for mudflat ecosystems and the many biogeochemical functions and services that they provide. These organisms have large surface-to-volume ratios relative to metazoans and are thus capable of rapidly interacting with their surrounding environment. A plethora of microbial respiratory processes (e.g. aerobic respiration, denitrification, the reduction of manganese, iron and sulfate, and methanogenesis) are responsible for the remineralization of organic matter (see Chaps. 2 and 4). The predominance of any given metabolic pathway is largely governed by the availability of electron acceptors, which in turn, is influenced by a range of abiotic (e.g. sediment grain size and mineralogy) and biotic (e.g. bioturbation) factors (Burdige 2007).

Bacteria typically dominate the biomass of marine sediments, with ~10^9 cells ml^{-1} of sediment (Schmidt et al. 1998). It is therefore perhaps not surprising that these 'tiny but mighty' organisms have been referred to as 'the engines that drive Earth's biogeochemical cycles' (Falkowski et al. 2008). Scalable estimates of bacterial biomass in estuarine and mudflat sediments are surprisingly scarce, given their biogeochemical significance, with values in surficial sediments ranging between <1 and ~5 g C m^{-2} (e.g. Austin and Findlay 1989; Van Duyl and Kop 1990; Mayor et al. 2013). Processing of detrital material by benthic microorganisms in mudflat ecosystems exerts a strong influence on the availability of key nutrients for primary producers, and these organisms thereby act as a crucial interface between the cycling of living and decaying organic matter (Zou et al. 2016). The subsequent release of climate-active gases, such as CO_2, N_2O and CH_4, from intertidal sediments represent significant terms in global budgets and hence these environments meaningfully interact with global climate (Bange et al. 1994; Frankignoulle et al. 1998; Mosier et al. 1998).

2 Microbial Interactions

Mudflats are home to numerous animals that are in part or entirely, and directly or indirectly, dependent upon benthic microbes and the myriad biochemical reactions that they govern. Equally, sediment microbes are strongly influenced by the metazoan organisms with which they cohabit. These interdependencies have been recognised for decades; MacGinitie (1932) opined that "we have not given bacteria sufficient credit for the part they play in the food supply of mud-flat and ocean-bottom animals". Shortly afterwards, Baier (1935) suggested that benthic detritivores derive their nourishment from the bacteria that decompose detritus, rather than from the detritus which they appear to feed upon. Later still it was reasoned that mudflat sediments produce ~11 g dry weight of bacterial biomass per cubic foot ($1\ \text{ft}^3 = 0.028\ \text{m}^3$) each day and must therefore "play an important role in the distribution and occurrence of the mud flat fauna and flora" (ZoBell and Feltham 1942). Many decades later, these early insights are now taken for granted. Nevertheless, despite the advent of many new tools to identify and quantitatively examine the role of benthic microorganisms, our understanding of the myriad prokaryotic-prokaryotic and prokaryotic-eukaryotic interactions remains far from complete (Van Colen et al. 2014).

2.1 *The 'Microbial Loop'*

Mudflat ecosystems receive significant quantities of terrigenous dissolved organic matter (DOM) (Cole et al. 2007). They also possess highly productive communities of phytoplankton and their benthic analogues, the microphytobenthos (MPB), which are typically comprised of epibenthic diatoms and cyanobacteria (Underwood and Kromkamp 1999; Chaps. 2, 4, 8). These two groups of primary producers release large quantities of DOM, particularly under nutrient-limited conditions (Joiris et al. 1982; Cook et al. 2007; Thornton 2014). In the MPB, >70% of their production may be released as extracellular polysaccharides (Goto et al. 2001). Bacteria rapidly utilise DOM as a substrate for growth (Smith and Underwood 1998; Middelburg et al. 2000) and the resulting biomass represents a major food source for nano- (2–20 μm) and micro- (20–200 μm) flagellates and ciliates, meiobenthos (63–1000 μm; e.g. foraminifera, copepods, nematodes) and even macrofauna (>1000 μm) (Kemp

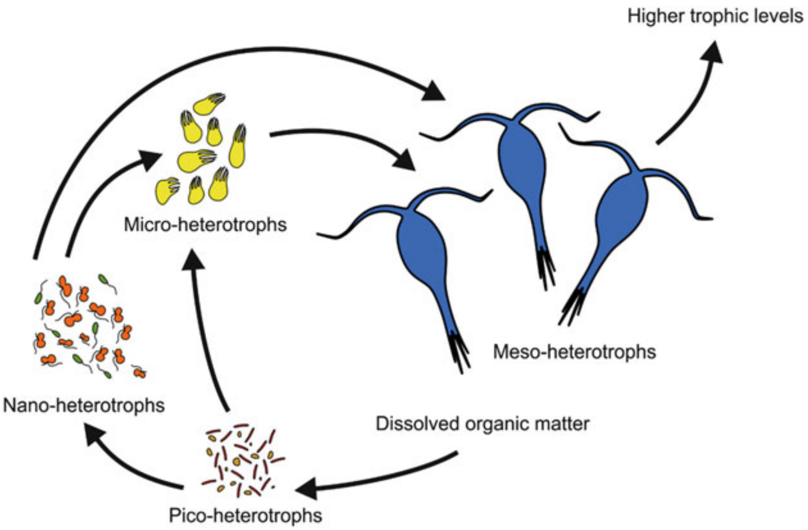

Fig. 3.1 Schematic of the 'microbial loop' (Azam et al. 1983). Dissolved organic matter, largely produced by photo-auto-heterotrophs, is retained within food webs and transferred to higher trophic levels via microorganisms. See text for further details.

1990; Heip et al. 1995; Hondeveld et al. 1995; Epstein 1997). This DOM-derived component of the benthic food web thereby serves as a mechanism through which a fraction of the exportable organic matter is retained within the sediments and contributes toward the sustenance of higher trophic levels.

Pelagic biologists recognise this classical paradigm as the 'microbial loop' (Azam et al. 1983; Fig. 3.1) and it has been the subject of intensive research in planktonic ecosystems over the proceeding decades (reviewed by Fenchel 2008). By contrast, only a handful of marine benthic studies explicitly refer to the 'microbial loop' (e.g. Danovaro 2000; Manini et al. 2003; Pusceddu et al. 2005; Pozzato et al. 2013). This apparent disparity in research effort may at least in part be attributed to the methodological complexities associated with studying the trophic interactions of organisms that depend on the specific redox conditions provided by their environment and which are easily disturbed during experimentation. Nevertheless, the global significance of benthic bacterial remineralization and production necessitates that further efforts be focussed toward mechanistically understanding how these organisms interact with the myriad components that constitute DOM and the organisms that produce it (Moran et al. 2016). For example, benthic bacteria display growth efficiencies between 4–81% (Hubas et al. 2007; Gontikaki et al. 2011; Mayor et al. 2012a, b) but the factors controlling this extensive range remain poorly understood. Environmental temperature, the availability of oxidants, and the quantity and quality of organic matter all influence microbial community composition and the rates at which they interact with organic matter (e.g. Arnosti et al. 1998; Pomeroy and Wiebe 2001; Arnosti 2004; Burdige 2007; Haynes et al. 2007; López-Urrutia and Morán 2007; Mayor et al. 2012a, b; Kujawinski et al. 2016) but a consensus view on their relative importance has not yet emerged. There is growing evidence to suggest that the composition and bioavailability of DOM is changing globally as a result of anthropogenic activities such as land use change, eutrophication and environmental warming (Engel et al. 2011; Thornton 2014; Parr et al. 2015; Moran et al. 2016). However, the paucity of knowledge on the processes influencing the functioning of the benthic microbial loop hinders our ability to meaningfully represent it in models and explore the ecological and biogeochemical implications of future environmental change.

2.2 Bioturbation

The physical properties of muddy sediments that typify mudflats (Chaps. 1, 2, and 8) provide a propitious substrate for burrowing animals, simultaneously providing a refuge from visual predation and reducing exposure to desiccation. However, the small interstitial spaces and cohesive nature of these sediments hinder the penetration of oxygenated water. Elevated levels of organic matter combined with high levels of microbial activity result in the rapid development of anoxic conditions, often only a few millimetres below the sediment's surface (Glud 2008). Burrowing benthic fauna frequently overcome this lack of oxygen by periodically flushing their burrows and chambers with fresh, oxygenated water (Chap. 6). This 'bioirrigation', in combination with other faunal activities, including locomotion, construction and feeding, results in the vertical and horizontal redistribution of sediment, organic matter, electron acceptors such as oxygen, and other solutes. These processes are collectively termed 'bioturbation' (see also Chaps. 5, 6, and 10), which has recently been defined as "*all transport processes carried out by animals that directly or indirectly affect sediment matrices. These processes include both particle reworking and burrow ventilation*" (Kristensen et al. 2012).

Bioturbation in marine sediments and its associated effects on benthic bacteria and biogeochemical processes have received considerable interest over the past few decades (e.g. Yingst and Rhoads 1980; Nealson 1997; Kristensen et al. 2012). Bioirrigation activities and the associated supply of oxygenated water represent a particularly important process that influences microbial community composition and the rate at which organic matter is remineralized. Recent research has demonstrated that benthic microbial community composition within a given faunal burrow, and hence the predominant biogeochemical pathways present, varies by faunal species identity and even by the specific location within a burrow (Bertics and Ziebis 2009, 2010; Laverock et al. 2010, 2011; Gilbertson et al. 2012; Lacoste et al. 2018). Where present, such effects have been attributed to specific redox microniches provided by the faunal activities and, to a lesser extent, the enhanced supply of organic matter (e.g. Bertics and Ziebis 2009; Chen et al. 2017). It is noteworthy that not all studies reveal strong macrofaunal-driven effects on benthic microbes and their biogeochemical functioning (e.g. Shen et al. 2017; Tada et al. 2017), indicating that species- or trait-specific effects likely operate. Care must therefore be taken when attempting to upscale observations from the laboratory to the real world (Carpenter 1996; Lohrer et al. 2015). Advances have been made in our understanding of how the identity and diversity of benthic faunal communities influence the community composition of sediment-dwelling microbes and their capacity to regenerate nutrients (Gilbertson et al. 2012; Bonaglia et al. 2014; Stock et al. 2014). Other contemporary research has demonstrated that the direct effects of anthropogenic stressors, such as environmental warming, ocean acidification and the presence of organic and inorganic pollutants, on benthic fauna can have profound direct and indirect consequences for microbially-mediated ecosystem functions and services such as carbon sequestration and nutrient regeneration (Godbold and Solan 2013; Godbold et al. 2017; Laverock et al. 2013; Mayor et al. 2013; Currie et al. 2017). The many developments in experimental observations of microbe-fauna interactions have, however, not been matched with developments in synthetic theory (Prosser et al. 2007; although see Allison and Martiny 2008) to explain such results. It is therefore not yet possible to derive generic predictions about how these interactions, and the concomitant effects on benthic biogeochemistry, will be affected by future environmental change.

2.3 Microbial Gardening

More than 50% of primary production is returned to the environment as dead and decaying particulate organic matter ('detritus' hereafter) (Mann 1988; Cebrián and Duarte 1995). Detritus therefore represents a dominant term in the global carbon cycle and is a major conduit through which organic matter is translocated between ecosystems (Bartels et al. 2012). Mudflat ecosystems receive significant quantities of both terrigenous and marine detritus, largely in the form of material derived from vascular plants (e.g. mangroves, cordgrasses, seagrasses, trees) and macroalgae (e.g. kelp). Animals that inhabit mudflat sediments are often considered to be detritivorous, but in many cases, the means by which these animals feed is more complex than the name of their feeding guild suggests (Plante et al. 1990).

Detritus is typically comprised of refractory, long-chain polysaccharides such as cellulose, hemicellulose and lignin that are difficult for metazoans to digest (Hylleberg Kristensen 1972) and contains little in the way of macro- or micronutrients that are essential for their healthy growth (Fenchel and Jørgensen 1977; Mann 1988; Moore et al. 2004; Mayor et al. 2011). At face value, deriving a nutritionally-balanced diet from this substrate alone therefore poses a considerable challenge to so-called 'detritivorous' animals (Phillips 1984). Closer inspection of detritus, however, reveals a diverse community of microorganisms that live on and within it. Collectively the 'detrital trophic complex', which includes bacteria, fungi, flagellates and ciliates, has the enzymatic capacity to catabolise refractory biomolecules such as lignin and cellulose.

Detritus-associated microbial communities, in contrast to the detritus itself, are readily digested by metazoans and their contents can be absorbed with relative ease

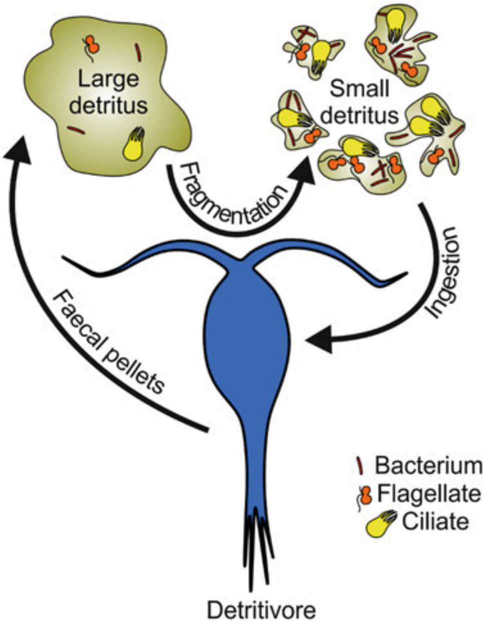

Fig. 3.2 Schematic of ‘microbial gardening’. Detritivorous metazoans stimulate the production of labile and nutritious microbial biomass by fragmenting, rather than ingesting large particles of detritus. Fragmentation of detritus increases the available surface area for microbial degradation, encouraging the growth of bacteria and other micro-heterotrophs (e.g. flagellates and ciliates) and the associated production of compounds such as essential fatty acids that are otherwise absent in detritus. See text for further details. Figure developed from Mayor et al. (2014).

(Phillips 1984). Furthermore, their ability to biosynthesise essential compounds such as amino acids and fatty acids renders their biomass nutritionally superior to detritus, resulting in the nutritional content of detritus increasing during the decay process (Harrison and Mann 1975). It is now widely accepted that detritivorous organisms obtain much of their energy and nutrition from the communities of detritus-associated microorganisms, rather than from the detritus itself (Fenchel and Jørgensen 1977; Phillips 1984; Plante et al. 1990; France 2011). Indeed, it is apparent that while detrital particles may be readily ingested, they often pass through the guts of so-called detritivores undigested, whereas organisms such as bacteria, flagellates and ciliates are readily removed (Fenchel 1970; Hylleberg 1975). Many detritivorous animals are adept at shredding or fragmenting particles of detritus (Anderson and Sedell 1979), a process that is known to further stimulate the proliferation of microbial communities by increasing the total surface area available to microbial degradation (Fenchel 1970); this process has been termed ‘microbial gardening’ (Hylleberg 1975) (Fig. 3.2), and has recently been invoked to explain the ecology and biogeochemistry of midwater ecosystems that are also fuelled by detritus (Mayor et al. 2014). Fragmentation as a strategy for increasing the nutritional content of detritus is a form of ‘trophic upgrading’ (Klein Breteler et al. 1999) that may be beneficial under certain circumstances. However, it is not without cost. Microbes typically display relatively low growth efficiencies (<30%; del Giorgio and Cole 1998) and thus remineralize much of the available substrate without benefit to metazoans. The merits of microbial gardening therefore represent a complex balance between the lability of the detrital substrate and an individual’s requirements for energy and nutrition (Anderson et al. 2017), and remain an area of ongoing research.

2.4 Microbial 'Priming'

It has long been recognised that the remineralization of recalcitrant organic matter within soils may be modified by the addition of fresh organic residues (e.g. Löhnis 1926; Broadbent 1947), a process that has become known as the 'priming effect' (Bingemann et al. 1953). These effects have been formally defined as "*strong short-term changes in the turnover of soil organic matter by comparatively moderate treatments of the soil*" and may occur due to a variety of reasons, including the input of organic or inorganic compounds, mechanical disturbance, and rewetting and drying effects (Kuzyakov et al. 2000). Recent years have seen a wealth of studies examining and describing a range of priming effects in terrestrial soils (see Kuzyakov et al. 2000; Kuzyakov 2010; Luo et al. 2015), including instances of both positive and negative priming (enhanced and depressed rates of remineralization, respectively; Fig. 3.3). Three, non-mutually exclusive mechanisms have been proposed to explain the observed instances of priming (Fig. 3.4), but the existence of these, and their relative importance, remain uncertain. Indeed, important differences have been shown to exist between the response of undisturbed soils *in situ* compared with disturbed soils often used in laboratory incubation studies with regards to their response to priming (Moinet et al. 2018). Nevertheless, priming effects appear capable of exerting significant influence on the global carbon cycle, potentially decreasing carbon sequestration in soils over the last century by ~50% (Guenet et al. 2018). Far less is known about priming effects in aquatic ecosystems, although recent reviews highlight the potential significance of positive priming in habitats such as mudflats, where recalcitrant terrigenous organic matter is likely

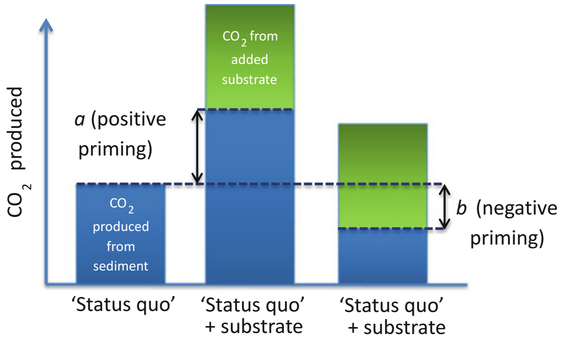

Fig. 3.3 Schematic illustration of the 'priming effect' in aquatic sediments (redrawn from Kuzyakov et al. 2000). Positive priming (**a**) occurs when remineralization of sediment organic matter increases following the introduction of a labile substrate. Negative priming (**b**) occurs when the addition of a labile substrate inhibits the remineralization of sediment organic matter.

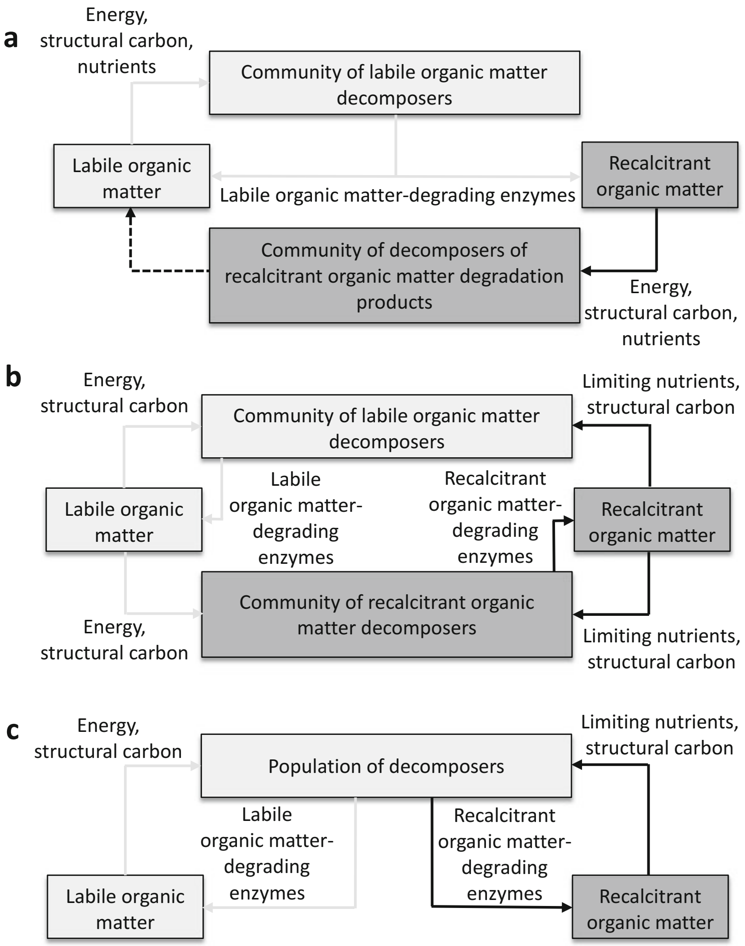

Fig. 3.4 Three alternative, but not mutually-exclusive, mechanisms by which priming occurs. Redrawn from Guenet et al. (2010). (**a**) Co-metabolism: Enzymes produced by microorganisms that degrade labile organic matter also catabolise recalcitrant organic matter into substrates that are utilised by a second community of microorganisms. (**b**) Mutualism: Enzymes produced by labile organic matter-degrading microorganisms provides energy to a second community of recalcitrant organic matter-degrading microorganisms that, in turn, liberates nutrients for both communities. (**c**) Degradation of labile organic matter by a single population of microorganisms provides sufficient energy for the generation of enzymes to extract nutrients from recalcitrant organic matter.

exposed to labile organic matter produced by marine microalgae (e.g. Guenet et al. 2010; Bianchi 2011). Further work is required to determine the significance of priming in aquatic ecosystems and to understand the mechanism(s) that govern how microbes elicit this effect.

3 Carbon-Based Isotope Techniques for Studying Mudflat Biogeochemistry

3.1 Bulk Isotopic (^{13}C) Methods

Carbon is the primary constituent of all organic matter and plays a major role in global climate. The cycling of this element has therefore been the subject of intense study over the past century. A particularly useful facet of carbon is that it exists in the natural environment as two stable isotopes, carbon-12 (^{12}C) and carbon-13 (^{13}C). These two atoms of the same element differ only in their number of neutrons and do not undergo radioactive decay. They naturally occur at a ratio of 98.9:1.1 (^{12}C:^{13}C), and their relative abundances in both organic and inorganic samples can be readily determined using isotope ratio mass spectrometry (IRMS) techniques. ^{12}C is referred to as being ‘light’, whereas ^{13}C is referred to as being ‘heavy’. Isotopic ratios are typically expressed using the more abundant isotope as the denominator (i.e. $^{13}C/^{12}C$) and are frequently reported relative to values of a known international reference material using the δ notation (‰); for carbon this reference is Vienna Pee Dee Belemnite (VPDB) (Coplen 1996).

The isotopic composition of carbon in organic matter initially reflects that of the inorganic sources used for autotrophic production and the effects of metabolic fractionation during this process. For example, different pathways of autotrophy (e.g. C3 and C4 pathways in terrestrial plants) result in organic matter with different isotopic signatures due to differential metabolic discrimination against $^{13}CO_{2(g)}$. Autotrophs using the C3 pathway on land and in the ocean produce isotopically distinct organic matter due to a range of factors that influence fractionation, including the dissolution of CO_2 in seawater, different carbon concentrating mechanisms, and the use of both dissolved $CO_{2(aq)}$ and $HCO_3^-{}_{(aq)}$ ions in seawater (Farquhar et al. 1989). The resulting isotopic differences between organic matter produced by different types of plants on land, and between primary producers on land and in the ocean, provides a powerful tool to discern the sources of organic matter consumed within ecosystems that receive organic matter from multiple sources, such as mudflats and estuaries. Carbon isotope fractionation during trophic transfer is often negligible (e.g. 0.4‰; Post 2002), and in such instances, $\delta^{13}C$ signatures of heterotrophic organisms can provide insight into their dietary carbon source(s). The apportioning of dietary substrates can be achieved by comparing the isotopic signatures of potential ‘end-members’ (i.e. $\delta^{13}C$ signatures of discrete sources of organic matter) to that of the consumer’s biomass using mass-balance isotope mixing models. Similarly, the source of metabolic substrate(s) being actively catabolised by organisms and ecosystems can be examined by comparing the isotopic composition of the evolved $CO_{2(g\ or\ aq)}$ to putative isotopic end-members (e.g. McCallister et al. 2006; Zetsche et al. 2011). Readers interested in the fundamentals of stable isotope ecology are referred to broader texts on this matter (e.g. Peterson and Fry 1987; Farquhar et al. 1989; Fry 2006; Karasov and del Rio 2007; Newton 2016).

3.2 Phospholipid Fatty Acid Techniques to Study Benthic Microbial Communities and Their Biogeochemistry

Phospholipids, which are composed of a phosphate ‘head’ joined to a pair of fatty-acid ‘tails’ via a glycerol molecule, are a major component of cellular membranes in prokaryotic and eukaryotic organisms. Pioneering work towards the end of the twentieth century demonstrated that bacteria produce specific phospholipid fatty acids (PLFAs) that can be used to derive estimates of their biomass, community composition, nutritional status and metabolic activity (Perry et al. 1979; White et al. 1979, 1996; Parkes and Taylor 1983; Taylor and Parkes 1983; Guckert et al. 1985, 1986, 1991; White 1988; Tunlid et al. 1989; Vestal and White 1989; Parkes et al. 1993). In essence, bacteria produce a range of iso- (i) and anteiso- (ai) branched PLFAs, many of which feature an odd number of carbon atoms (e.g. 15:1i, 15:1ai), and the abundance of these branched compounds can therefore be used a proxy for bacterial biomass. Similarly, the overall composition of PLFAs in environmental samples can provide information about the resident microbial communities and how these change in response to exogenous factors (e.g. Vestal and White 1989; Frostegård et al. 1993). Concentrations of individual PLFAs have been suggested to indicate the presence of specific groups of bacteria, e.g. aerobes, anaerobes, sulfate-reducers, etc. (see Table 2 in Vestal and White (1989) for putative biomarker PLFAs). However, it is apparent that the composition of PLFAs in bacterial monocultures can change depending on the environmental conditions and substrates used for growth (e.g. Guckert et al. 1986, 1991) and there is growing awareness that putative biomarker PLFAs are more abundant in other bacterial groups than previously thought. Therefore, great caution must be used when attempting to ascribe changes in the composition of PLFAs to shifts in the abundance of specific microbial groups (Frostegård et al. 2011). PLFA-based techniques lack the species-specificity of DNA- and RNA-based molecular tools but remain widely used to study benthic microbial communities as this approach is considered to relate only to the extant community, which may represent $\leq 30\%$ of the total number of bacterial cells (Luna et al. 2002). This is because, in contrast to genetic material, PLFAs in dead organisms degrade within hours (White et al. 1979).

A considerable advantage of PLFA analysis is that it is possible to discern the stable isotope composition of individual PLFAs using gas chromatography combustion IRMS (GC-C-IRMS). This approach is conceptually analogous to the IRMS analysis of bulk carbon and can thus provide information on the likely sources of carbon used for biosynthesis and specific metabolic pathways that result in isotopic fractionation (Teece et al. 1999; Pancost and Damsté 2003). The application of this technique has helped elucidate the trophic link between microphytobenthos and benthic bacteria (Cook et al. 2004) and fostered the understanding that macrophytes are generally not the primary carbon source for the majority of benthic bacteria in coastal environments (Boschker et al. 1999; Bouillon and Boschker 2006). GC-C-IRMS analysis of sediment PLFAs has been used to study how interactions between fauna and contaminants influence benthic bacterial community composition and metabolic functioning (Mayor et al. 2013). More recently these techniques have been used to detect aquaculture-derived organic wastes, which are isotopically-distinct to the autochthonous organic matter, in marine sediments, and their resulting effects on bacterial biomass (Mayor et al. 2017). Interpretation of the mechanisms underlying data from such studies remains a major challenge because the processes that control the relative composition of sediment-extracted PLFAs, in terms of both their relative abundance and isotopic composition, remain poorly understood (Lerch et al. 2011). Nevertheless, GC-C-IRMS analysis of PLFAs is a powerful tool for quantitatively tracing the sources of organic matter in benthic microbial communities and we suggest that their application is likely to increase in the coming years as access to the required facilities increases and the associated analytical costs decrease. Combining compound-specific isotope analysis (CSSIA) of PLFAs with high-throughput sequencing of environmental DNA offers considerable promise, and will likely yield new insights into how the composition of microbial communities relate to the wider ecological and biogeochemical functioning of benthic ecosystems. Such an approach will be particularly useful in coastal regions and other ecosystems that receive isotopically distinct sources of organic matter (Mayor et al. 2017).

3.3 Stable Isotope (^{13}C) Addition Experiments

The scarcity of ^{13}C in the natural environment can be exploited by adding this heavy isotope as a deliberate tracer to study the rates and pathways of carbon cycling in benthic ecosystems. Short-term (typically hours to days) studies that use single additions of ^{13}C-enriched material to natural communities are frequently referred to as ‘pulse-chase’ experiments. This is because they begin with an initial ‘pulse’ of ^{13}C-labelled material and subsequently ‘chase’ this into different components of the ecosystem by quantifying changes in their isotopic composition after a known period of time. The sensitivity of typical IRMS techniques is such that even relatively small changes in the isotopic signatures of material are readily discernible. Recent years have seen a steady increase in the use of stable isotope pulse-chase experiments, involving the addition of ^{13}C in either inorganic or organic forms, to study the ecology and biogeochemistry of intertidal ecosystems. Additions of ^{13}C-labelled bicarbonate to intertidal sediments have allowed the quantification of carbon fixation rates by the microphytobenthos and the subsequent transfer of this organic matter via dissolved and particulate pathways to benthic bacteria and metazoan consumers (Middelburg et al. 2000; Miyatake et al. 2014; Oakes and Eyre 2014; Oakes et al. 2016). An early example of an organic carbon isotope enrichment study added ^{13}C-labelled acetate and methane to benthic microbial communities and, using GC-C-IRMS analysis of bacterial PLFAs, directly linked specific bacterial groups with sulphate reduction and methane oxidation (Boschker et al. 1998). More recent studies have added ^{13}C-enriched phytodetritus to coastal benthic ecosystems to quantify the roles of different groups of benthic organisms and the rates at which organic matter is remineralised (Moodley et al. 2005; Evrard et al. 2012; Mayor et al. 2012a).

Pulse-chase experiments are, at least in theory, quantitative; a known quantity of ^{13}C is added at the outset and it is possible to quantify the amount of this tracer that is incorporated into the dissolved and particulate pools of organic and inorganic matter using a variety of IRMS techniques. Quantifying the amounts of carbon that are incorporated into faunal and bacterial biomass, and remineralized to dissolved inorganic carbon (DI^{13}C), permits the biogeochemical significance of these groups of organisms to be assessed and compared. Many of the studies to achieve this in benthic ecosystems have, to date, highlighted the predominance of bacteria in carbon processing (Moodley et al. 2005; Mayor et al. 2012a, b), further consolidating the importance of bacteria in the biogeochemical cycling that occurs in marine sediments.

References

Allison SD, Martiny JBH (2008) Colloquium paper: resistance, resilience, and redundancy in microbial communities. Proc Natl Acad Sci USA 105:11512–11519

Anderson NH, Sedell JR (1979) Detritus processing by macroinvertebrates in stream ecosystems. Annu Rev Entomol 24:351–377

Anderson TR, Pond DW, Mayor DJ (2017) The role of microbes in the nutrition of detritivorous invertebrates: a stoichiometric analysis. Front Microbiol 7:1–13

Arnosti C (2004) Speed bumps and barricades in the carbon cycle: substrate structural effects on carbon cycling. Mar Chem 92:263–273

Arnosti C, Jørgensen BB, Sageman J, Thamdrup B (1998) Temperature dependence of microbial degradation of organic matter in marine sediments: polysaccharide hydrolysis, oxygen consumption, and sulfate reduction. Mar Ecol Prog Ser 165:59–70

Austin HK, Findlay SE (1989) Benthic bacterial biomass and production in the Hudson River estuary. Microb Ecol 18:105–116

Azam F, Fenchel T, Field J, Gray J, Meyer-Reil L, Thingstad F (1983) The ecological role of water-column microbes in the Sea. Mar Ecol Prog Ser 10:257–263

Baier CR (1935) Studien zur hydrobakteriologie stehender binnengewasser. Arch Hydrobiol 29:183–264

Bange HW, Bartell UH, Rapsomanikis S, Andreae MO (1994) Computed with two different exchange models lie in the range of 11-18 Tg CH TM (phosphorus). North 8:465–480

Bartels P, Cucherousset J, Steger K, Eklov P, Tranvik LJ, Hillebrand H (2012) Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. Ecology 93:1173–1182

Bertics VJ, Ziebis W (2009) Biodiversity of benthic microbial communities in bioturbated coastal sediments is controlled by geochemical microniches. ISME J 3:1269–1285

Bertics VJ, Ziebis W (2010) Bioturbation and the role of microniches for sulfate reduction in coastal marine sediments. Environ Microbiol 12:3022–3034

Bianchi TS (2011) The role of terrestrially derived organic carbon in the coastal ocean: a changing paradigm and the priming effect. Proc Natl Acad Sci USA 108:19473–19481

Bingemann CW, Varner JE, Martin WP (1953) The effect of the addition of organic materials on the decomposition of an organic soil. Soil Sci Soc Am J 17:34–38

Bonaglia S, Nascimento FJA, Bartoli M, Klawonn I, Brüchert V (2014) Meiofauna increases bacterial denitrification in marine sediments. Nat Commun 5:5133

Boschker HTS, Nold SC, Wellsbury P, Bos D, de Graaf W, Pel R, Parkes RJ, Cappenberg TE (1998) Direct linking of microbial populations to specific biogeochemical processes by 13C-labelling of biomarkers. Nature 392:396–400

Boschker HTS, de Brouwer JFC, Cappenberg TE (1999) The contribution of macrophyte-derived organic matter to microbial biomass in salt-marsh sediments: stable carbon isotope analysis of microbial biomarkers. Limnol Oceanogr 44:309–319

Bouillon S, Boschker HTS (2006) Bacterial carbon sources in coastal sediments: a cross-system analysis based on stable isotope data of biomarkers. Biogeosciences 3:175–185

Broadbent FE (1947) Nitrogen release and carbon loss from soil organic matter during decomposition of added plant residues. Soil Sci Soc Am Proc 12:246–249

Burdige DJ (2007) Preservation of organic matter in marine sediments: controls, mechanisms, and an imbalance in sediment organic carbon budgets? Chem Rev 107:467–485

Cai W-J (2011) Estuarine and coastal ocean carbon paradox: CO_2 sinks or sites of terrestrial carbon incineration? Annu Rev Mar Sci 3:123–145

Carpenter SR (1996) Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77:677–680

Cebrián J, Duarte CM (1995) Plant growth-rate dependence of detrital carbon storage in ecosystems. Science (New York, N.Y.) 268:1606–1608

Chen X, Andersen TJ, Morono Y, Inagaki F, Jørgensen BB, Lever MA (2017) Bioturbation as a key driver behind the dominance of bacteria over archaea in near-surface sediment. Sci Rep 7:1–14

Cole JJ, Prairie YT, Caraco NF, McDowell WH, Tranvik LJ, Striegl RG, Duarte CM, Kortelainen P, Downing JA, Middelburg JJ, Melack J (2007) Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. Ecosystems 10:171–184

Cook PLM, Revill AT, Butler ECV, Eyre BD (2004) Carbon and nitrogen cycling on intertidal mudflats of a temperate Australian estuary. II. Nitrogen cycling. Mar Ecol Prog Ser 280:39–54

Cook PLM, Veuger B, Böer S, Middelburg JJ (2007) Effect of nutrient availability on carbon and nitrogen incorporation and flows through benthic algae and bacteria in near-shore sandy sediment. Aquat Microb Ecol 49:165–180

Coplen TB (1996) New guidelines for reporting stable hydrogen, carbon, and oxygen isotope-ratio data. Geochim Cosmochim Acta 60:3359–3360

Currie AR, Tait K, Parry H, de Francisco-Mora B, Hicks N, Mark Osborn A, Widdicombe S, Stahl H (2017) Marine microbial gene abundance and community composition in response to ocean acidification and elevated temperature in two contrasting coastal marine sediments. Front Microbiol 8:1599

Danovaro R (2000) Benthic microbial loop and meiofaunal response to oil-induced disturbance in coastal sediments: a review. Int J Environ Pollut 13:380

Del Giorgio PA, Cole JJ (1998) Bacterial growth efficiency in natural aquatic systems. Annu Rev Ecol Syst 29:503–554

Duyl FCV, Kop AJ (1990) Seasonal patterns of bacterial production and biomass in intertidal sediments of the western Dutch Wadden Sea. Mar Ecol Prog Ser 59:249–261

Engel A, Händel N, Wohlers J, Lunau M, Grossart HP, Sommer U, Riebesell U (2011) Effects of sea surface warming on the production and composition of dissolved organic matter during phytoplankton blooms: results from a mesocosm study. J Plankton Res 33:357–372

Epstein SS (1997) Microbial food webs in marine sediments. I. Trophic interactions and grazing rates in two tidal flat communities. Microb Ecol 34:188–198

Evrard V, Huettel M, Cook PLM, Soetaert K, Heip CHR, Middelburg JJ (2012) Importance of phytodetritus and microphyto benthos for heterotrophs in a shallow subtidal sandy sediment. Mar Ecol Prog Ser 455:13–31

Falkowski PG, Fenchel T, DeLong EF (2008) The microbial engines that drive earth's biogeochemical cycles. Science 320:1034–1039

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annu Rev Plant Physiol Plant Mol Biol 40:503–537

Fenchel T (1970) Studies on the decomposition of organic detritus derived from the turtle grass *Thalassia testudinum*. Limnol Oceanogr 15:14–20

Fenchel T (2008) The microbial loop - 25 years later. J Exp Mar Biol Ecol 366:99–103

Fenchel T, Jørgensen BB (1977) Detritus food chains of aquatic ecosystems: the role of bacteria. Adv Microb Ecol 1:1–58

France RL (2011) Leaves as "crackers", biofilm as "peanut butter": exploratory use of stable isotopes as evidence for microbial pathways in detrital food webs. Oceanol Hydrobiol Stud 40:110–115

Frankignoulle M, Abril G, Borges A, Bourge I, Canon C, Delille B, Libert E, Théate JM (1998) Carbon dioxide emission from European estuaries. Science 282:434–436

Frostegård Å, Bååth E, Tunlid A (1993) Shifts in the structure of soil microbial communities in limed forests as revealed by phospholipid fatty acid analysis. Soil Biol Biochem 25:723–730

Frostegård Å, Tunlid A, Bååth E (2011) Use and misuse of PLFA measurements in soils. Soil Biol Biochem 43:1621–1625

Fry B (2006) Stable isotope ecology. Springer, Berlin

Gilbertson WW, Solan M, Prosser JI (2012) Differential effects of microorganism-invertebrate interactions on benthic nitrogen cycling. FEMS Microbiol Ecol 82:11–22

Glud RN (2008) Oxygen dynamics of marine sediments. Mar Biol Res 4:243–228

Godbold JA, Solan M (2013) Long-term effects of warming and ocean acidification are modified by seasonal variation in species responses and environmental conditions. Philos Trans R Soc 368:20130186

Godbold JA, Hale R, Wood CL, Solan M (2017) Vulnerability of macronutrients to the concurrent effects of enhanced temperature and atmospheric pCO_2 in representative shelf sea sediment habitats. Biogeochemistry 135:89–10

Gontikaki E, Mayor DJ, Thornton B, Black K, Witte U (2011) Processing of 13C-labelled diatoms by a bathyal community at sub-zero temperatures. Mar Ecol Prog Ser 421:39–50

Goto N, Mitamura O, Terai H (2001) Biodegradation of photosynthetically produced extracellular organic carbon from intertidal benthic algae. J Exp Mar Biol Ecol 257:73–86

Guckert JB, Antworth CP, Nichols PD, White DC (1985) Phospholipid, ester-linked fatty acid profiles as reproducible assays for changes in prokaryotic community structure of estuarine sediments. FEMS Microbiol Lett 31:147–158

Guckert JB, Hood MA, White DC (1986) Phospholipid ester-linked fatty acid profile changes during nutrient deprivation of *Vibrio cholerae*: increases in the trans/cis ratio and proportions of cyclopropyl fatty acids. Appl Environ Microbiol 52:794–801

Guckert JB, Ringelberg DB, White DC, Hanson RS, Bratina BJ (1991) Membrane fatty acids as phenotypic markers in the polyphasic taxonomy of methylotrophs within the Proteobacteria. J Gen Microbiol 137:2631–2641

Guenet B, Danger M, Abbadie L, Lacroix G (2010) Priming effect: bridging the gap between terrestrial and aquatic ecology. Ecology 91:2850–2861

Guenet B, Camino-Serrano M, Ciais P, Tifafi M, Maignan F, Soong JL, Janssens IA (2018) Impact of priming on global soil carbon stocks. Glob Change Biol:1–11

Harrison PG, Mann KH (1975) Detritus formation from eelgrass (*Zostera marina L.*): the relative effects of fragmentation, leaching, and decay. Limnol Oceanogr 20:924–934

Haynes K, Hofmann TA, Smith CJ, Ball AS, Underwood GJC, Osborn AM (2007) Diatom-derived carbohydrates as factors affecting bacterial community composition in estuarine sediments. Appl Environ Microbiol 73:6112–6124

Heip CHR, Goosen NK, Herman PMJ, Kromkamp J, Middelburg JJ, Soetaert K (1995) Production and consumption of biological particles in temperate tidal estuaries. https://pure.knaw.nl/portal/en/publications/production-and-consumption-of-biological-particles-in-temperate-tidal-estuaries(766ddea7-098f-4095-b17d-6d4eb2961dcc).html

Hondeveld BJM, Nieuwland G, Van Duyl FC, Bak RPM (1995) Impact of nanoflagellate bacterivory on benthic bacterial production in the North Sea. Neth J Sea Res 34:275–287

Hubas C, Artigas LF, Davoult D (2007) Role of the bacterial community in the annual benthic metabolism of two contrasted temperate intertidal sites (Roscoff Aber Bay, France). Mar Ecol Prog Ser 344:39–48

Hylleberg J (1975) Selective feeding by *Abarenicola pacifica* with notes on *Abarenicola vagabunda* and a concept of gardening in lugworms. Ophelia 14:113–137

Hylleberg Kristensen J (1972) Carbohydrases of some marine invertebrates with notes on their food and on the natural occurrence of the carbohydrates studied. Mar Biol 14:130–142

Joiris C, Billen G, Lancelot C, Daro MH, Mommaerts JP, Bertels A, Bossicart M, Nijs J, Hecq JH (1982) A budget of carbon cycling in the Belgian coastal zone: relative roles of zooplankton, bacterioplankton and benthos in the utilization of primary production. Neth J Sea Res 16:260–275

Karasov WH, del Rio CM (2007) Physiological ecology: how animals process energy, nutrients, and toxins. Princeton University Press, Princeton

Kemp PF (1990) The fate of benthic bacterial production. Aquat Sci 2:109–124

Klein Breteler WCM, Schogt N, Baas M, Schouten S, Kraay GW (1999) Trophic upgrading of food quality by protozoans enhancing copepod growth: role of essential lipids. Mar Biol 135:191–198

Kristensen E, Penha-Lopes G, Delefosse M, Valdemarsen T, Quintana CO, Banta GT (2012) What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar Ecol Prog Ser 446:285–302

Kujawinski EB, Longnecker K, Barott KL, Weber RJM, Kido Soule MC (2016) Microbial community structure affects marine dissolved organic matter composition. Front Mar Sci 3:1–15

Kuzyakov Y (2010) Priming effects: interactions between living and dead organic matter. Soil Biol Biochem 42:1363–1371

Kuzyakov Y, Friedel JK, Stahr K (2000) Review of mechanisms and quantification of priming effects. Soil Biol Biochem 32:1485–1498

Lacoste É, Piot A, Archambault P, McKindsey CW, Nozais C (2018) Bioturbation activity of three macrofaunal species and the presence of meiofauna affect the abundance and composition of benthic bacterial communities. Mar Environ Res 136:62–70

Laverock B, Smith CJ, Tait K, Osborn AM, Widdicombe S, Gilbert JA (2010) Bioturbating shrimp alter the structure and diversity of bacterial communities in coastal marine sediments. ISME J 4:1531–1544

Laverock B, Gilbert JA, Tait K, Osborn AM, Widdicombe S (2011) Bioturbation: impact on the marine nitrogen cycle. Biochem Soc Trans 39:315–320

Laverock B, Kitidis V, Tait K, Gilbert JA, Osborn AM, Widdicombe S (2013) Bioturbation determines the response of benthic ammonia-oxidizing microorganisms to ocean acidification. Philos Trans R Soc B Biol Sci 368:20120441

Lerch TZ, Nunan N, Dignac MF, Chenu C, Mariotti A (2011) Variations in microbial isotopic fractionation during soil organic matter decomposition. Biogeochemistry 106:5–21

Löhnis F (1926) Nitrogen availability of green manures. Soil Sci 22:253–290

Lohrer AM, Thrush SF, Hewitt JE, Kraan C (2015) The up-scaling of ecosystem functions in a heterogeneous world. Sci Rep 5. https://doi.org/10.1038/srep10349

López-Urrutia Á, Morán XAG (2007) Resource limitation of bacterial production distorts the temperature dependence of oceanic carbon cycling. Ecology 88:817–822

Luna GM, Manini E, Danovaro R (2002) Large fraction of dead and inactive bacteria in coastal marine sediments: comparison of protocols for determination and ecological significance. Appl Environ Microbiol 68:3509–3513

Luo Z, Wang E, Smith C (2015) Fresh carbon input differentially impacts soil carbon decomposition across natural and managed systems. Ecology 96:2806–2813

MacGinitie GE (1932) The role of bacteria as food for bottom animals. Science 76:490

Manini E, Fiordelmondo C, Gambi C, Pusceddu A, Danovaro R (2003) Benthic microbial loop functioning in coastal lagoons: a comparative approach. Oceanol Acta 26:27–38

Mann KH (1988) Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. Limnol Oceanogr 33:910–930

Mayor DJ, Cook KB, Thornton B, Walsham P, Witte UFM, Zuur AF, Anderson TR (2011) Absorption efficiencies and basal turnover of C, N and fatty acids in a marine Calanoid copepod. Funct Ecol 25:509–518

Mayor DJ, Thornton B, Hay S, Zuur AF, Nicol GW, McWilliam JM, Witte UFM (2012a) Resource quality affects carbon cycling in deep-sea sediments. ISME J 6:1740–1748

Mayor DJ, Thornton B, Zuur AF (2012b) Resource quantity affects benthic microbial community structure and growth efficiency in a temperate intertidal mudflat. PLoS One 7:2–7

Mayor DJ, Gray NB, Elver-Evans J, Midwood AJ, Thornton B (2013) Metal-macrofauna interactions determine microbial community structure and function in copper contaminated sediments. PLoS One 8:e64940

Mayor DJ, Sanders R, Giering SLC, Anderson TR (2014) Microbial gardening in the ocean's twilight zone: detritivorous metazoans benefit from fragmenting, rather than ingesting, sinking detritus. BioEssays 36:1132–1137

Mayor DJ, Gray NB, Hattich GSI, Thornton B (2017) Detecting the presence of fish farm-derived organic matter at the seafloor using stable isotope analysis of phospholipid fatty acids. Sci Rep 7:5146

McCallister SL, Guillemette F, del Giorgio PA (2006) A system to quantitatively recover bacterioplankton respiratory CO_2 for isotopic analysis to trace sources and ages of organic matter consumed in freshwaters. Limnol Oceanogr Methods 4:406–415

Middelburg JJ, Barranguet C, Boschker HTS, Herman PMJ, Moens T, Heip CHR (2000) The fate of intertidal microphytobenthos carbon: an in situ 13C-labeling study. Limnol Oceanogr 45:1224–1234

Miyatake T, Moerdijk-Poortvliet TCW, Stal LJ, Boschker HTS (2014) Tracing carbon flow from microphytobenthos to major bacterial groups in an intertidal marine sediment by using an in situ 13C pulse-chase method. Limnol Oceanogr 59:1275–1287

Moinet GYK, Midwood AJ, Hunt JE, Whitehead D, Hannam KD, Jenkins M, Brewer MJ, Adams MA, Millard P (2018) Estimates of rhizosphere priming effects are affected by soil disturbance. Geoderma 313:1–6

Moodley L, Middelburg JJ, Soetaert K, Boschker HTS, Herman PMJ, Heip CHR (2005) Similar rapid response to phytodetritus deposition in shallow and deep-sea sediments. J Mar Res 63:457–469

Moore JC, Berlow EL, Coleman DC, De Suiter PC, Dong Q, Hastings A, Johnson NC, McCann KS, Melville K, Morin PJ, Nadelhoffer K, Rosemond AD, Post DM, Sabo JL, Scow KM, Vanni MJ, Wall DH (2004) Detritus, trophic dynamics and biodiversity. Ecol Lett 7:584–600

Moran MA, Kujawinski EB, Stubbins A, Fatland R, Aluwihare LI, Buchan A, Crump BC, Dorrestein PC, Dyhrman ST, Hess NJ, Howe B, Longnecker K, Medeiros PM, Niggemann J, Obernosterer I, Repeta DJ, Waldbauer JR (2016) Deciphering ocean carbon in a changing world. Proc Natl Acad Sci USA 113:3143–3151

Mosier A, Kroeze C, Nevison C, Oenema O, Seitzinger S (1998) Closing the global N_2O budget : nitrous oxide emissions through the agricultural nitrogen cycle inventory methodology. Nutr Cycling Agroecosyst 52:225–248

Nealson KH (1997) Sediment bacteria: who's there, what are they doing, and what's new? Annu Rev Earth Planet Sci 25:403–434

Newton J (2016) Stable isotopes as tools in ecological research. eLS. Wiley, Chichester

Oakes JM, Eyre BD (2014) Transformation and fate of microphytobenthos carbon in subtropical, intertidal sediments: potential for long-term carbon retention revealed by 13C-labeling. Biogeosciences 11:1927–1940

Oakes JM, Rysgaard S, Glud RN, Eyre BD (2016) The transformation and fate of sub-Arctic microphytobenthos carbon revealed through 13C-labeling. Limnol Oceanogr 61:2296–2308

Pancost RD, Sinninghe Damsté JS (2003) Carbon isotopic compositions of prokaryotic lipids as tracers of carbon cycling in diverse settings. Chem Geol 195:29–58

Parkes RJ, Taylor J (1983) The relationship between fatty acid distributions and bacterial respiratory types in contemporary marine sediments. Estuar Coast Shelf Sci 16

Parkes RJ, Dowling NJE, White DC, Herbert RA, Gibson GR (1993) Characterization of sulphate-reducing bacterial populations within marine and estuarine sediments with different rates of sulphate reduction. FEMS Microbiol Lett 102:235–250

Parr TB, Cronan CS, Ohno T, Findlay SEG, Smith SMC, Simon KS (2015) Urbanization changes the composition and bioavailability of dissolved organic matter in headwater streams. Limnol Oceanogr 60:885–900

Perry GJ, Volkman JK, Johns RB (1979) Fatty acids of bacterial origin in contempary marine sediments. Geochim Cosmochim Acta 43:1715–1725

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293–320

Phillips NW (1984) Role of different microbes and substrates as potential suppliers of specific, essential nutrients to marine detritivores. Bull Mar Sci 35:283–298

Plante CJ, Jumars PA, Baross JA (1990) Digestive associations between marine detritivores and bacteria. Annu Rev Ecol Syst 21:93–127

Pomeroy LR, Wiebe WJ (2001) Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. Aquat Microb Ecol 23:187–204

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718

Pozzato L, Van Oevelen D, Moodley L, Soetaert K, Middelburg JJ (2013) Sink or link? The bacterial role in benthic carbon cycling in the Arabian Sea's oxygen minimum zone. Biogeosciences 10:6879–6891

Prosser JI, Bohannan BJM, Curtis TP, Ellis RJ, Firestone MK, Freckleton RP, Green JL, Green LE, Killham K, Lennon JJ, Osborn AM, Solan M, van der Gast CJ, Young JPW (2007) The role of ecological theory in microbial ecology. Nat Rev Microbiol 5:384

Pusceddu A, Fiordelmondo C, Danovaro R (2005) Sediment resuspension effects on the benthic microbial loop in experimental microcosms. Microb Ecol 50:602–613

Schmidt JL, Deming JW, Jumars PA, Keil RG (1998) Constancy of bacterial abundance in surficial marine sediments. Limnol Oceanogr 43:976–982

Shen H, Jiang G, Wan X, Li H, Qiao Y, Thrush S, He P (2017) Response of the microbial community to bioturbation by benthic macrofauna on intertidal flats. J Exp Mar Biol Ecol 488:44–51

Sholkovitz ER (1976) Flocculation of dissolved organic and inorganic matter during the mixing of river water and seawater. Geochim Cosmochim Acta 40:831–845

Smith DJ, Underwood GJC (1998) Exopolymer production by intertidal epipelic diatoms. Limnol Oceanogr 43:1578–1591

Stock W, Heylen K, Sabbe K, Willems A, De Troch M, Savage C (2014) Interactions between benthic copepods, bacteria and diatoms promote nitrogen retention in intertidal marine sediments. PLoS One 9:e111001

Tada K, Koomklang J, Ichimi K, Yamaguchi H (2017) Negligible effect of the benthic fauna on measuring the nutrient upward fluxes from coastal sediments. J Oceanogr 73:397–402

Taylor J, Parkes RJ (1983) The cellular fatty-acids of the sulfate-reducing bacteria, *Desulfobacter* Sp, *Desulfobulbus* Sp and *Desulfovibrio*-Desulfuricans. J Gen Microbiol 129:3303–3309

Teece MA, Fogel ML, Dollhopf ME, Nealson KH (1999) Isotopic fractionation associated with biosynthesis of fatty acids by a marine bacterium under oxic and anoxic conditions. Org Geochem 30:1571–1579

Thornton DCO (2014) Dissolved organic matter (DOM) release by phytoplankton in the contemporary and future ocean. Eur J Phycol 49:20–46

Tunlid A, Ringelberg DB, Phelps TJ, Low C, White DC (1989) Measurement of phospholipid fatty acids at picomolar concentrations in biofilms and deep subsurface sediments using gas chromatography and chemical ionization mass spectrometry. J Microbiol Methods 10:139–153

Underwood GJC, Kromkamp J (1999) Primary production by phytoplankton and microphytobenthos in estuaries. Adv Ecol Res 29:93–153

Van Colen C, Underwood GJC, Serôdio J, Paterson DM (2014) Ecology of intertidal microbial biofilms: mechanisms, patterns and future research needs. J Sea Res 92:2–5

Vestal JR, White DC (1989) Lipid analysis in microbial ecology. BioScience 39:535–541

White DC (1988) Validation of quantitative analysis for microbial biomass, community structure, and metabolic activity. Arch Hydrobiol 31:1–18

White DC, Davis WM, Nickels JS, King JD, Bobbie RJ (1979) Determination of the sedimentary microbial biomass by extractible lipid phosphate. Oecologia 40:51–62

White DC, Stair JO, Ringelberg DB (1996) Quantitative comparisons of in situ microbial biodiversity by signature biomarker analysis. J Ind Microbiol 17:185–196

Whitman WB, Coleman DC, Wiebe WJ (1998) Prokaryotes: the unseen majority. Proc Natl Acad Sci USA 95:6578–6583

Yingst JY, Rhoads DC (1980) The role of bioturbation in the enhancement of bacterial growth rates in marine sediments. Marine benthic dynamics. University of South Carolina Press, Columbia

Zetsche E, Thornton B, Midwood AJ, Witte U (2011) Utilisation of different carbon sources in a shallow estuary identified through stable isotope techniques. Cont Shelf Res 31:832–840

ZoBell CE, Feltham CB (1942) The bacterial flora of a marine mud flat as an ecological factor. Ecology 23:69–78

Zou K, Thébault E, Lacroix G, Barot S (2016) Interactions between the green and brown food web determine ecosystem functioning. Funct Ecol 30:1454–1465

Chapter 4
Microphytobenthic Biofilms: Composition and Interactions

Cédric Hubas, Claire Passarelli, and David M. Paterson

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Abstract Microphytobenthic biofilms in mudflats are characterised by a wide variety of microorganisms and the production of large quantities of extracellular polymeric substances (EPS). In this chapter, the diversity of microphytobenthos (MPB) is reviewed and the complex interactions that take place in mudflat biofilms between microalgae and bacteria are discussed. Microbial interaction in natural

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biofilms is an emerging field of study in mudflat ecosystems. Although emphasis is placed on EPS and EPS-mediated interactions, because they have received most of the research attention, more direct interactions such as communication and defence are also discussed. Most studies to date have dealt with monospecific or multispecific laboratory biofilms, and environmental studies are still very rare. The development of this field of study in mudflat ecosystems is clearly a major requirement in our understanding of the functioning of mudflat biofilms.

1 Introduction

Microphytobenthic biofilms in mudflats are characterised by the production of large quantities of extracellular polymeric substances (EPS), forming a matrix at the sediment surface and incorporating a wide variety of microorganisms. Diatoms are by far the most abundant taxa of the microphytobenthos (MPB) but "microphytobenthic biofilms" are much more complex than first appears. Diatoms are merely the tip of the biofilm iceberg, since MPB comprise a large diversity of eukaryotic and prokaryotic organisms which interact in multiple ways, and contribute to the functioning of the whole biofilm community. Biofilm communities are composed of a wide range of microbes which could be classified in several ways, including size and lifestyle (i.e. picoheterobenthos, picophytobenthos, microphytobenthos and microheterobenthos, see Paterson et al. 2009). MPB is the one that has received the most attention in depositional systems, which are complex and highly organised ecosystems where opposing gradients of oxygen and sulphide provide rapidly-changing ecological niches and favour the development of different functional groups of microorganisms that display various forms of respiration. Many of these microbial groups have not yet received the attention they deserve. For example, the purple sulphur bacteria (i.e. prokaryotic picophytobenthos) contribute significantly to the carbon cycle of intertidal sediments (Hubas et al. 2013, 2017), although they are not well-studied.

Due to the difficulty of applying the species concept in microbiology (Rossello-Mora and Amann 2001), the full extent of the microphytobenthic assemblage diversity has not yet been characterized. Interaction between the members of the MPB community is therefore still an emerging field of study. The aim of the present chapter is to provide an overview of the complex interactions that take place in mudflat biofilms between microalgae and bacteria. We first describe the interactions that are mediated by extracellular polymeric substances (EPS). This field of study is relatively well-documented and the roles of the EPS in the functioning of mudflat biofilms have been discussed in detail, although their fine chemical composition is less well understood. We then consider the "direct" interactions between microbes, and especially those that involve the production of secondary metabolites.

Fig. 4.1 Left: in sufficient density, diatoms colour the surface of a sediment matrix. In this case, a culture grown on glass beads. Centre: the diversity of diatom frustules (cell walls) used in creating a montage of cell shapes visible only by microscopy (slide by K. Kemp). Right: fine structure on the valve surface of a common benthic diatom (*Navicula* sp.) demonstrated by scanning electron microscopy. The raphe (longitudinal slit in the silica frustule) is visible along the central axis of the valve. Scale bar = 10 μm (SEM by IR Davidson, University of St Andrews).

2 Composition and Diversity of Microphytobenthos

2.1 Microphytobenthos: Too Diverse to Study?

There is a significant challenge in fully appreciating the range and diversity of organisms that comprise the microphytobenthos. The word itself provides a clue, in that "microphytobenthos" is a cumulative, generic, hybrid term, bringing together an essentially unrelated group of organisms that are (usually) invisible to the naked eye (*micro* describes a unit of 1 millionth of a meter), that are designated by the ancient Greek term "phyto" (pertaining to or derived from plants) and that are associated with the bottom (benthos = ancient Greek for depth). Each part of this classification can be discussed in great detail, and many planktonic organisms are now assigned to even smaller (size) groupings such as the pico- and even nano- size ranges (Meng et al. 2011). The 'micro' prefix is also misleading since the larger epipelic diatoms may reach more than 500 μm in length and, under the right conditions, are individually barely visible to the naked eye. In addition, the accumulation of even very small pigmented cells can make them visible to the trained eye, as an obvious pigment on the surface of sediments (Fig. 4.1), which can be sufficiently dense that it can also be discerned by remote sensing (Paterson et al. 1998).

The designation "phyto" in the term 'microphytobenthos' is now related more to the mode of energy capture than to phylogeny. The MPB are now taken to include photosynthetic prokaryotes and also some mixotrophic organisms (Sanders 1991), such as free-living protozoans, including the foraminifera that can photosynthesise due to the presence of algal symbionts (Lee 2001). To summarise, MPB comprises a diverse group in terms of size, morphology, and ecology; their common denominator is the mudflat habitat. There is no sharp distinction between a "biofilm" and a "microbial mat"; rather, one merges into the other, and different disciplines (geologists, sedimentologists, medical researchers, mudflat ecologists) often mean different things while using the same terminology (see Chap 1). In general, although a microbial mat begins as a biofilm, it evolves toward a more substantial and permanent structure, lasting for months if not years (see Chap. 8), whereas a biofilm is less physically substantial, with higher turnover and less longevity. Indeed, in intertidal systems, MPB cells may accumulate at the sediment surface when the tide is out during daylight and migrate back into the sediment before the tide returns (Admiraal 1984; Paterson and Hagerthey 2001). This predictable diurnal formation and dispersion of a thick layer of cells at the sediment surface had led to the term "transient biofilms" (Krumbein et al. 2003) for such MPB systems (in order to reduce ambiguity, we propose to use the term '*transient epibenthic biofilm*' to designate these communities—see Chap. 1). Samples of MPB returned to the laboratory sometimes continue this migratory behaviour for a period of days, suggesting there is an inherent genetic control to the pattern of migration. Epipelic diatom migration was noted as early as 1907 by Flavel and Bohn, and Round summarised this behaviour in 1984, but there is still a lack of knowledge of the exact mechanisms of control, movement and coordination, despite the decades that have passed.

The most commonly-cited and most abundant MPB are diatoms and cyanobacteria, with some authors occasionally including flagellates, euglenids and other protists (Paterson and Hagerthey 2001; Giere 2009). With care, a microscopist will find a wide variety of MPB in most samples, but it requires skill and patience to recognise the full array. For added difficulty, the sampling techniques appropriate to observing the different groups of MPB vary and can greatly bias the results for some groups of organisms. For example, diatomists tend to use strong acid to clean samples for clearer observation of the siliceous diatom cell walls, which will then exclude all soft-bodied members of the MPB. Even when fresh samples are observed, very few researchers are comprehensive in their reports. Provide unadulterated slides to different colleagues and they can't help but highlight their interests; diatomists report on the diatoms in great detail while other microbiologists might concentrate on the cyanobacteria. Flagellates and other small mobile protists are less well-studied and much more difficult to sample, being highly mobile and very fragile. In conclusion, the diversity of organisms in the MPB is impressive, and great care and skill are required to study them fully. The following section therefore deals only with the major components of the MPB, diatoms and cyanobacteria, for the reasons outlined above. More specialized texts can be consulted for greater detail on the less-studied groups (Adl et al. 2007; Giere 2009).

2.2 Diatoms

The evolutionary history of the diatoms is complex (Medlin 2016), and no precise time can be placed on their emergence. It is suggested that after a complex chain of endosymbiotic events, possibly with varied endosymbionts, the heterokont algae (which include the diatoms) began to radiate from no earlier than 250 million YBP,

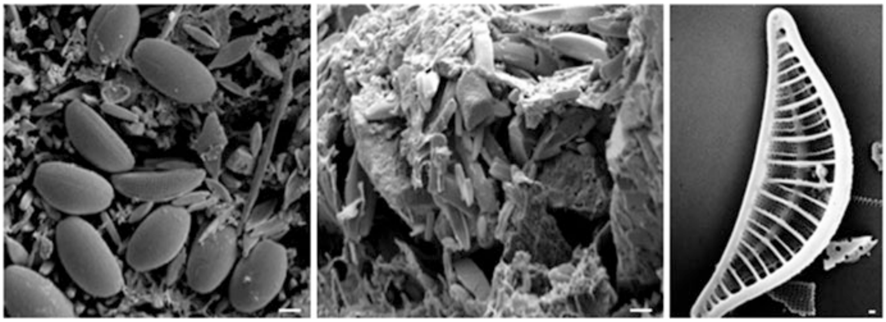

Fig. 4.2 Electron micrographs of diatoms: Left: A group of epipelic diatoms on the surface of intertidal sediment. Centre: A profile of a sediment sample, showing diatoms between the sediment grains. Right: Detail of the fine structure of the inside of a diatom valve. Scale bar = 10 μm.

at the time of the Permian–Triassic extinction event, or "the Great Dying". The diatoms have since evolved into one of the most diverse (in species terms), important, and beautiful of the algal groups. The cell is surrounded by an often-ornate silica cell wall, the patterning of which can be used to distinguish between species.

How many species of diatoms are in existence is a surprisingly complex question. At first glance, a species that can be told apart by the patterning of the cell walls (Figs. 4.1 and 4.2) should be a taxonomist's dream, but this dream can quickly become a nightmare due to the number of species, the very close resemblance of many similar forms, and the possibility that some species may vary in size and shape due to factors such as temperature and age (Round et al. 1990). For example, some diatoms reduce in size as they undergo asexual reproduction (Round 1981). Added to this is the difficulty of maintaining a primary catalogue of species names and descriptions across a global community when researchers often reach different conclusions about the designation of individual morphotypes (Mann and Droop 1996). So how many species of diatom are there? Given that many may be undiscovered, and the possible confusion of morpho-types and definitive species, the proposed numbers of species range from a conservative estimate of 20,000 (Guiry 2012), to a more consequent 200,000 (Mann and Droop 1996), and an extreme and unsubstantiated 2 million.[1]

Species determination of diatoms has largely been done using morphological characteristics based on the structure of the cell wall. The siliceous patterning of the valves, with ridges, grooves and perforations, can be very intricate (Figs. 4.2 and 4.3) and creates a strong protective capsule around the cell. Some workers have tried to include more characteristics for taxonomic discrimination, including detail from live material such as chloroplast structure, rather than the preserved valves; this is rather rare (Bedoshvili et al. 2009).

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[1] http://westerndiatoms.colorado.edu/about/what_are_diatoms. Accessed Sept 2017.
http://www.itcamefromthepond.com/2014/03/26/paddy-patterson. Accessed May 2018.

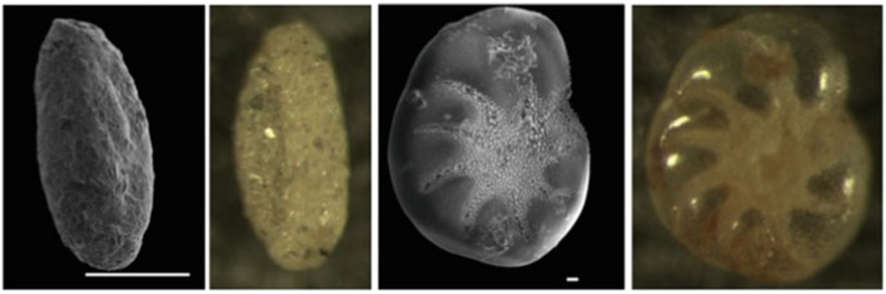

Fig. 4.3 Paired scanning electron and light micrographs of two benthic species of Foraminifera. Left: an agglutinating species that forms a "shell" from sediment particles. Scale bar = 100 μm. Right: a calcifying form that creates a test by bio-deposition. Scale bar = 10 μm (images courtesy of Dr N. Khanna).

2.3 Cyanobacteria

Cyanobacteria are important components of the MPB. They have the ability to form recognisable and resilient mats and have been the subject of a great deal of biogeochemical research, partly because many species have the ability to fix nitrogen (Stal 2015), making them an important link in nutrient recycling, especially in oligotrophic habitats. The cyanobacteria have a very long evolutionary history (Shih 2015), and their activity, through the development of oxygenic photosynthesis (Harel et al. 2015), led to the oxygenation of the Earth's atmosphere and the beginning of the "oxygenic ecology" that we recognise today. The precise point of cyanobacterial evolution is very ancient and difficult to determine, but is estimated to be between 3.4 and 3 billion YBP (Shih 2015). Evidence of their emergence is retained in the fossil record as the laminated microbially-derived structures known as stromatolites. These early bacterial assemblages trapped sedimentary grains and created lasting laminations in the depositional environment that later became preserved as fossils (Noffke and Paterson 2007; Riding 2011; see Chap. 8). These very early and developing ecosystems may represent one of the first examples of ecosystem engineering, whereby organisms, including bacteria (Larson et al. 2009) alter their physical surroundings (Lubarsky et al. 2010). There is also evidence that development of photosynthesis may have enhanced the sediment-binding capacity of cyanobacterial biofilms by the associated production and secretion of the EPS, contributing to the adhesive potential of the early biofilms (Paterson et al. 2008). The cyanobacteria therefore have a very ancient lineage; however, they show much more limited radiation than other MPB groups such as the diatoms. There are estimated to be 2000–8000 species of cyanobacteria, comprising both unicellular and filamentous species. Often, the cells are arranged inside a sheath of polymeric material, and in some species there can also be some differentiation of cells into reproductive units (akinetes) and specialist nitrogen-fixing cells (heterocysts). Interestingly, some cyanobacteria that do not have heterocysts can still fix nitrogen (Stal 2015). Recognising the different species of cyanobacteria by microscopy is also a highly skilled task, as morphology and pigmentation may vary depending on conditions, and some forms may be difficult to assign to known species groups (Whitton 1992).

2.4 Other MPB

There is a serious dearth of information on some of the less well-studied microphytobenthos; however, the lack of study does not necessarily mean that they are unimportant. For example, recent studies on benthic Foraminifera reveal surprisingly high diversity (Khanna 2014). In addition, these same organisms are capable of both heterotrophic and autotrophic energy capture, generally through the development of symbiosis with an algal species (Ziegler and Uthicke 2011). In addition to a truly symbiotic relationship, some Foraminifera also sequester and use chloroplasts from prey species, and can assimilate carbon from their captive chloroplast for several days after ingestion. This is not a true symbiosis, but it has the effect that such forms which regularly graze on algae can also use sunlight directly.

2.5 How Should We Measure MPB Diversity?

The advance of a new technology often appears to offer easy solutions to current problems. While still providing exciting new prospects, in many cases, these advances do not quite deliver on all expectations. A current example is the use of molecular techniques such as “Next Generation Sequencing” (NGS) as an approach to biodiversity research. This technology has provided a step change in the amount of genetic information that can be acquired, enabling novel phylogenetic analysis (Medlin 2016); however, it has limitations in terms of biodiversity (Pompanon and Samadi 2015). A sample of sediment contains DNA and RNA from living microbes, but also traces of both molecules, often degraded, found outside of living cells. These fragments may provide a clue to other life forms that recently shared this habitat (so called environmental DNA [e-DNA]). The problem lies in attribution, validation and analysis of these pools of information. Molecular analysis can separate the genetic information (genetic barcodes), providing a catalogue of “species” present. This can be extremely accurate where the species are well-known, but remains a list of numbers where they are not. However, the molecular field is advancing rapidly (Corlett 2017) and excellent examples of its use for different fractions of the MPB are accumulating (e.g. Pawlowski et al. 2014). For some groups, information is lacking to fully employ the methodology (Pompanon and Samadi 2015). As a relevant example, the diatoms themselves may contain 200,000 species, and few of these are fully characterised in molecular terms; in addition, we still require the skills to describe and assign taxa to the correct species. The assignment of molecular profiles to a specific taxon is limited by the previous identification and sequencing, and we have a long way to go to achieve this goal for the diatoms. This would require a monumental effort, and also the retention of taxonomic skills that are becoming increasingly rare. Even as we still need to "observe and classify" in order to validate and place molecular analyses in context, these skills are disappearing with the scientists who possess them.[2]

In summary, to fully understand the ecology, diversity, and function of the MPB, both approaches—observation and analysis—must be combined in a multidisciplinary effort.

3 Microphytobenthos in the Biofilm: EPS and EPS-Mediated Interactions

3.1 The Biofilm Matrix: EPS

3.1.1 General Composition and Structure

The biofilm matrix is composed of a diversity of large molecules generically referred to as extracellular polymeric substances (EPS, Fig. 4.4). Microphytobenthic EPS are mainly composed of carbohydrates, as well as some proteins and various other molecules. They also contain DNA which (as with other components of the EPS) is actively secreted by microorganisms (Whitchurch et al. 2002). EPS is also able to absorb a large diversity of smaller molecules and ions, which also increase the molecular diversity of the biofilm matrix (Wotton 2004a). Bacterial EPS contains relatively more protein and a larger diversity of components than MPB EPS (Decho 1990). Microphytobenthic carbohydrates are mainly heteropolymers, with a vast diversity of component monomers (Decho 1990) and a wide range of molecular weights, from carbohydrates containing a few sugars to highly complex molecules. The relative proportion of the different fractions will determine the physicochemical structure of the matrix (Underwood and Paterson 2003). Different types of EPS have been operationally distinguished as capsular EPS (material closely associated with the cell wall), bound-EPS (tightly-bound long-chain material), and less refractory, small chain, easy-extracted molecules (colloidal EPS). The most complex molecules form the capsule around the cell and are associated with the cell wall, while bound-EPS are found further from the cell, often as a densely packed network. Colloidal EPS forms a looser network around cells and sediment grains, with a highly diverse composition.

Colloidal EPS can be extracted by water at room temperature, while bound-EPS extraction requires hot water or bicarbonate (Underwood and Paterson 2003). However, these protocols have also been shown to release intracellular material

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[2] http://westerndiatoms.colorado.edu/about/what_are_diatoms. Accessed Sept 2017.

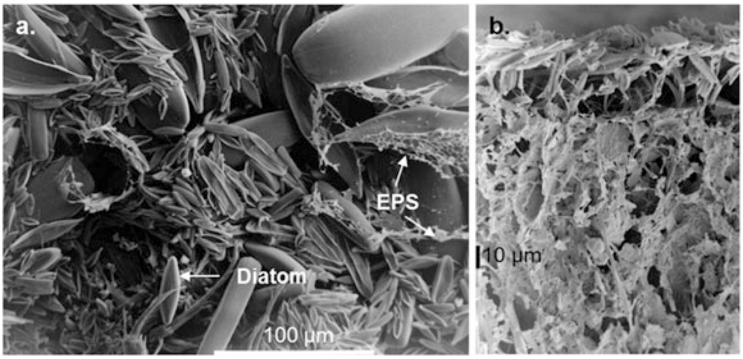

Fig. 4.4 LTSEM (Low Temperature Scanning Electron Microscopy) images of a microphytobenthic biofilm on sediment, showing EPS (dehydrated during preparation) binding sediment particles together. (**a**) Surface of the biofilm. (**b**) Fracture face; the sediment surface is at the top. Adapted from Passarelli et al. (2014).

(Chiovitti et al. 2004). A more recent method uses cationic resin: during extraction, this resin traps the bivalent cations linking the molecules together, allowing the extraction of bound-EPS (Takahashi et al. 2009). Addition of ethanol to the extract can then precipitate EPS of low to high molecular weight (Underwood and Paterson 2003).

3.1.2 Diversity of EPS Composition

The composition of EPS is under loose genetic control (Decho 1990). For example, two molecules coded by the same gene complex can have different compositions. EPS composition is dependent on the cells' physiological state, growth stage, physical environmental conditions (temperature, for instance) and ion and nutrient concentrations (Decho 1990; Underwood et al. 2004). Diversity of EPS composition can also be linked to the diversity of the producing assemblage (Fig. 4.5; Decho 1990; Hoagland et al. 1993; Oakes et al. 2010). The carbohydrates from colloidal fractions are richer in glucose than those of bound EPS (82% and 37% of glucose, respectively; Taylor et al. 1999). Taylor et al. (1999) identified seven main neutral monosaccharides in both fractions: glucose, rhamnose, galactose, xylose, fucose and mannose. Glucuronic and galacturonic acid as well as myo- and scyllo-inositol have also been described (Underwood et al. 2004; Pierre et al. 2010; Passarelli et al. 2015). A high proportion of glucose in carbohydrates is usually associated with a high photosynthetic production (Hanlon et al. 2006).

At a seasonal scale, it seems that environmental parameters controlling photosynthesis are the main factors governing EPS composition (Passarelli et al. 2015). In particular, glucose accumulates in carbohydrates in summer, while carbohydrates display a higher diversity in terms of base monomers during the rest of the year. Nutrient concentrations in pore water and light exposure have also been demonstrated

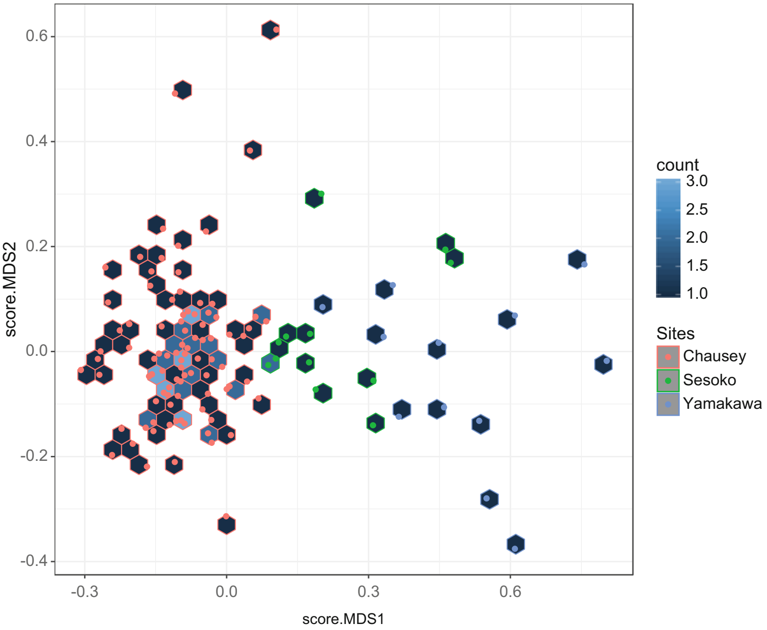

Fig. 4.5 Is the carbohydrate composition of EPS a fingerprint of the microbial community? Shown is a non-metric multidimensional scaling of various EPS samples from different types of biofilms: intertidal sandy sediment of the Chausey archipelagos (from Passarelli et al. 2015) and coral biofilms from Japan—Sesoko and Yamakawa (unpublished). Bray-Curtis dissimilarity index (stress 0.16). The position of the samples on this ordination was calculated from the % monosaccharide composition of the samples (galacturonic-acid, glucuronic-acid, fucose, galactose, glucose, mannose, muo-inositol, rhamnose, scyllo-inositol and xylose). The high dispersion within each site is mainly due to changes in the carbohydrate composition between seasons. Note that sandy sediments and coral biofilms (which are different in terms of microbial assemblages) are well-separated by the nMDS ordination.

to influence EPS composition (De Brouwer and Stal 2002; Underwood et al. 2004). In natural environments, EPS are also degraded by bacteria and consumed by other organisms, which will affect both their concentration and composition (see Sect. 3.2.1).

3.1.3 EPS Production Mechanisms and Regulation

EPS production in microphytobenthos has mainly been studied in benthic diatoms, which produce copious amounts of mucilage that motile species also use for locomotion (Underwood and Paterson 2003). In diatoms, EPS are synthesized in the Golgi apparatus, then externally secreted via specialized vesicles (Underwood and Paterson 2003; Wotton 2004a). In pennate diatoms, most EPS are secreted through the raphe (Fig. 4.1). EPS production by diatoms in cultures is higher during the stationary growth phase compared to the exponential phase (Decho 1990; Underwood and Paterson 2003). Moreover, EPS synthesis is controlled by the environment. For instance, EPS production is higher under nutrient limitation; and it appears that the secretion of carbohydrates allows the diatoms to “dump” photosynthetically-fixed carbon when illuminated under low nutrient conditions, preventing “growth” (Stal 2003; Cook et al. 2007). Under stress, microphytobenthos also increase their EPS, which acts as a protection mechanism (see Sect. 3.1.4). In the natural environment, EPS production varies with tidal, daily and seasonal cycles; for example, higher production of EPS at the end of low tide prepares the microorganisms for immersion (van Duyl et al. 1999).

EPS is ultimately a product of photosynthesis, and several studies have shown that carbohydrate production is positively correlated with the rate of primary production (Smith and Underwood 1998; Staats et al. 2000; Perkins et al. 2001). Inhibiting photosynthesis drastically reduces EPS production (Staats et al. 2000); yet, EPS can be produced even in the dark (Smith and Underwood 1998, 2000; van Duyl et al. 1999, 2000; Staats et al. 2000; Underwood et al. 2004). It seems that previous exposure to light allows accumulation of cellular storage material, conferring the ability to produce EPS in darkness (Perkins et al. 2001; Smith and Underwood 2000). Diatoms are also able to control the percentage of fixed carbon which will be released into the EPS pool.

Different EPS fractions exhibit different behaviours in relation to light (Smith and Underwood 2000; Underwood and Paterson 2003). Bound EPS, for example, is produced only in the presence of light; its concentration decreases in the dark (de Brouwer et al. 2002; Orvain et al. 2003). Colloidal EPS are produced both with and without light (Perkins et al. 2001). In the dark or during immersion, concentrations diminish, which can be linked to solubilisation and/or consumption by microorganisms (Orvain et al. 2003). Bound and colloidal EPS have different tidal and seasonal dynamics; their control therefore seems to be independent (Hanlon et al. 2006; Orvain et al. 2014; Passarelli et al. 2015). EPS production varies seasonally, with highest concentrations in the sediment in early summer and lowest in winter (Passarelli et al. 2015). This dynamic is linked to higher photosynthetic biomass and higher photosynthetic production in summer.

3.1.4 EPS Roles in Microphytobenthos

In mudflats, epipelic diatoms migrate through the sediments in relation to tidal and light cycles (Decho 1990; Underwood and Paterson 2003). Populations move towards the sediment surface and light at low tide, and move away from the surface, deeper into the sediment when the tide is coming in; this behaviour is regarded as an adaptation which avoids resuspension. Some epipsammic diatoms also display these movements, though at a lower amplitude. Many diatoms are facultatively mixotrophic, consuming organic matter from the environment in the dark (Staats et al. 2000; Taylor et al. 2013), and also moving toward a food source. Locomotion is therefore central to the ecology of epipelic diatoms. While the exact mechanisms are not fully elucidated, carbohydrate production is necessary for this mobility (Smith and Underwood 2000). The most widely-accepted model of diatom locomotion proposes that the mucilage, secreted through the raphe, hydrates, swells and adheres to the substratum (Underwood and Paterson 2003). The posterior end of the polymer strand remains attached to the plasmalemma. This attachment point is translocated along the plasmalemma, powered by an actin/myosin motility system. Actin cables interact with myosin attached to the extracellular EPS to generate a gliding movement (Poulsen et al. 1999). Through this process epipelic diatoms secrete copious amounts of mucilage (EPS), leaving strands attached to the substratum.

EPS can also be responsible for the more permanent attachment of sessile microorganisms to sediment particles (Decho 1990; Sutherland 2001). Bacteria often use fimbria or attachment pili to adhere to a host surface; this limits their resuspension in turbulent environments, and, for diatoms, therefore protects their frustule. For diatoms, after a first stage of reversible attachment, these microorganisms produce a more rigid EPS which more permanently attaches to a sediment particle (Sauer et al. 2007). EPS composition is thus important in this regard, and some mutants cannot attach to sediment despite the production of large quantities of the molecules. EPS can bind the sediment particles together, forming the matrix of the biofilm (Flemming and Wingender 2010). This process has an importance beyond its role for microorganisms, as it contributes to the stabilisation of intertidal sediments (Paterson 1989). EPS can also diminish sediment roughness by filling the space between particles and smoothing the surface of particles (de Winder et al. 1999). EPS can also coat sediment particles, making them behave in a cohesive fashion (Grabowski et al. 2011). As a matrix develops, EPS can attach to several particles and link them together (Sutherland 2001; Fig. 4.4), forming a network which traps cells. All of these processes limit sediment erosion and promote sediment stabilisation, and diatom EPS production appears to be responsible for the majority of the stabilization effect, as opposed to bacteria (Yallop et al. 1994; Lundkvist et al. 2007a, b). Indeed, field- and laboratory-based studies have demonstrated a positive correlation between EPS concentrations in the sediment and various measures of sediment stability (Decho 1990; Sutherland et al. 1998; Paterson and Hagerthey 2001; Lundkvist et al. 2007b; Stal 2010). Since sediment stability increases during the stationary phase of diatom growth, mudflat sediment erosion may even be linked to diatom growth phase (Sutherland et al. 1998); for these and other reasons, MBP, and in particular the diatom component, may be considered ecosystem engineers (see Chaps. 8, 10).

For microphytobenthos and bacteria, the EPS matrix is both a living environment and also a mechanism of protection (Fig. 4.6). Tidal flats are a highly variable environment, with marked shifts and strong gradients of chemical and physical conditions (light, oxygen, salinity, temperature etc.) over hourly to seasonal time scales, and from micro- to macro- spatial scales. In the face of this variability, EPS can act as a buffer, maintaining more stable conditions in the immediate surroundings of cells (Decho 1990; Wotton 2004b; Bhaskar and Bhosle 2005). For example, some EPS are highly hygroscopic molecules, able to absorb and hold water and therefore protect organisms from dessication (Potts 1994).

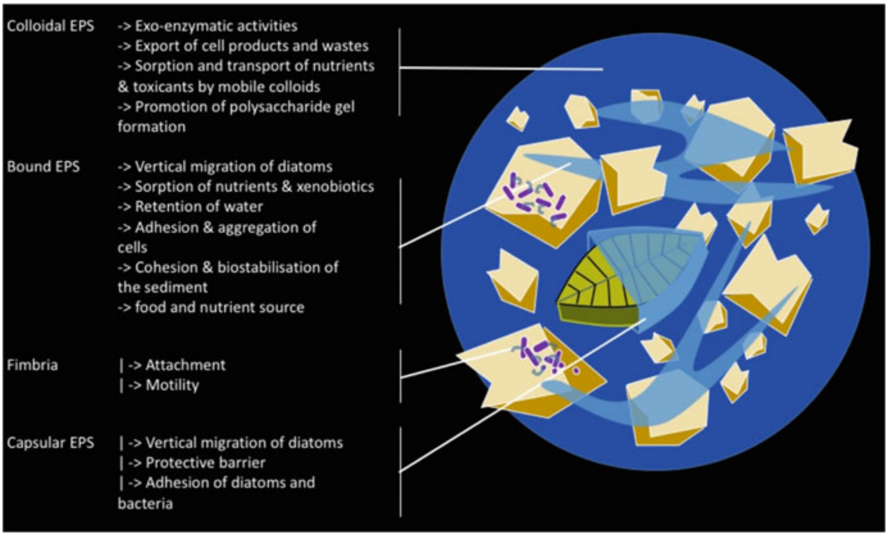

Fig. 4.6 Different kinds of EPS in mudflat biofilms and their associated roles and functions. Adapted for mudflats from Haber and Brenner (1993), Decho (2000), and Flemming and Wingender (2010).

EPS can also absorb various molecules, ions in particular, but also heavy metals and other pollutants. The strength of the link between EPS and these molecules is dependent on pH and salinity, as well as on EPS surface charge and the structure of the MBP network. Molecules absorbed onto EPS do not reach the cells, which is why biofilms can grow in contaminated environments where other organisms often cannot (Sutherland 2001). EPS has also been shown to provide limited protection against antibiotics through the same mechanism (Lubarsky et al. 2010). Furthermore, EPS production may actually increase in the presence of pollutants, e.g. nanoparticles (Joshi et al. 2012).

3.2 EPS, Key Mediators of Interactions Between Microphytobenthos and Bacteria

3.2.1 Trophic Interactions: Microphytobenthic EPS as a Trophic Resource for Bacteria

A significant trophic interaction between microphytobenthos and bacteria through EPS is indirect. EPS can constitute a trophic resource, rich in carbon (carbohydrates in particular) and also nitrogen (proteins), but the size of the molecules makes it impossible for bacteria to assimilate them (Hoppe 1983; Laspidou and Rittmann 2002; McKew et al. 2013). Bacteria produce a large array of extracellular enzymes which degrade EPS into smaller molecules that they can then assimilate. For instance, the β-glucosidase enzyme can break the glycosidic linkage between two sugars in a carbohydrate polymer while other exo-enzymes degrade proteins of phosphate-containing compounds. These enzymes play key roles in determining the fate of EPS; for instance, separation of sugars by bacterial β-glucosidase is the rate-limiting step of carbohydrate degradation in EPS (McKew et al. 2013).

Extracellular enzymes are not in direct contact with cells, but they are contained within the EPS matrix, and therefore stay close to the producing cells (Meyer-Reil 1994). Bacteria can benefit from enzymes produced by the previous generation of microorganisms, which reduces the energy required to produce these enzymes (Decho 2000). Bacteria do not necessarily assimilate all of the small molecules released by the extracellular enzymes and these smaller molecules are therefore available for other microorganisms, and also for meio- and macrofauna. It has even been suggested that very different phyla of organisms, such as bacteria and nematodes, can contribute to and benefit from a common pool of extracellular enzymes (*enzyme sharing* concept; Riemann and Helmke 2002).

Both the composition and structure (branching, succession of monomers) of EPS influence their degradability (Oakes et al. 2010). Most studies have focused on carbohydrate degradation, since these are major components of EPS and an important source of carbon for consumers. Portions of carbohydrates rich in glucose are, for example, more easily degraded than those containing large numbers of deoxymonosaccharides (fucose and rhamnose; Giroldo et al. 2003; Bellinger et al. 2009). Glucose and galactose indeed constitute points of access to EPS for extracellular enzymes (Taylor et al. 2013). This preferential degradation and assimilation of some sugars also means that the composition of EPS varies throughout its degradation, and these changes can alter the effects of EPS within the biofilm.

To understand the fate of EPS carbon inside the biofilm, diatoms can be cultured with ^{13}C-bicarbonate; they then produce ^{13}C-EPS that can be purified and fed onto a biofilm, and the fate of the ^{13}C incorporated into the EPS can be followed. Such studies have shown that bacteria are the main EPS degraders, with a massive and rapid transfer of carbon fixed by diatoms to bacteria. When in contact with labelled EPS, bacteria incorporate labelled carbon into their fatty acids within 4 to 6 h (Bellinger et al. 2009; Taylor et al. 2013). After 30 h, fatty acids of diatoms also become labelled, meaning diatoms are able to assimilate organic carbon from their environment, and also from the EPS they produce themselves (Taylor et al. 2013). The longer delay suggests that they are less efficient than bacteria at assimilating EPS, and also that they may not be able to degrade EPS themselves, therefore only using carbon released into the matrix by bacterial extracellular enzymes. In total, 60% of carbon photosynthetically fixed by microphytobenthos is transferred to bacteria within 36 h (Oakes et al. 2010).

3.2.2 EPS Roles in Bacterial-Algal Interactions

Not all bacterial groups are involved in strong EPS-related trophic interactions (i.e. not all EPS production by microphytobenthos can affect the nature of the bacterial assemblages in surrounding sediment). EPS has been shown to influence bacteria in other ways, such as the growth stimulation of specialist bacteria, e.g. the Actinobacteria-related groups (Haynes et al. 2007). By adding ^{13}C-EPS to sediment slurries, Taylor et al. (2013) also showed that certain genera among the Alphaproteobacteria and Gammaproteobacteria classes became highly enriched in ^{13}C in the presence of ^{13}C-EPS. Low molecular weight EPS can be degraded in most conditions, but most high molecular-weight EPS are degraded in anaerobic conditions by diverse assemblages of bacteria, including sulphate reducers and methanogens (McKew et al. 2013).

It has been proposed that the immediate environment of microalgae forms a "phycosphere", a special habitat rich in exudates in which some bacterial species, named "satellite bacteria", preferentially grow (Schäfer et al. 2002; see Sect. 4.4). Due to their preference for a given type of exudates (e.g. monomer composition, complexity of the polymer), some bacterial species can indeed become more closely associated with certain microalgal species. Studies on phytoplankton have shown that some diatom species are associated with a very distinct bacterial assemblage, while others have similar assemblages of satellite bacteria (Sapp et al. 2007). The reasons for such associations are unclear, but the driver may be the composition of exudates produced by the algae, rather than other parameters such as inorganic nutrient concentrations. Gammaproteobacteria and Bacteroides are closely associated with diatoms in many environments (freshwater and marine, planktonic and benthic, etc.; Bruckner et al. 2008) while in microphytobenthic biofilms, Alphaproteobacteria are also common (Taylor et al. 2013; Decleyre et al. 2015).

Besides their effect on bacterial community composition, diatoms and their EPS secretions also seem to influence bacterial abundances, productivity, and enzymatic activity (Agogué et al. 2014; Orvain et al. 2014; Decleyre et al. 2015); however, the data are not always consistent. Two field studies recently reported dissonant results: Decleyre et al. (2015) described a tenfold increase of bacterial abundances associated with a twofold increase of microphytobenthic biomass, while Orvain et al. (2014) found that concentrations of bound EPS were negatively correlated with bacterial abundances. Similarly, a negative correlation was observed between bound EPS and bacterial production and enzymatic activities in tidal mesocosms (Agogué et al. 2014). Manipulative studies in more controlled environments are necessary to determine the exact mechanisms of such interactions, but the highly diverse, patchy and variable nature of microphytobenthic biofilms make such experiments difficult.

Finally, it is worth noting that bacteria can also influence diatoms and their EPS production. The influences of bacteria on diatoms are diverse and highly dependent on species and conditions. Bacteria can either increase or hinder diatom growth; they can modify their adhesion to their substratum, and also modulate the production and composition of EPS (Bruckner et al. 2008). For example, Bruckner et al. (2008) isolated Bacteroidetes which, when in co-culture with the diatom *Cymbella microcephala*, decreased the concentration of soluble EPS, but also increased the quantity of bound EPS. During the earlier stages of biofilm formation, there also seems to be a synergy between diatoms and bacteria in terms of EPS production, especially for the protein component (Agogué et al. 2014; Orvain et al. 2014); this synergy results in the production of a "cooperative" micro-ecosystem ("the biofilm") where bacteria and diatoms directly interact.

4 How Direct Microbial Interactions Affect Biofilm Fitness

4.1 Synergistic vs. Antagonistic Effects

Mudflat biofilms are characterized by a complex assemblage of microbial species, and the interactions between these microorganisms critically influence the development and shape of the entire community. In biofilms, interspecies interactions involve communication, and metabolic cooperation or competition. Interactions can be synergistic, or antagonistic (such as competition for nutrients, virulence), which ultimately limits the growth of one or several species. The latter is observed when the interaction between microbial cells induces a total effect (i.e. organic matter degradation, primary production) greater than the sum of the individual effects. Examples include biofilm formation by aggregation through the production of EPS (metabolic cooperation, Elias and Banin 2012), or coordination to better utilize nutrients or withstand harsh conditions.

An increase of the fitness of all partners is generally observed as a result of a synergistic effect. Such cooperation can evolve if the evolutionary fitness of two or more partners are aligned (Buckling and Brockhurst 2008). For example, the production of EPS may not only assist in establishing the biofilm, but also promote greater biofilm growth than the comparable single-species biofilms, suggesting that cells not only promote their own adhesion, migration, and growth, but also those of other microbial species. This was suggested by Lubarsky et al. (2010), who investigated the engineering effect (i.e. adhesive capacity and cohesive strength of the biofilm) of microbial assemblages. They discovered that exopolymer concentrations were significantly greater when bacteria and axenic diatoms were co-cultured, compared to single cultures. In another study by Hubas et al. (2010), the complexity of MPB assemblages was identified as a potential bio-stabilization force in marine sediments. The authors showed that the assemblage complexity, rather than the presence of any particular organism, strongly impacts biofilm structure, both in terms of microbial abundance/biomass, and exopolymer content. With increasing complexity, the number of potential interactions also increases, leading to a general enhancement of the diversity of trophic links and energy pathways. This is considered to improve the ability of a given community to withstand external perturbations (Paine 1969).

As may be understood from the above examples, most biofilm studies examine mono-species cultures (Elias and Banin 2012); a very limited number of studies involve actual mudflat biofilms. Interactions in natural communities are far more complex than those observed under controlled monoculture conditions, and often involve negative and/or positive feedback loops as well as indirect effects. Together, these processes influence the complex responses of communities to external perturbation and biodiversity losses (Worm and Duffy 2003). In addition, the expression of many genes in biofilms is ultimately density-dependent and the quorum (i.e. the minimum number of members of a given species necessary to conduct the function of that group) modulates the magnitude and direction (i.e. negative vs. positive) of these feedback loops (see Sect. 4.2). In this context, understanding the interactions in mudflat biofilms (and thereby, how biofilm diversity affects its general functioning) and whether these interactions are intrinsically synergistic or antagonistic is genuinely challenging.

4.2 Communication . . .

4.2.1 Communication Between Bacteria

Communication between microbes generally takes the form of quorum sensing (QS), a social behaviour that enables interactions between the members of the microbial communities. Quorum sensing relies on the production and release of signalling molecules called autoinducers, which increase in concentration as a function of cell density (Camilli and Bassler 2006). The detection of these autoinducers often involves diffusion back into cells and binding to specific receptors, allowing bacteria to express specific genes in a coordinated manner (Miller and Bassler 2001; Waters and Bassler 2005). Biofilm development and QS are closely interconnected processes, especially through the production of EPS (Branda et al. 2005; Solano et al. 2014), although the effect of QS may vary in opposite ways (i.e. enhancement or inhibition), depending on the species considered and the environmental conditions. Quorum sensing signalling pathways are very complex, and several types of secondary metabolites have been identified as QS molecules (Keller and Surette 2006). In *Pseudomonas aeruginosa*, for example, three complete QS circuits (involving N-Acyl homoserine lactone signalling molecules), LasI/LasR, RhlI/RhlR and PqsABCDH/PqsR are involved in the regulation of EPS production, with the LasI/R circuit hierarchically positioned upstream of the RhlI/R circuit (Solano et al. 2014). The transcription factors LasR, RhlR, and PqsR detect their respective signal molecules, leading to a feed-forward autoinduction loop and also to either positive or negative regulation of target gene transcription. An additional level of complexity arises in microbial assemblages when considering that some quorum-sensing systems are used mainly for intraspecies communication, while others support interspecies communication (Bassler and Losick 2006).

The type 2 autoinducers (AI-2) are considered universal and can mediate interspecies communication, while other signalling molecules such as type 1 autoinducers (AI-1), are mainly used in intraspecific communication. N-Acyl homoserine lactones (AHLs or AI-1) are fatty acid amides of variable chain length (C4 to C18) or their oxygenated derivatives with 3-amino-γ-butyrolactone (N-acyl homoserine lactones), and their exact composition gives the signal its specificity (Rolland et al. 2016). Many other types of metabolites have been identified, such as the p-coumaroyl homoserine lactones (Schaefer et al. 2008), furanosyl diester borate (AI-2, Chen et al. 2002), quinolones (Pesci et al. 1999), peptides, and γ-butyrolactones (Onaka et al. 1995). AI-2s are all derived from a common precursor, 4,5-dihydroxy-2,3 pentanedione (DPD), the product of the S-ribosylhomocysteine (LuxS) enzyme, which spontaneously cyclicize to produce a collection of stereoisomers that presumably allow bacteria to respond to both endogenic and allogeneic AI-2s.

In nature, a great diversity of QS molecules are found in microbial mats (Decho et al. 2009, 2010). It is hypothesized that signalling pathways could be modified due to geochemical and/or biological modifications of the signalling molecules. This modification could result in a disruption of the intended communication if signals are no longer recognized, or, alternatively, an activation of another communication pathway that may result in the expression of a different gene if a modified signal is able to interact with a different receptor (Decho et al. 2010). There is clearly a lack of studies in mudflats to validate or invalidate such a hypothesis. As mentioned above, most studies have dealt with monospecific, or, at best, multispecific laboratory biofilms; natural environmental investigations are still very rare (Gerbersdorf and Wieprecht 2015). The development of this field of study is clearly a major gateway to the understanding of mudflat biofilm function.

4.2.2 Other Forms of Communication

Bacteria are not the only microbes capable of inter-individual communication. Growing evidence suggests that diatoms produce cell-to-cell signalling molecules (mainly pheromones involved in sexual reproduction), which share many features with quorum-sensing molecules (i.e. hydrophobic, diffusion across cell membranes, and presumably coordination of gene expression between gametes). Several types of gamones are produced by freshwater and marine diatoms. Examples include hormosirene, dictyopterine A, and finavarrene, which are produced by *Gomphonema parvulum* (Pohnert and Boland 1996); fucoserratene, which is produced by *Asterionella formosa* (Hombeck and Boland 1998); ectocarpene, which is produced by *Skeletonema* sp. (Derenbach and Pesando 1986); or yet-unidentified sex pheromones (Sato et al. 2011). Benthic diatoms also produce pheromones. In the benthic pennate diatom *Seminavis robusta*, pheromones trigger the switch from mitosis to meiosis in the opposing mating type, coupled with the transcriptional induction of proline biosynthesis genes, and the release of the proline-derived attraction pheromone (Moeys et al. 2016). However, there is once again a lack of information from natural assemblages, and once again, the development of this approach is a major gateway in the understanding of the functioning of natural mudflat biofilms. For example, is the migration pattern observed in mudflat biofilms somehow modulated by the production of signalling molecules? Indeed, epipelic diatoms show partially endogenous vertical migratory rhythms, which are synchronized with diurnal and tidal cycles (see Sect. 3.1.4), whereas epipsammic diatoms do not (Admiraal 1984; Serôdio et al. 1997). It has been shown that these different behaviours correspond to different photoregulatory strategies: the epipelic community of muddy sediments employing both physiological and behavioural photoprotection, while the epipsammic community of sandy sediments uses exclusively physiological mechanisms (Cartaxana et al. 2011). Physiological mechanisms imply the reversible de-epoxidation of pigment diadinoxanthin (DD) into the energy-dissipating form diatoxanthin (DT), diverting excessive light energy from photosystem II reaction centres, thereby limiting damage to the photosynthetic apparatus (Goss and Jakob 2010). These recent findings in chemical microbial ecology shed new light on how microbes may interact in natural assemblages. Indeed, we now consider them a social group that responds to environmental stimuli in a coordinated manner. It is likely that macroscopic manifestation of microbial activities such as the vertical migration of diatoms, or the development of massive mats of bacteria visible to the naked eye (Hubas et al. 2013) may be regulated by signalling molecules.

4.3 . . . and Defence

In biofilms, interspecies interactions involve communication and metabolic cooperation, but also competition for nutrients and space. An increasing number of studies indicate that benthic microbes do produce defence and virulence factors. In a recent study, Doghri et al. (2017) demonstrated that benthic diatom EPS may inhibit biofilm formation in some bacterial strains, while promoting it in others. Colloidal and bound EPS secreted by axenic *Navicula phyllepta* cultures were tested for their effects on the in vitro formation of biofilms by three marine bacteria, including one from a French Atlantic intertidal mudflat known for its strong in vitro biofilm-forming ability. *Navicula phyllepta*-bound EPS synthesized during the stationary phase specifically inhibited the biofilm formation by the *Flavobacterium* sp. bacterial strain, whereas they stimulated biofilm development by two other bacterial strains. Saccharidic molecules were found to be responsible for these activities. In addition, diatoms are known to produce a variety of halogenated compounds, which are involved in allelopathic interactions between competing species. The production of these compounds is linked to haloperoxidase activity, and it has been shown recently in the benthic diatom *Nitzschia pellucida* that this system may also be involved in diatom-bacteria interactions via the H_2O_2-dependent inactivation of a type of quorum sensing (QS) molecule (i.e., N-β-ketoacylated homoserine lactones | AHLs). In this case, diatoms are responsible for a loss of the QS activity by cleavage of the halogenated N-acyl chain of the autoinducers (Syrpas et al. 2014). This observation supports the Decho et al. (2010) hypothesis that specific microbial activities could modify QS signalling pathways, and result in a disruption of the intended communication. Microbial interactions in mudflat ecosystems are thus seen to be extremely complex.

Many diatoms secrete free fatty acids (FFAs) and esters that can act as antibacterial compounds and influence bacterial community structure. FFAs display a broad spectrum of activity ranging from growth inhibition (inhibition of enzyme activity or nutrient uptake) to direct cell lysis (Desbois and Smith 2010). However, the antibacterial effects of FFAs are frequently observed during bioassay-guided fractionation of extracts from a variety of organisms, and no studies to date have attempted to determine the diversity of FFAs in natural microbial mats (including mudflats), or the concentration at which they are expected to have a bactericidal effect. The role of single-cell eukaryotic FFAs against bacteria is poorly known, but an interesting hypothesis has been proposed by Desbois and Smith (2010). In microalgae, "scarifying" microbial cells may confer some protection to the whole population. FFAs released from a microalgal cell that has been damaged by a pathogen will act on pathogens in the local vicinity, reducing their numbers. Indeed, fatty acids are abundant in the phospholipids that constitute the cell membrane. If microalgae are lysed due to the feeding activity of grazers or to bacteria virulence, it is expected that a large quantity of FFAs are released from the cell membranes by lipolytic enzymes. It is known that these FFAs are toxic to invertebrate grazers of diatom epilithic biofilms (Jüttner 2001), but they could potentially offer similar protection against pathogenic bacteria or viruses.

4.4 The Phycosphere

4.4.1 Definition and Functioning

The phycosphere is a region where EPS-mediated interactions between bacteria and diatoms take place. The term phycosphere corresponds to a region that is located in the close vicinity of a microalgal cell or colony. This term was first introduced in the early 1970s by Bell and Mitchell (1972) as an equivalent of the "rhizosphere" of terrestrial ecosystems. The concept is that there is a region extending outward from an algal cell for an undefined distance, in which bacterial growth is stimulated by the extracellular products of the algae. Since the introduction of this concept, numerous studies have demonstrated that this high-nutrient environment creates an "attached" microbiome with phylogenetic groups that are significantly different from the free-living bacterial populations. However, whether the compositions of the bacterial communities are strictly species-specific for microalgae (i.e. host-specific) is still under debate. According to Bruckner et al. (2008), diatoms may be regarded generally as a microhabitat to which Proteobacteria and Bacteroidetes have particularly adapted, regardless of whether the diatoms are planktonic or benthic, freshwater- or saltwater, or terrestrial. It seems, indeed, that the quality and quantity of microalgal exudates is the most significant driver in structuring the phycosphere bacterial diversity (Sapp et al. 2007).

There is also strong evidence that quorum sensing occurs in microbial communities that inhabit the phycosphere and that long-chain AHLs (more than eight carbons in the acyl side chain) are the dominant mode of communication in phytoplankton-associated bacteria, above AI-2 and other signalling molecules (Rolland et al. 2016). The roles of quorum sensing in the phycosphere are numerous and sometime contradictory. Generally speaking, QS is recognised as an efficient way to regulate the attachment of cells to a substratum and the development of biofilms through the production of EPS molecules as well as the dispersion of the cells, through the production of tensioactive rhamnolipids (Pasmore and Costerton 2003; Branda et al. 2005; Battin et al. 2007; Flemming et al. 2016), and thereby QS is expected to play a key role in the colonization of the phycosphere by bacteria. It is also well established that QS is involved in the biosynthesis of antimicrobial compounds (see Sect. 4.3) and thus is expected to have a strong impact on the bacterial population, both within the phycosphere and on the algal host. Various algicides and antibiotics, such as proteases, have been identified from bacteria that inhabit the phycosphere (Amin et al. 2012; Rolland et al. 2016). In addition, some algicidal bacteria are also known to enter the phycosphere and lyse diatoms, e.g. *Saprospira* spp. induce cell lysis of *Chaetoceros ceratosporum* by direct contact. The bacteria use gliding motility to move toward the diatom and induce lysis via the production of microtubule-like structures (Furusawa et al. 2003). In response to pathogens, algae produce antibacterial compounds such as free fatty acids (see Sect. 4.3) or perform quorum quenching (QS interference), which reduces the virulence (Rolland et al. 2016).

4.4.2 The Concept of Phycosphere in Mudflat Biofilms

Studies dealing with benthic diatoms and their associated microbiome are still very rare, and the gaps in current knowledge are even more striking for natural biofilms. In the context of MPB it is worth noting that the secretion of extracellular products is not limited to the immediate cell neighbourhood, but rather everywhere in the biofilm, forming a coherent matrix. Thus the question arises if the concept of phycosphere is entirely applicable to mudflat diatoms (Fig. 4.7). If it is, then we should expect that bacterial assemblages that develop near microalgae be intrinsically different in terms of diversity and functioning than those that develop on EPS bound to sediment particles. Considering that EPS compositions are different between the different EPS fractions, and that pathogenic bacteria and viruses develop near the microalgae, it is likely that bacterial assemblages would differ. Alternatively, transfers of cells, genes or even signalling molecules between both compartments are possible, and this might reduce the dissimilarity between the microbial assemblages. In a recent study, Leinweber and Kroth (2015) combined scanning electron and bright-field microscopy together with Energy-dispersive X-ray (EDX) spectroscopy to reveal that capsular EPS of the freshwater benthic diatom *Achnanthidium minutissimum* developed from fibrillar precursors, and that bacteria preferentially attach to encapsulated rather than non-encapsulated diatoms. This supports the idea of the existence of a phycosphere mediated by the capsular EPS in benthic diatoms. Alternatively, the bound EPS of the biofilm could represent an extension of the phycosphere: a place where dormant pathogenic bacteria and viruses are protected in a nutrient-rich environment, awaiting the opportunity to infect a host.

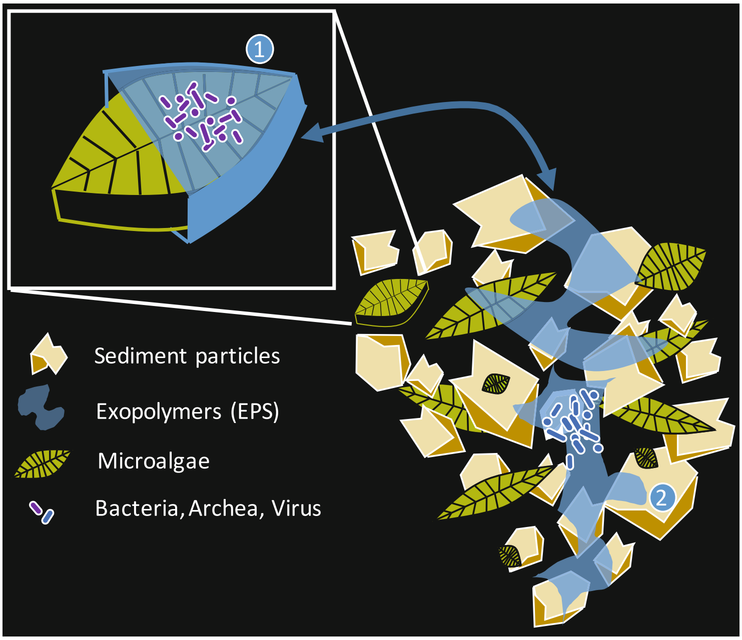

Fig. 4.7 Where is the phycosphere in mudflats? Mudflat biofilms are composed of a complex mixture of mineral particles (silt, sand and clay), living microbes (bacteria, Archaea and microalgae) and extracellular polymeric substances. By analogy with phytoplankton, it is expected that a specific bacterial assemblage (i.e. in comparison to free-living bacterial cells that develop in pore water) develop in the close vicinity of microalgae (**1**). It is also expected that the high production of exopolymers by diatoms over several hundreds of microns during vertical migration creates living space that favors the growth of specific bacterial assemblages (**2**). Whether these microbial assemblages are intrinsically different in terms of diversity and/or functioning remains an open question.

5 Conclusion

From the preceding considerations, the diversity of the microphytobenthos (MPB) and the interactions between microalgae and bacteria are shown to be extremely complex. The understanding of microbial interaction within natural biofilms is an emerging field of study in mudflat ecosystems, and the categorization of the microbial interactions adopted in this chapter (i.e. direct vs. EPS-mediated) is somewhat artificial, because most small molecules used in communication and defence in microbial ecosystems could themselves be considered as colloidal or dissolved EPS. This should invite us to consider that, in the biofilm, EPS plays a central role as the mediator of microbial functions, and thereby the associated ecosystem services.

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References

Adl SM, Leander BS, Simpson AGB, Archibald JM, Anderson OR, Bass D, Bowser SS, Brugerolle G, Farmer MA, Karpov S, Kolisko M, Lane CE, Lodge DJ, Mann DG, Meisterfeld R, Mendoza L, Moestrup Ø, Mozley-Standridge SE, Smirnov AV, Spiegel F, Collins T, Sullivan J (2007) Diversity, nomenclature, and taxonomy of protists. Syst Biol 56:684–689

Admiraal W (1984) The ecology of estuarine sediment-inhabiting diatoms. Prog Phycol Res 3:269–322

Agogué H, Mallet C, Orvain F, De Crignis M, Mornet F, Dupuy C (2014) Bacterial dynamics in a microphytobenthic biofilm: a tidal mesocosm approach. J Sea Res 92:36–45

Amin SA, Parker MS, Armbrust EV (2012) Interactions between diatoms and bacteria. Microbiol Mol Biol Rev 76:667–684

Bassler BL, Losick R (2006) Bacterially speaking. Cell 125:237–246

Battin TJ, Sloan WT, Kjelleberg S, Daims H, Head IM, Curtis TP, Eberl L (2007) Microbial landscapes: new paths to biofilm research. Nat Rev Microbiol 5:76–81

Bedoshvili YD, Popkova TP, Likhoshway YV (2009) Chloroplast structure of diatoms of different classes. Cell Tissue Biol 3:297–310

Bell W, Mitchell R (1972) Chemotactic and growth responses of marine bacteria to algal extracellular products. Biol Bull 143:265–277

Bellinger B, Underwood GJC, Ziegler S, Gretz MR (2009) Significance of diatom-derived polymers in carbon flow dynamics within estuarine biofilms determined through isotopic enrichment. Aquat Microb Ecol 55:169–187

Bhaskar PV, Bhosle NB (2005) Microbial extracellular polymeric substances in marine biogeochemical processes. Curr Sci 88:45–53

Branda SS, Vik S, Friedman L, Kolter R (2005) Biofilms: the matrix revisited. Trends Microbiol 13:20–26

Bruckner CG, Bahulikar R, Rahalkar M, Schink B, Kroth PG (2008) Bacteria associated with benthic diatoms from Lake Constance: phylogeny and influences on diatom growth and secretion of extracellular polymeric substances. Appl Environ Microbiol 74:7740–7749

Buckling A, Brockhurst MA (2008) Kin selection and the evolution of virulence. Heredity (Edinb) 100:484–488

Camilli A, Bassler BL (2006) Bacterial small-molecule signalling pathways. Science (80–) 311:1113–1116

Cartaxana P, Ruivo M, Hubas C, Davidson I, Serôdio J, Jesus B (2011) Physiological versus behavioural photoprotection in intertidal epipelic and epipsammic benthic diatom communities. J Exp Mar Biol Ecol 405:120–127

Chen X, Schauder S, Potier N, Van Dorsselaer A, Pelczer I, Bassler BL, Hughson FM (2002) Structural identification of a bacterial quorum-sensing signal containing boron. Nature 415:545–549

Chiovitti A, Molino P, Crawford S a, Teng R, Spurck T, Wetherbee R (2004) The glucans extracted with warm water from diatoms are mainly derived from intracellular chrysolaminaran and not extracellular polysaccharides. Eur J Phycol 39:117–128

Cook P, Veuger B, Böer S, Middelburg J (2007) Effect of nutrient availability on carbon and nitrogen incorporation and flows through benthic algae and bacteria in near-shore sandy sediment. Aquat Microb Ecol 49:165–180

Corlett R (2017) A bigger toolbox: biotechnology in biodiversity conservation. Trends Biotechnol 35:55–65

De Brouwer JFC, Stal LJ (2002) Daily fluctuations of exopolymers in cultures of the benthic diatoms *Cylindrotheca closterium* and *Nitzschia* sp. (Bacillariophyceae). J Phycol 38:464–472

de Brouwer JF, Ruddy GK, Jones TER, Stal LJ (2002) Sorption of EPS to sediment particles and the effect on the rheology of sediment slurries. Biogeochemistry 6:57–71

de Winder B, Staats N, Stal L, Paterson D (1999) Carbohydrate secretion by phototrophic communities in tidal sediments. J Sea Res 42:131–146

Decho A (1990) Microbial exopolymer secretions in ocean environments: their role(s) in food webs and marine processes. Oceanogr Mar Biol Annu Rev 28:73–153

Decho AW (2000) Microbial biofilms in intertidal systems: an overview. Cont Shelf Res 20:1257–1273

Decho AW, Visscher PT, Ferry J, Kawaguchi T, He L, Przekop KM, Norman RS, Reid RP (2009) Autoinducers extracted from microbial mats reveal a surprising diversity of N-acylhomoserine lactones (AHLs) and abundance changes that may relate to diel pH. Environ Microbiol 11:409–420

Decho AW, Norman RS, Visscher PT (2010) Quorum sensing in natural environments: emerging views from microbial mats. Trends Microbiol 18:73–80

Decleyre H, Heylen K, Sabbe K, Tytgat B, Deforce D, Van Nieuwerburgh F, Van Colen C, Willems A (2015) A doubling of microphytobenthos biomass coincides with a tenfold increase in denitrifier and total bacterial abundances in intertidal sediments of a temperate estuary. PLoS One 10:e0126583

Derenbach JB, Pesando D (1986) Investigations into a small fraction of volatile hydrocarbons: III. Two diatom cultures produce ectocarpene, a pheromone of brown algae. Mar Chem 19:337–341

Desbois AP, Smith VJ (2010) Antibacterial free fatty acids: activities, mechanisms of action and biotechnological potential. Appl Microbiol Biotechnol 85:1629–1642

Doghri I, Lavaud J, Dufour A, Bazire A, Lanneluc I, Sablé S (2017) Cell-bound exopolysaccharides from an axenic culture of the intertidal mudflat *Navicula phyllepta* diatom affect biofilm formation by benthic bacteria. J Appl Phycol 29:165–177

Elias S, Banin E (2012) Multi-species biofilms: living with friendly neighbours. FEMS Microbiol Rev 36:990–1004

Flemming H-C, Wingender J (2010) The biofilm matrix. Nat Rev Microbiol 8:623–633

Flemming H, Wingender J, Szewzyk U, Steinberg P, Rice SA, Kjelleberg S (2016) Biofilms: an emergent form of bacterial life. Nat Rev Microbiol 14:563–575

Furusawa G, Yoshikawa T, Yasuda A, Sakata T (2003) Algicidal activity and gliding motility of *Saprospira* sp. SS98-5. Can J Microbiol 49:92–100

Gerbersdorf SU, Wieprecht S (2015) Biostabilization of cohesive sediments: revisiting the role of abiotic conditions, physiology and diversity of microbes, polymeric secretion, and biofilm architecture. Geobiology 13:68–97

Giere O (2009) Meiobenthology: the microscopic motile fauna of aquatic sediments, 2nd edn. Springer, Berlin, 527 p

Giroldo D, Vieira AAH, Paulsen BS (2003) Relative increase of deoxy sugar during microbial degradation of an extracellular polysaccharide released by a tropical freshwater *Thalassiosira* sp (Bacillariophyceae). J Phycol 39:1109–1115

Goss R, Jakob T (2010) Regulation and function of xanthophyll cycle-dependent photoprotection in algae. Photosynth Res 106:103–122

Grabowski RC, Droppo IG, Wharton G (2011) Erodibility of cohesive sediment: the importance of sediment properties. Earth Sci Rev 105:101–120

Guiry MD (2012) How many species of algae are there? J Phycol 48:1057–1063

Haber S, Brenner H (1993) Effect of entrained colloidal particles in enhancing the transport of adsorbable chemical contaminants. J Colloid Interface Sci 155:226–246

Hanlon ARM, Bellinger B, Haynes K, Xiao G, Hofmann TA, Gretz MR, Ball AS, Osborn AM, Underwood GJC (2006) Dynamics of extracellular polymeric substance (EPS) production and loss in an estuarine, diatom-dominated, microalgal biofilm over a tidal emersion-immersion period. Limnol Oceanogr 51:79–93

Harel A, Karkar S, Cheng S, Falkowski PG, Bhattacharya D (2015) Deciphering primordial cyanobacterial genome functions from protein network analysis. Curr Biol 25:628–634

Haynes K, Hofmann TA, Smith CJ, Ball AS, Underwood GJC, Osborn AM (2007) Diatom-derived carbohydrates as factors affecting bacterial community composition in estuarine sediments. Appl Environ Microbiol 73:6112–6124

Hoagland KD, Rosowski JR, Gretz MR, Roemer SC (1993) Diatom extracellular polymeric substances: function, fine structure, chemistry, and physiology. J Phycol 29:537–566

Hombeck M, Boland W (1998) Biosynthesis of the algal pheromone fucoserratene by the freshwater diatom *Asterionella formosa* (Bacillariophyceae). Tetrahedron 54:11033–11042

Hoppe H-G (1983) Significance of exoenzymatic activities in the ecology of brackish water: measurements by means of methylumbelliferyl-substrates. Mar Ecol Prog Ser 11:299–308

Hubas C, Sachidhanandam C, Rybarczyk H, Lubarsky H, Rigaux A, Moens T, Paterson D (2010) Bacterivorous nematodes stimulate microbial growth and exopolymer production in marine sediment microcosms. Mar Ecol Prog Ser 419:85–94

Hubas C, Jesus B, Ruivo M, Meziane T, Thiney N, Davoult D, Spilmont N, Paterson DM, Jeanthon C (2013) Proliferation of purple sulphur bacteria at the sediment surface affects intertidal mat diversity and functionality. PLoS One. https://doi.org/10.1371/journal.pone.0082329

Hubas C, Boeuf D, Jesus B, Thiney N, Bozec Y, Jeanthon C (2017) A nanoscale study of carbon and nitrogen fluxes in mats of purple sulfur bacteria: implications for carbon cycling at the surface of coastal sediments. Front Microbiol 8:1995

Joshi N, Ngwenya BT, French CE (2012) Enhanced resistance to nanoparticle toxicity is conferred by overproduction of extracellular polymeric substances. J Hazard Mater 241–242:363–370

Jüttner F (2001) Liberation of 5,8,11,14,17-eicosapentaenoic acid and other polyunsaturated fatty acids from lipids as a grazer defence reaction in epilithic diatom biofilms. J Phycol 37:744–755

Keller L, Surette MG (2006) Communication in bacteria: an ecological and evolutionary perspective. Nat Rev Microbiol 4:249–258

Khanna N (2014) The biological response of foraminifera to ocean acidification. PhD dissertation, University of St Andrews

Krumbein WE, Paterson DM, Zavazin G (eds) (2003) Fossil and Recent biofilms: a natural history of life on earth. Kluwer Academic, Dordrecht. ISBN 1-4020-1597-6. 504 pp

Larson F, Lubarsky H, Gerbersdorf SU, Paterson DM (2009) Surface adhesion measurements in aquatic biofilms using magnetic particle induction: MagPI. Limnol Oceanogr Methods 7:490–497

Laspidou CS, Rittmann BE (2002) A unified theory for extracellular polymeric substances, soluble microbial products, and active and inert biomass. Water Res 36:2711–2720

Lee JJ (2001) Living sands: symbiosis between foraminifera and algae. In: Seckbach J (ed) Symbiosis. Cellular origin, life in extreme habitats and astrobiology, vol 4. Kluwer Academic, Dordrecht, pp 489–506

Leinweber K, Kroth PG (2015) Capsules of the diatom *Achnanthidium minutissimum* arise from fibrillar precursors and foster attachment of bacteria. PeerJ 3:e858

Lubarsky HV, Hubas C, Chocholek M, Larson F, Manz W, Paterson DM, Gerbersdorf SU (2010) The stabilisation potential of individual and mixed assemblages of natural bacteria and microalgae. PLoS One 5:e13794

Lundkvist M, Gangelhof U, Lunding J, Flindt MR (2007a) Production and fate of extracellular polymeric substances produced by benthic diatoms and bacteria: a laboratory study. Estuar Coast Shelf Sci 75:337–346

Lundkvist M, Grue M, Friend PL, Flindt MR (2007b) The relative contributions of physical and microbiological factors to cohesive sediment stability. Cont Shelf Res 27:1143–1152

Mann DG, Droop SJM (1996) Biodiversity, biogeography and conservation of diatoms. Hydrobiologia 336:19–32

McKew BA, Dumbrell AJ, Taylor JD, McGenity TJ, Underwood GJC (2013) Differences between aerobic and anaerobic degradation of microphytobenthic biofilm-derived organic matter within intertidal sediments. FEMS Microbiol Ecol 84:495–509

Medlin LK (2016) Evolution of the diatoms: major steps in their evolution and a review of the supporting molecular and morphological evidence. Phycologia 55:79–103

Meng Z, Xu K, Lei Y (2011) Community composition, distribution, and contribution of microbenthos in offshore sediments from the Yellow Sea. Cont Shelf Res 31:1437–1446

Meyer-Reil L-A (1994) Microbial life in sedimentary biofilms the challenge to microbial ecologists. Mar Ecol Prog Ser 112:303–311

Miller MB, Bassler BL (2001) Quorum sensing in bacteria. Annu Rev Microbiol:165–199

Moeys S, Frenkel J, Lembke C, Gillard JTF, Devos V, Van den Berge K, Bouillon B, Huysman MJJ, De Decker S, Scharf J, Bones A, Brembu T, Winge P, Sabbe K, Vuylsteke M, Clement L, De Veylder L, Pohnert G, Vyverman W (2016) A sex-inducing pheromone triggers cell cycle arrest and mate attraction in the diatom *Seminavis robusta*. Sci Rep 6:19252

Noffke N, Paterson D (2007) Microbial interactions with physical sediment dynamics, and their significance for the interpretation of Earth's biological history. Geobiology 6:1–4

Oakes JM, Eyre BD, Middelburg JJ, Boschker HTS (2010) Composition, production, and loss of carbohydrates in subtropical shallow subtidal sandy sediments: rapid processing and long-term retention revealed by 13C-labeling. Limnol Oceanogr 55:2126–2138

Onaka H, Ando N, Nihira T, Yamada Y, Beppu T, Horinouchi S (1995) Cloning and characterization of the A-factor receptor gene from *Streptomyces griseus*. J Bacteriol 177:6083–6092

Orvain F, Galois R, Barnard C, Sylvestre A, Blanchard G, Sauriau P-G (2003) Carbohydrate production in relation to microphytobenthic biofilm development: an integrated approach in a tidal mesocosm. Microb Ecol 45:237–251

Orvain F, De Crignis M, Guizien K, Lefebvre S, Mallet C, Takahashi E, Dupuy C (2014) Tidal and seasonal effects on the short-term temporal patterns of bacteria, microphytobenthos and exopolymers in natural intertidal biofilms (Brouage, France). J Sea Res 92:6–18

Paine RT (1969) A note on trophic complexity and community stability. Am Nat 103:91–93

Pasmore M, Costerton JW (2003) Biofilms, bacterial signalling, and their ties to marine biology. J Ind Microbiol Biotechnol 30:407–413

Passarelli C, Olivier F, Paterson DM, Meziane T, Hubas C (2014) Organisms as cooperative ecosystem engineers in intertidal flats. J Sea Res 92:92–101

Passarelli C, Meziane T, Thiney N, Boeuf D, Jesus B, Ruivo M, Jeanthon C, Hubas C (2015) Seasonal variations of the composition of microbial biofilms in sandy tidal flats: focus of fatty acids, pigments and exopolymers. Estuar Coast Shelf Sci 153:29–37

Paterson D (1989) Short-term changes in the erodibility of intertidal cohesive sediments related to the migratory behaviour of epipelic diatoms. Limnol Oceanogr 34:223–234

Paterson DM, Hagerthey SE (2001) Microphytobenthos in contrasting coastal ecosystems: biology and dynamics. In: Reise K (ed) Ecological comparisons of sedimentary shores. Springer, Berlin, pp 105–125

Paterson DM, Wiltshire KH, Miles A, Blackburn TH, Davison I, Yates MG, McGrorty S, Eastwood JA (1998) Microbiological mediation of spectral reflectance from intertidal cohesive sediments. Limnol Oceanogr 43:1207–1221

Paterson DM, Aspden RJ, Visscher PT, Consalvey M, Andres MS, Decho AW, Stolz J, Reid RP (2008) Light-dependant biostabilisation of sediments by stromatolite assemblages. PLoS One 3: e3176. https://doi.org/10.1371/journal.pone.0003176

Paterson DM, Aspden RJ, Black KS (2009) Intertidal flats: ecosystem functioning of soft sediment systems. In: Perillo GME, Wolanski E, Cahoon DR, Brinson MM (eds) Coastal wetlands: an integrated ecosystem approach. Elsevier, Amsterdam, pp 317–338

Pawlowski J, Lejzerowicz F, Esling P (2014) Next-generation environmental diversity surveys of foraminifera: preparing the future. Biol Bull 227:93–106

Perkins R, Underwood G, Brotas V, Snow G, Jesus B, Ribeiro L (2001) Responses of microphytobenthos to light: primary production and carbohydrate allocation over an emersion period. Mar Ecol Prog Ser 223:101–112

Pesci EC, Milbank JB, Pearson JP, McKnight S, Kende AS, Greenberg EP, Iglewski BH (1999) Quinolone signalling in the cell-to-cell communication system of *Pseudomonas aeruginosa*. Proc Natl Acad Sci USA 96:11229–11234

Pierre G, Graber M, Orvain F, Dupuy C, Maugard T (2010) Biochemical characterization of extracellular polymeric substances extracted from an intertidal mudflat using a cation exchange resin. Biochem Syst Ecol 38:917–923

Pohnert G, Boland W (1996) Biosynthesis of the algal pheromone hormosirene by the fresh-water diatom *Gomphonema parvulum* (Bacillariophyceae). Tetrahedron 52:10073–10082

Pompanon F, Samadi S (2015) Next generation sequencing for characterizing biodiversity: promises and challenges. Genetica 143:133–138

Potts M (1994) Desiccation tolerance of prokaryotes. Microbiol Rev 58:755–805

Poulsen NC, Spector I, Spurck TP, Schultz TF, Wetherbee R (1999) Diatom gliding is the result of an actin-myosin motility system. Cell Motil Cytoskeleton 44:23–33

Riding R (2011) The nature of stromatolites: 3,500 million years of history and a century of research. Springer, Berlin, pp 29–74

Riemann F, Helmke E (2002) Symbiotic relations of sediment-agglutinating nematodes and bacteria in detrital habitats: the enzyme-sharing concept. Mar Ecol 23:93–113

Rolland JL, Stien D, Sanchez-Ferandin S, Lami R (2016) Quorum sensing and quorum quenching in the phycosphere of phytoplankton: a case of chemical interactions in ecology. J Chem Ecol 42:1201–1211

Rossello-Mora R, Amann R (2001) The species concept for prokaryotes. FEMS Microbiol Ecol 25:39–67

Round FE (1981) The ecology of algae. Cambridge University Press, Cambridge, 653 pp

Round FE, Crawford RM, Mann DG (1990) The diatoms: biology & morphology of the genera. Cambridge University Press

Sanders RW (1991) Mixotrophic protists in marine and freshwater ecosystems. J Protozool 38:76–81

Sapp M, Schwaderer AS, Wiltshire KH, Hoppe H-G, Gerdts G, Wichels A (2007) Species-specific bacterial communities in the phycosphere of microalgae? Microb Ecol 53:683–699

Sato S, Beakes G, Idei M, Nagumo T, Mann DG, Anderson O (2011) Novel sex cells and evidence for sex pheromones in diatoms. PLoS One 6:e26923

Sauer K, Rickard AH, Davies DG (2007) Biofilms and biocomplexity. Microbe 2:347–353

Schaefer AL, Greenberg EP, Oliver CM, Oda Y, Huang JJ, Bittan-Banin G, Peres CM, Schmidt S, Juhaszova K, Sufrin JR, Harwood CS (2008) A new class of homoserine lactone quorum-sensing signals. Nature 454:595–599

Schäfer H, Abbas B, Witte H, Muyzer G (2002) Genetic diversity of “satellite” bacteria present in cultures of marine diatoms. FEMS Microbiol Ecol 42:25–35

Serôdio J, Marques da Silva J, Catarino F (1997) Non-destructive tracing of migratory rhythms of intertidal benthic microalgae using in vivo chlorophyll a fluorescence. J Phycol 33:542–553

Shih PM (2015) Cyanobacterial evolution: fresh insight into ancient questions. Curr Biol 25:R192–R193

Smith DJ, Underwood GJC (1998) Exopolymer production by intertidal epipelic diatoms. Limnol Oceanogr 43:1578–1591

Smith DJ, Underwood GMC (2000) The production of extracellular carbohydrates by estuarine benthic diatoms: the effects of growth phase and light and dark treatment. J Phycol 36:321–333

Solano C, Echeverz M, Lasa I (2014) Biofilm dispersion and quorum sensing. Curr Opin Microbiol 18:96–104

Staats N, Stal L, de Winder B, Mur L (2000) Oxygenic photosynthesis as driving process in exopolysaccharide production of benthic diatoms. Mar Ecol Prog Ser 193:261–269

Stal LJ (2003) Microphytobenthos, their extracellular polymeric substances, and the morphogenesis of intertidal sediments. Geomicrobiol J 20:463–478

Stal LJ (2010) Microphytobenthos as a biogeomorphological force in intertidal sediment stabilization. Ecol Eng 36:236–245

Stal LJ (2015) Nitrogen fixation in cyanobacteria. In: eLS encyclopedia of life science. Wiley, Chichester, pp 1–9

Sutherland I (2001) Biofilm exopolysaccharides: a strong and sticky framework. Microbiology 147:3–9

Sutherland TF, Grant J, Amos CL (1998) The effect of carbohydrate production by the diatom *Nitzschia curvilineata* on the erodibility of sediment. Limnol Oceanogr 43:65–72

Syrpas M, Ruysbergh E, Blommaert L, Vanelslander B, Sabbe K, Vyverman W, De Kimpe N, Mangelinckx S (2014) Haloperoxidase mediated quorum quenching by *Nitzschia cf pellucida*: study of the metabolization of N-acyl homoserine lactones by a benthic diatom. Mar Drugs 12:352–367

Takahashi E, Ledauphin J, Goux D, Orvain F (2009) Optimising extraction of extracellular polymeric substances (EPS) from benthic diatoms: comparison of the efficiency of six EPS extraction methods. Mar Freshw Res 60:1201

Taylor IS, Paterson DM, Mehlert A (1999) The quantitative variability and monosaccharide composition of sediment carbohydrates associated with intertidal diatom assemblages. Biogeochemistry 45(3):303–327

Taylor JD, Mckew BA, Kuhl A, McGenity TJ, Underwood GJC (2013) Microphytobenthic extracellular polymeric substances (EPS) in intertidal sediments fuel both generalist and specialist EPS-degrading bacteria. Limnol Oceanogr 58:1463–1480

Underwood GJC, Paterson DM (2003) The importance of extracellular carbohydrate production by marine epipelic diatoms. Adv Bot Res 40:183–240

Underwood GJC, Boulcott M, Raines CA, Waldron K (2004) Environmental effects on exopolymer production by marine benthic diatoms: dynamics, changes in composition, and pathways of production. J Phycol 40:293–304

van Duyl FC, de Winder B, Kop AJ, Wollenzien U (1999) Tidal coupling between carbohydrate concentrations and bacterial activities in diatom-inhabited intertidal mudflats. Mar Ecol Prog Ser 191:19–32

van Duyl FC, de Winder B, Kop AJ, Wollenzien U (2000) Consequences of diatom mat erosion for carbohydrate concentrations and heterotrophic bacterial activities in intertidal sediments of the Ems-Dollard estuary. Cont Shelf Res 20:1335–1349

Waters CM, Bassler BL (2005) Quorum sensing: cell-to-cell communication in bacteria. Annu Rev Cell Dev Biol 21:319–346

Whitchurch CB, Tolker-Nielsen T, Ragas PC, Mattick JS (2002) Extracellular DNA required for bacterial biofilm formation. Science 295:1487–1487

Whitton BA (1992) Diversity, ecology, and taxonomy of the cyanobacteria. In: Prokaryotes P (ed) Biotechnology handbooks 6. Springer, Boston, MA, pp 1–51

Worm B, Duffy JE (2003) Biodiversity, productivity and stability in real food webs. Trends Ecol Evol 18:628–632

Wotton RS (2004a) The ubiquity and many roles of exopolymers (EPS) in aquatic systems. Sci Mar 68:13–21

Wotton RS (2004b) The essential role of exopolymers (EPS) in aquatic systems. Oceanogr Mar Biol 42:57–94

Yallop ML, de Winder B, Paterson DM, Stal LJ (1994) Comparative structure, primary production and biogenic stabilization of cohesive and non-cohesive marine sediments inhabited by microphytobenthos. Estuar Coast Shelf Sci 39:565–582

Ziegler M, Uthicke S (2011) Photosynthetic plasticity of endosymbionts in larger benthic coral reef Foraminifera. J Exp Mar Biol Ecol 407:70–80

Chapter 5
Meiofauna: An Inconspicuous but Important Player in Mudflat Ecology

Tom Moens and Peter G. Beninger

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Abstract Due to their inconvenient size and nature (too small for easy whole-organism work; too large for, and not amenable to, most microbiology techniques), meiofauna tend to perpetually slip through the cracks of mainstream marine ecology. The resulting knowledge gap is probably as considerable as the ecological importance

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of this group. In this chapter we first present the available techniques for sampling, extraction, and preservation of mudflat meiofauna, and then consider their spatial and temporal dynamics. Although their trophic ecology is obviously of prime importance, meiofauna influence the mudflat ecosystem through many other types of interactions which, at least in part, result from their high taxonomic and functional diversity. These include cryptobioturbation, which has far-reaching effects on sediment characteristics and stability; microbial grazing and fecal pellet production, which impact mudflat microbial ecology and nutrient cycling; and meiofauna-macrofauna interactions, which evolve as the macrofauna grow and develop. An increased awareness of the roles of meiofauna is essential to a comprehensive understanding of mudflat ecology.

1 Introduction

There is an increasing awareness of the ecological importance of soft-bottom meiofauna to the marine ecosystem (Watzin 1983; Pati et al. 1999; Danovaro et al. 2007; Nascimento et al. 2012; Schratzberger and Ingels 2018), especially in the intertidal, where meiobenthic populations are most abundant and productive (Vranken et al. 1986; Vincx 1996; Giere 2009). In particular, benthic meiofauna represent an important food source for higher trophic levels, to which more than 75% of their total production may be transferred (Danovaro et al. 2007). Due to their small size, high turnover and high abundance, meiofaunal organisms are also efficient environmental sentinels (Coull and Chandler 1992; Schratzberger et al. 2000; Moreno et al. 2008a, b; Zeppilli et al. 2015).

Progress in the ecology of mudflat meiofauna has been hampered by the relatively recent awareness of the ubiquity and diversity of these organisms, the difficulty in extracting them completely from the sediment (up to the late 1970s), and the inherent difficulty in studying organisms too small to easily recognize and count (Giere 2009). These difficulties render all the more remarkable Giere's (2009) seminal work on sediment meiofauna.

The introduction and generalization of improved extraction techniques (de Jonge and Bouwman 1977) have rendered the study of meiofauna much more accessible, but their small size and the difficulty of lower-level taxonomic identification still hinder progress in ecological research. Although geologically-interesting groups such as the Foraminifera may have journals specifically devoted to them, a 1980–2011 survey of the papers published in the leading marine ecology journal *Marine Ecology Progress Series* showed that the percent of all papers concerning meiofauna peaked at 6 in 1990, decreasing to a mere 0.4 in 2011, compared to 10–55 for macrofauna papers over the same period. At the time of writing, the percent of articles concerning meiofauna was 0 for the first six volumes in 2018, while those concerning macrofauna had increased to almost 80% (including a seabird special issue; Fig. 5.1). This contrasts with a refreshing recent special meiofauna issue of

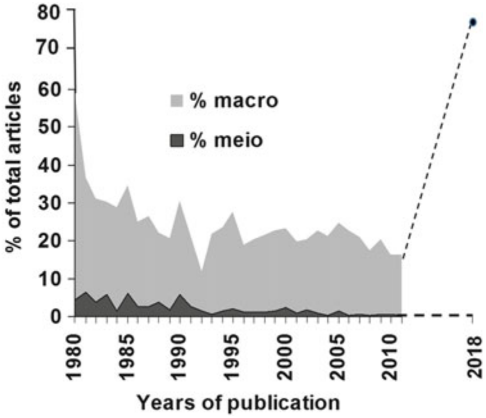

Fig. 5.1 Percentage of all articles in the journal *Marine Ecology Progress Series* concerning meiofauna and macrofauna, 1980–2011, and in 2018 up to June. P. Beninger, unpublished data.

another mainstream marine ecology journal, the *Journal of Experimental Marine Biology and Ecology* (Lampadariou et al. 2018).

In this chapter, we will first examine the methods currently available for descriptive and quantitative study of mudflat meiobenthos; the spatio-temporal variability, trophic and other functional ecology of this living fraction; and finally the ecological interactions which involve meiofauna in the mudflat habitat. Of the relatively little that is known of mudflat meiofaunal ecology, most concerns two dominant metazoan taxa: nematodes and harpacticoid copepods. We will thus focus almost exclusively on these two groups.

2 Sampling, Preservation and Extraction Procedures

2.1 Sampling Procedures

Sampling meiofauna on intertidal mudflats is usually performed at low tide and does not require expensive equipment or sophisticated procedures. Hand coring is a straightforward and effective sampling technique. Corers are typically made of Perspex or another hard, robust and translucent material (Fig. 5.2). When the sediment contains many hard inclusions such as stones, or when larger sediment depths need to be sampled, metal corers may be preferred since these can be hammered into the sediment. The luer or bottom end of the corer should be beveled and should ideally be inserted in a nicely vertical orientation into the sediment; corer withdrawal from cohesive sediments may be facilitated by slightly tilting and rotating the corer during withdrawal. Once the corer is inserted, it should be closed from the top with an air-tight stopper (Fig. 5.2). In some cases (e.g. very fine, water-saturated mud sediment), it may be necessary to also close the corer from below before withdrawal from the sediment. This implies digging and removing the surrounding sediment until a stopper can be inserted.

Fig. 5.2 Sampling equipment for meiofauna field sampling. Perspex hand corers with air-tight stoppers, a 'microcore' with a piston (here simply a sawn-off syringe) and recipients for sample storage. Photo by Tania Campinas Bezerra.

It is important to be aware that coring may compact and even partly 'squeeze' sediments. The use of a piston with which a slight suction on the sediment can be exerted during withdrawal may counteract this, but this is easier to apply to corers with a very small diameter (e.g. a sawn-off syringe; Fig. 5.2) than to larger ones (Somerfield et al. 2005). Withdrawal of corers from the sediment, and of sediment from the corers, may also cause significant vertical displacement of sediment and, particularly, interstitial water and fauna. Allowing the sediment to gently slide down from the corer usually causes fewer such effects than pushing it up through the corer with a piston. Nevertheless, the latter procedure is much easier to vertically slice a sediment core; a half-open graded Perspex cylinder can be screwed onto the corer and a piston pump system can be used to push the sediment upward in a controlled way. In order to avoid the sediment compaction and porewater drainage resulting from this procedure, the lower end of the corer can be closed with potter's clay (Cleven 1999). This effectively closes the corer from below with a stopper which perfectly fits the size of the corer and can be pushed up by a piston, and it avoids that the pressure (and hence compaction) from the piston pump directly acts on the sediment (Cleven 1999).

While the above procedures are adequate to section sediments in strata of 1–2 cm thick, and hence to address issues of vertical distribution or migration of meiofauna (e.g. Steyaert et al. 2001, 2003), very detailed vertical profiles (down to one or a few mm) have been obtained using a modified corer attached to a micrometer screw (Joint et al. 1982). Such fine-scale profiles may, for instance, be required when studying interactions between meioafuna and microalgae in the surface layers of mudflats (Warwick and Gee 1984). However, such screw micrometers are extremely sensitive to blockage by sediment particles and therefore must be kept as clean as possible. Sampling of surface sediments at sub-millimeter scales can be performed using a cryolander, allowing undisturbed profiles with a vertical resolution of ca. 0.1 mm (Wiltshire et al. 1997). This technique has not hitherto be implemented for meiofauna, but might be of use in reconstructing the fine-scale relation between microphytobenthic biofilms and the meiofauna feeding on, or living inside them.

Two obvious issues are the preferred size of the corers to be used for sampling, and the number of replicate samples to be obtained. This obviously depends on the research question. Meiofauna are typically very patchily distributed at scales of a few cm^2, sometimes even less (Findlay 1981, 1982; Blanchard 1990; Pinckney and Sandulli 1990; Boldina et al. 2014, and Chaps. 8 and 15). Hence, the relationship between meiofauna and microalgae or other food sources, or with sediment microtopography (Sun et al. 1993), may be much better revealed by a larger number of small samples than by a few larger-sized samples (Moens et al. 1999a). Corers with a diameter as small as 1 cm may be adequate for such purposes. If the focus is on a description of community abundance, composition and biodiversity, a smaller number (preferably no less than 4) of larger-sized samples may be more suitable, or large compound samples may be collected, homogenised and subsampled to obtain one replicate (Heip et al. 1985). A very commonly used corer diameter for meiofauna inventories measures 3.5 cm and covers a surface area of 10 cm^2. Montagna et al. (2017) found no difference in density estimates of nematodes, copepods and total meiofauna between corers with diameters of 2.2, 3.1, 5.5 and 6.7 cm, but cautioned that the numbers of meiofaunal taxa other than nematodes were quite low when corer diameter dropped below 5.5 cm, potentially hampering statistical power of data analyses. Hence, the abundance of meiofauna is another factor to consider when choosing an optimal sample size. To our knowledge, no study similar to that of Montagna et al. (2017) has compared meiobenthos diversity estimates or community composition assessments generated by differently sized corers. In any case, since the abundance and the patch size of meiofauna may vary tremendously with factors such as sediment granulometry or habitat type, there is no universally-suitable corer size for every habitat and research question.

In addition to the above-mentioned considerations concerning corer size, if the research question entails any aspect contingent on the proper spatial representation of the meiofauna (spatial distribution, biomass, annual productivity, etc.), the equally-important question of spatial lag (distance between cores) must be addressed. Assuming that sampling occurs in linear transects, a sample lag of at least 5 m should be used, and several replicate samples may be taken at each sampling station, provided this is done almost simultaneously for all replicates (Boldina et al. 2014). In turn, the appropriate inter-replicate spatial lag may be initially investigated and standardized once ascertained. A summary of such a sampling strategy is provided in Fig. 5.3.

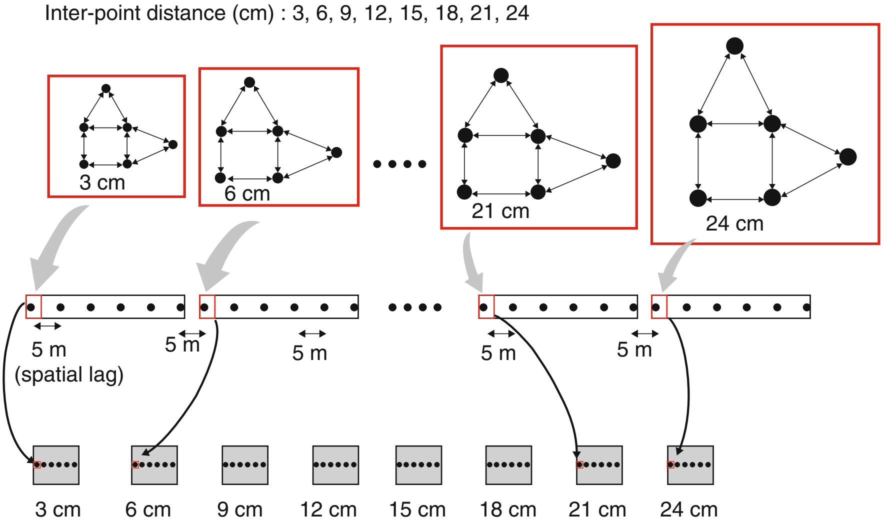

Fig. 5.3 Example of a mudflat meiofauna sampling protocol, where the research question requires adequate spatial representation. Sampling stations are separated by 5-m intervals, and different inter-replicate distances are applied at each sampling station, in order to determine the characteristics of meiofaunal patchiness. From Boldina et al. (2014), with permission from Elsevier.

2.2 Sample Preservation

Optimal sample preservation procedures differ among meiobenthic taxa (Higgins and Thiel 1988; Somerfield et al. 2005). Soft-bodied taxa in particular require different preservation procedures than hard- or semi-hard-bodied taxa such as copepods and nematodes. The latter two taxa can be adequately preserved by covering the sediment sample with a formaldehyde solution with a final concentration of 4%. In this way, samples can be stored for up to several years. However, it is imperative that they are stored in air-tight containers to avoid evaporation, which would otherwise result in drying of the sample, formation of paraformaldehyde ‘crystals’, and the release of a toxic vapour (formaldehyde is carcinogenic and should not be inhaled). Formaldehyde polymerization is a normal process but is counteracted by the addition of methanol in commercial grade formaldehyde (Bedino 2003). It is nevertheless enhanced by factors such as light (hence long-term storage of samples in a dark environment is advisable) and pH: as pH decreases, polymerization increases (Bedino 2003). Therefore, it is also advisable to use formaldehyde which has been buffered, for instance with borax (Pfannkuche and Thiel 1988; Garraffoni et al. 2017); a pH no less than 8.2 will at the same time ensure that organisms with calcified structures remain intact. Some nematode taxa tend to react to the addition of formaldehyde by curling; if preserved in this position, important morphological features may be poorly visible. Preserving with hot (ca 70 °C) formaldehyde usually guarantees that the vast majority of nematodes is nicely stretched out, but the heating of the formaldehyde increases vaporization and precautions should therefore be taken to avoid inhalation.

Technically speaking, glutaraldehyde is probably a superior alternative to formaldehyde, as it may also effectively preserve protists and soft-bodied meiofauna (Pfannkuche and Thiel 1988). Although glutaraldehyde penetrates tissues more slowly, this is not much of an issue with meiofauna-size organismes. Moreover, its long-term preservation capacity is better than that of formaldehyde (Bedino 2003), it is not volatile and—although it does pose health risks—it is not carcinogenic. However, it is considerably more expensive and therefore seldom used for routine preservation of meio- and macrofauna samples. While a 70–80% solution of ethanol in glycerol may also adequately preserve harpacticoid copepods (Higgins and Thiel 1988) and—in contrast to aldehydes—DNA (allowing DNA-based community analyses to be performed), it typically leads to shrinking and discoloration of nematodes, rendering them even more difficult to identify. Preservation of samples intended for molecular analyses, e.g. for metabarcoding of meiobenthic communities (Creer et al. 2016; Fonseca et al. 2017), should avoid the use of formaldehyde. Freezing at −80 °C, or preservation in ethanol or DESS [dimethyl sulfoxide, disodium EDTA, and saturated NaCl—Yoder et al. (2006), Beknazarova et al. (2017)], are the preferred options here.

2.3 Extraction Procedures

2.3.1 Extraction of Preserved Samples

An adequate extraction of meiofauna from the sediments, with which they are sometimes tightly associated, is a crucial but non-evident task; indeed, as mentioned above, this has historically been one of the most difficult obstacles to quantitative meiofauna research. The degree of difficulty of this task depends on factors such as sediment granulometry and detritus content, but also on the indigenous meiofaunal taxa, and on whether or not they should remain alive. Here, we restrict ourselves to the dominant meiofaunal taxa, i.e. nematodes and harpacticoid copepods, acknowledging that the approaches taken may be suboptimal for use in, for instance, turbellarians, ostracods or foraminiferans. We refer to Higgins and Thiel (1988) and Somerfield et al. (2005) for an overview of sample preservation and extraction procedures for other meiofaunal taxa.

When samples have been chemically preserved (see Sect. 2.2), and meiofauna are therefore dead, elutriation of meiofauna depends mostly on sediment granulometry. In coarse sediments, or more generally in sediments with only a very small silt-clay fraction, vigorously stirring the sample with water (e.g. by applying a jet of tap water) and then decanting it over a suitable sieve after a short (10–30 s) period to allow sediment particles to settle, may be sufficient to obtain the vast majority of nematodes and copepods, provided the procedure is repeated up to ten times. When there is a substantial silt-clay fraction, the same procedure is less than suboptimal because of the slow sedimentation of silt, clay and detritus, and because of the often intricate association of meiofauna with detritus particles or sediment aggregates. The latter are sometimes hard to sieve out and may conceal some meiofauna. Sediments that contain many aggregates may therefore be pretreated using sample sonication (Thiel et al. 1975) and/or incubation and shaking with Calgon™, a water softening agent (Barnett 1980), to fragment the sediment aggregates. For sediments with a high silt fraction, the addition of kaolin powder improves extraction efficiency, because the kaolin binds silt-clay particles, thus enhancing their sedimentation (Heiner and Neuhaus 2007; Giere 2009).

The above treatments are only a first step; meiofauna will then have to be extracted via isopycnic elutriation techniques, which are based on the difference in the specific density of meiofauna *vs.* that of most sediment particles (the latter considerably exceeds the specific density of meiofauna, with the exception of shelled taxa). Therefore, the sample is thoroughly mixed with a solution which approximates the specific density of the meiofauna. This can be achieved with sugar (Heip et al. 1974), with chemicals like $MgSO_4$ (Vincx unpubl.), but most commonly and efficiently with colloidal silica gels such as Ludox™ or Ludox HS40 (Du Pont) (Heip et al. 1985; Vincx 1996; Du et al. 2009; Xu et al. 2010; Boldina et al. 2014; Montagna et al. 2017). Whatever the solution used, it is important that it has a density which equals or only slightly exceeds that of meiofauna. When a sediment sample is well-mixed and shaken with, for instance, Ludox of the correct specific density, the heavier sediment particles will slowly sink to the bottom, whereas the meiofauna will remain suspended in, or float on top of, the Ludox fraction. This fraction can then be gently poured over a suitable sieve to collect the meiofauna. It is best to repeat this procedure up to 3 or 4 rinses so as to obtain the vast majority of meiofaunal specimens in the sample. Extraction efficiency may thus amount to $\geq$97% (Pfannkuche and Thiel 1988; Boldina et al. 2014). Still, Heip et al. (1974) have argued that each such extraction step yields a fixed proportion of the remaining nematodes/copepods from the sample, which would allow estimation of the abundance of the whole sample even after a single Ludoxing cycle. In most labs, the density separation of meiofauna and sediment can be enhanced by centrifugation, allowing the complete extraction of multiple samples a day. However, even in the absence of a suitable centrifuge, the procedure still works well; it will only take considerably more time to ensure that all sediment particles properly sink to the bottom, and a more delicate handling of the recipient to avoid resuspension of settled sediment.

It is important to thoroughly rinse sediment samples with tap water prior to addition of Ludox, since Ludox gels on contact with seawater. This problem is less prominent when using a different type of Ludox, Ludox® AM (Pfannkuche and Thiel 1988), but it is nevertheless advisable to routinely wash samples with tap water prior to Ludoxing. The pre-washing with tap water also removes a considerable portion of the silt-clay fraction and most of the preservative. When working with muddy samples, care should be taken not to overload the sieve (which would lead to spilling of some meiofauna), and gently tapping the sieve from below may prevent clogging. In addition, it is advisable to check the tap water for presence of meiofaunal taxa (particularly nematodes). This can be done by allowing tap water to run over a suitable sieve for 5–10 min and subsequently checking the contents of that sieve (Somerfield et al. 2005).

Ludox is most commonly prepared with a specific density of 1.13–1.18 (Heip et al. 1985; Vincx 1996). The former value is based upon the specific density of the nematode *Enoplus communis* (Wieser 1960), wheras slightly higher values take into account that the Ludox solution can become somewhat diluted by the interstitial water present in the sediment sample. While it is unlikely that the specific density of other nematodes would deviate substantially from that of *Enoplus*, other meiofauna taxa may have deviant specific densities [shelled taxa such as ostracods and foraminiferans, for instance, typically have a higher specific density (Somerfield et al. 2005)]. While the above specific density of Ludox efficiently separates meiofauna from sediments, it does not always separate meiofauna from various types of detritus. Much of the larger detrital material can be removed by washing samples through a 1-mm sieve nested on top of the meiofauna sieve, but this procedure also entails the risk of losing larger meiofauna which are retained on the 1-mm sieve. Hence, when plenty of detritus is present in the samples, elutriation should be performed in a solution with a higher specific density. In such cases, Ludox can be replaced by $MgSO_4$ at a specific density of 1.25 or higher (Vincx, pers. comm.). While this clearly results in a better separation of meiofauna from detritus, it has not been rigorously tested to what extent this affects the extraction efficiency of meiofauna.

The extraction efficiency of meiofauna may be greatly affected by seemingly small ‘details’. The two Ludox types mentioned above, i.e. Ludox™ and Ludox HS40, may yield significantly different extraction efficiencies, with the latter outperforming the former (Du et al. 2009). Since density centrifugation with Ludox HS40 can be combined with quantitative protargol staining (QPS), which is commonly used to quantify ciliates and diatoms in sediment samples (Montagnes and Lynn 1993), a Ludox HS40-QPS protocol can simultaneously yield adequate estimates of meiofauna, ciliates and diatoms (Du et al. 2009; Xu et al. 2010). The volume ratio of Ludox to sample is also important: a sample is ideally mixed thoroughly with at least a fourfold volume of Ludox (Heip et al. 1985; Somerfield et al. 2005; Giere 2009). However, efficient extraction was also obtained with a Ludox:sample ratio $\leq$2:1 by applying a 5-min vortexing to fluidize the sediment and create a density gradient in which meiofauna rise to the surface prior to the centrifugation step (Burgess 2001). Operator experience and performance may also significantly affect extraction efficiency. Rohal et al. (2018) compared the performance of two operators who had received the same training and had the same level of experience. Their extraction efficiencies of muddy samples, while being almost identical for copepods and several other meiofaunal taxa, differed by as much as 20% for nematodes of the order *Desmoscolecida* and by almost 17% for other nematodes. Furthermore, both operators extracted *Desmoscolecida* with much lower efficiency (12–20%) than other nematodes, a result which might be linked to the prominent presence of non-living particles that stick to the nematode cuticles (Rohal et al. 2018).

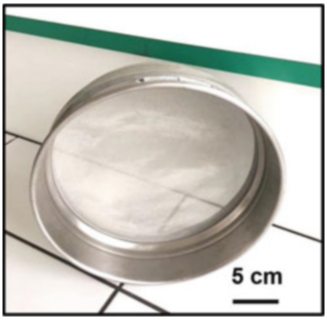

Fig. 5.4 A typical sieve used to retain extracted meiofauna. Photo PG Beninger.

Mesh size of the sieves used to retain meiofauna (Fig. 5.4) is a more obvious cause of variation in extraction efficiency between studies. While some laboratories maintain a tradition of using a 63-μm mesh, this significantly underestimates meiofauna abundances compared to smaller mesh sizes (Leduc et al. 2010; Montagna et al. 2017). Although this effect is probably more pronounced for deep-sea than for intertidal meiofauna, given the typically much smaller body sizes of the former, it may nevertheless be significant for mudflat meiofauna as well. Moreover, mesh size will obviously not bias abundance estimates to the same extent for differently sized organisms; abundances of smaller taxa/individuals (e.g. juveniles) will be considerably more underestimated by coarser meshes than those of larger taxa. As a consequence, assessments of assemblage composition, of size spectra, of adult/juvenile ratios etc. will be affected by mesh size (Leduc et al. 2010). Most commonly, mesh sizes of 38–45 μm are used, but for an optimal collection, mesh sizes down to 20 μm would be better. The main problem is that when working with muddy sediments, such fine mesh sizes retain large portions of silt and hence easily become clogged.

On a cautionary note, it is important to realise that Ludox is a silica gel, and that silica dust is both irritating to skin and respiratory tracts and is also carcinogenic. It is therefore imperative to avoid any spilling and drying of Ludox, since direct contact with, or inhalation of the resulting silica dust can be harmful.

2.3.2 Extraction of Live Meiofauna

While meiofauna samples for inventories or monitoring purposes tend to be numerous, and are usually preserved with some chemical fixative for longer-term preservation, experimental studies often require large quantities of live meiofauna.

Some of the above isopycnic elutriation techniques have been used in the past to obtain living meiofauna as well, and can further be enhanced by first applying a $MgCl_2$-solution isosmotic with the habitat water to anaesthetise the meiofauna (Hulings and Gray 1971; Garraffoni et al. 2017). Protocols using sugar and salt solutions do, however, impose extreme osmotic stress and therefore should be performed rapidly and with utmost precision to harvest living meiofauna; silica solutions tend to be toxic to meiofauna. A specific silica gel called Cecasol 40C

(Sobrep) has proven less toxic (De Ley and Mundo-Ocampo 2004), but in our experience, substantial species-specific mortality or damage nevertheless occurs. The same may hold for the silica-sorbitol mixture Percoll (Rzeznik-Orignac et al. 2004), which has been proposed as a very efficient solution for isopycnic separation of both preserved and living meiofauna (Schwinghamer 1981). It is therefore doubtful whether an isopycnic separation protocol exists which maintains most meiofauna alive and active.

Alternative methods exist for the extraction of living meiofauna based on their behaviour in certain imposed gradients. It is important, however, to realize that none of these methods will yield a complete or quantitative extraction of meiofauna, and that most or all are inherently selective: some species/taxa will be extracted in substantial numbers, whereas others may be largely or completely missed.

For nematodes, most such behaviour-based methods are Baermann-type extraction protocols which rely on the motility of the organisms to separate them from sediment and detritus (Baermann 1917; Viglierchio and Schmitt 1983; Gray 1984). Both funnel- and tray-type deployments are used, the latter probably being more efficient at extracting substantial volumes of sediment and at avoiding asphyxiation (Couch 1988; Mangubhai and Greenwood 2004; De Ley and Mundo-Ocampo 2004). Most commonly, sediment is placed on top of a mesh or sieve which in turn is supported or held in place by various means. One of the simplest and perhaps most efficient forms consists of a tray with a metal insert; the insert has large pores (e.g. 0.5 cm diam.) and supports a single or double layer of tissue paper, the edges of which extend over the edge of the insert and into the tray (Mangubhai and Greenwood 2004). Sediment is gently spread out over the tissue paper [note that the thickness of the sediment layer may substantially affect the efficiency of extraction, and that the type of mesh (here tissue paper) will determine to what extent fine sediment and detritus particles end up in the tray along with the nematodes], and aerated habitat water is subsequently poured carefully into the base of the tray, until the water level touches the mesh from underneath, thus keeping the sediment moist from below. Nematodes tend to migrate downward through the mesh into the water in the tray and remain trapped there (Fig. 5.5). Migration can be further enhanced by the application at the sediment surface of some trigger which the nematodes try to avoid, such as cold temperature [e.g. the seawater-ice method (Uhlig et al. 1973)], heat and/or light (Armonies and Hellwig 1986; Couch 1988). However, this may also

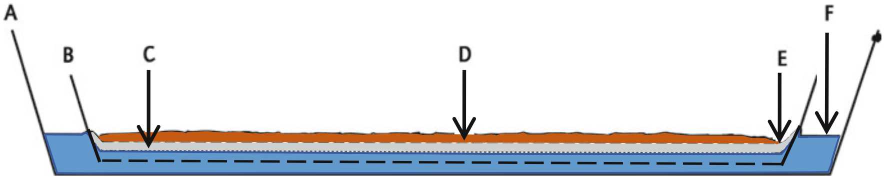

Fig. 5.5 A modified Baermann tray for the extraction of living nematodes from soils/sediments. A: recipient tray; B: metal or plastic insert with large pores; C: coarse (e.g. 200 μm) and fairly solid mesh supporting D: single- or double-ply tissue paper; E: thin layer of sediment; F: water of appropriate salinity. Schematic modified from Fan et al. (2016).

adversely affect the extraction, because some nematodes easily become immobilized under such stressful conditions (Moens unpubl.). Addition of a layer of sterile sand or glass beads in between mesh and sample is advisable for obtaining clean nematode suspensions when dealing with sediments with a high portion of silt and/or fine detritus (Uhlig et al. 1973; Rzeznik-Orignac et al. 2004).

Alternatively, many nematodes will also move into a layer of sterile sandy sediment or glass beads put on top of a muddy sediment sample, particularly if the sediment is not oxygenated from below (Wu and Moens unpubl.). The bottom line is that several simple and relatively fast (24–48 h) protocols exist which allow the extraction of good numbers of living nematodes suitable for experiments, but that none of these protocols is very efficient or quantitative, and that all are selective: some nematode species, particularly the more motile ones, will be obtained in good numbers, while others will not be obtained at all.

Similar principles as for nematodes can be used to harvest large numbers of harpacticoid copepods, free of sediment and debris, from sediments. However, different triggers may prove more efficient to induce copepod movement, and hence different setups may be more practical. Many harpacticoid copepods appear positively phototactic (in contrast to nematodes) and readily move towards light. In this way, clean suspensions full of copepods can be obtained within less than 1 h (Svensson et al. 2010). Once again, it must be stressed that there is as yet no method which will quantitatively extract all live meiofaunal taxa, or even one of the taxa. However, this still allows for much descriptive work, and for the instruction of students, whereas extraction of dead (fixed) meiofauna allows for a great deal of quantitative research.

2.3.3 Staining

In ecological studies, it is usually necessary to distinguish between live and dead meiofauna. Since counting live organisms is usually not practical, and in any event not feasible (due to the possibility of counting the same motile individuals twice), it is necessary to be able to distinguish, post-hoc, between live and dead individuals at the time of fixation. Due to lack of motility in fixed specimens, and because most meiofauna possess some form of cuticle or exoskeleton, many live and dead individuals are visually indistinguishable. For several decades, the simple, inexpensive Rose Bengal (RB) staining procedure has been used for this purpose (Walton 1952), on the assumption that its protein-staining affinity allowed the ready distinction between empty exoskeletons and live (at time of sampling) meiofauna. However, RB-staining proteins may persist for months, or even years, in dead meiofauna, introducing a source of overestimation bias for live meiofauna, and a concomitant underestimation of dead meiofauna. The much more laborious QPS staining technique (Du et al. 2009; Xu et al. 2010) suffers from the same problem. This problem was progressively recognized (see review by Murray and Bowser 2000); a true vital staining technique (Cell Tracker Green—CTG) was eventually developed for Foraminifera (Bernhard et al. 2006), and later used for nematodes and copepods (Grego et al. 2013). Based on the activation of fluorescence after chemical modification of the marker molecule by an enzyme which is only active in living cells, the CTG technique very specifically stains live meiofauna. Comparisons with the RB technique have shown very considerable overestimations of the living fraction in sampled meiofaunal taxa: a nearly 50% mean difference, with extreme values up to 97% in the case of foraminiferans, and 100–400% mean difference for copepods in anoxic layers of the sediment (Bernhard et al. 2006; Grego et al. 2013).

To summarize, on the one hand there is a simple and inexpensive technique which may severely bias estimations of living meiofauna, and on the other hand, there is a rather more time-consuming technique, involving dark incubation in the presence of CTG, at the temperature at which the meiofauna were sampled, prior to fixation and counting. Some authors have continued to use the RB technique, reporting their results as ‘Live (RB stained)’ rather than ‘Live’ (Caulle et al. 2014). Although such a semantic sidestep may be valid when the objective is simply to distinguish between ‘dead for a long time’ and ‘live or recently dead’, it is not valid for many ecological studies.

3 Spatial Distribution

3.1 Large-Scale Horizontal Distribution Patterns and Intertidal Zonation

At scales of meters to kilometers (mesoscale), the principal drivers of meiobenthos community patterns comprise mainly physical-chemical properties of the sediment matrix (e.g., Steyaert et al. 2003), such as salinity, tidal exposure, sediment grain size and a number of variables (in)directly liked to it, such as oxygenation and physical disturbance (Hicks and Coull 1983; Heip et al. 1985; Moens et al. 2013).

Salinity is among the main structuring factors in mudflats, with particularly pronounced effects on meiobenthic species diversity, which tends to increase with increasing salinity in estuaries (Soetaert et al. 1994, 1995). Oligo- to mesohaline waters are typically characterized by a lower species diversity, but examples of Remane’s minimum (Remane 1934) are not common. This concept posits that the upper salinity tolerance limits of freshwater species are usually very low (well below a salinity of 10 psu), and the lower tolerance limits of marine species highly variable, with some species disappearing in mesohaline sediments, while others extend nearly all the way to the inland freshwater reaches (Heip et al. 1985). Relatively few species survive in the oligo-mesohaline zone. Moreover, this mid-section of estuaries also typically exhibits higher salinity fluctuations during each tidal cycle than both the poly- and oligohaline reaches (Kaiser et al. 2011), a variability which may challenge the tolerance limits of many species and could therefore lead to a (very) low diversity. Nevertheless, other environmental factors may affect and modify such a unimodal diversity-salinity relationship.

The tidal immersion-emersion cycle also causes significant changes in sediment temperature, water content, oxygen and hydrodynamics, which generate horizontal distribution patterns (zonation) (Armonies and Reise 2000; Gheskiere et al. 2004; Maria et al. 2013a, b) and vertical stratification (Steyaert et al. 2001; Maria et al. 2012).

The impacts of hydrodynamics and low-tide exposure may typically create opposing disturbance gradients across the intertidal zone. In the lower intertidal, organisms are often more exposed to wave action, while in the upper intertidal, they are more prone to suffer from the larger variability in temperature, moisture etc. during low tide exposure (Armonies and Reise 2000; Kaiser et al. 2011). In the intermediate intertidal zone, wave action and low-tide exposure are generally more at equilibrium, resulting in a higher abundance and diversity, particularly on sandy beaches (Nicholas and Hodda 1999; Armonies and Reise 2000; Gheskiere et al. 2004; Gingold et al. 2010). Such across-shore zonation patterns can be considered examples of the Intermediate Disturbance Hypothesis (IDH), which postulates that maximum species diversity occurs at intermediate disturbance levels; here, disturbance is not so intense that it eliminates species, but is sufficient to prevent a dominance of competitive interactions which might otherwise lead to diversity loss through competitive exclusion (Connell 1978). The processes governing disturbance-diversity relations are manifold, and may comprise, among others, hydrodynamic activity, organic enrichment, abiotic stress in the form of reduced oxygen availability, increased temperature fluctuations etc., but also predator-prey and competitive interactions. Schratzberger et al. (2009) confirmed IDH-like patterns for various types of sediment disturbance.

From an IDH perspective, mudflats tend to be hydrodynamically sheltered and are therefore more dominated by competitive interactions, unless other types of disturbance, like predation, become severe. Whereas diversity exhibits a unimodal relationship with disturbance under the IDH model, the Intermediate Productivity Model (IPM; Grime (1973)) similarly predicts a unimodal relationship between resource availability and diversity. At very low food inputs, resource availability is simply insufficient to sustain a more diverse community, whereas at very high inputs, conditions are optimal for a limited number of opportunistic species which have superior competitive abilities under a particular set of conditions. Highest diversity is hence to be expected at intermediate levels of food supply.

Mudflats often combine—albeit not necessarily on a year-round basis—a high productivity of MPB with the deposition of significant quantities of suspended particulate organic matter, resulting in a high availability of nutritious food. In addition, the decomposition of much of this organic matter *in situ*, and the usually prevailing mild hydrodynamics, often create low-oxygen conditions, even near the surface of mudflat sediments. This combination of biotic (competition) and abiotic (hypoxia) factors typically results in a lower species richness in muddy compared to more sandy intertidal sediments (*sensu* Folk et al. (1970) 'sandy mud' or 'muddy sand'). However, due to the high resource availability, total densities of meiofauna in muddy sediments may substantially exceed those of sandy sediments. Still, meiobenthic species richness in mudflat sediments is not typically (very) low, except under conditions of strong pollution, suggesting that other stressors cause a substantial level of disturbance; these other stressors may be abiotic as well as biotic.

Sediment granulometry is intimately linked with hydrodynamics, with finer-grained sediments occurring mostly where hydrodynamic impacts are low and deposition of fines from the water column is enhanced. Finer and coarser-grained sediments, such as muddy and sandy tidal flat sediments, usually harbor distinct meiobenthic assemblages: for nematodes and harpacticoid copepods, muddy sediments tend to be dominated by relatively robust species that can burrow through the sediment or thrive mostly as sediment dwellers at or very near the surface (Tita et al. 1999), whereas nematodes from sandy habitats comprise a mix of slender species that move through the interstitial spaces in the sand, and larger and bulkier species, many of the latter being predators/omnivores (Heip et al. 1985; Tita et al. 1999; Vanaverbeke et al. 2011; Moens et al. 2013). For harpacticoid copepods, sandy sediments often comprise a substantial portion of slender, almost vermiform species (Hicks and Coull 1983). The depositional nature and hypoxic conditions of muddy sediments often favour non-selective deposit-feeding nematodes, while their prominent MPB biofilms are typically inhabited by high abundances of a limited number of epistrate-feeding genera (Commito and Tita 2002; Van Colen et al. 2009).

As mentioned above, coarser sediments frequently have a high abundance of predatory/omnivorous and of very slender species. The latter often comprise selective deposit feeders; however, general trends in the proportional abundances of this feeding group are difficult to draw, which is at least in part a consequence of the high tolerance to hypoxia of a few genera of selective deposit-feeders, such as *Terschellingia* and *Leptolaimus*. *Terschellingia* in particular is very well-represented in sediments which range in granulometry from silt-clay rich to medium sandy with a negligible silt-clay fraction (Materatski et al. 2015; Sahraean et al. 2017), suggesting its distribution is not so much dependent on granulometry or food availability, but rather on hypoxia/anoxia, conditions under which these nematodes may benefit from the disappearance of potential competitors. Alternatively, *Terschellingia* may thrive under conditions which favour chemoautotrophic prokaryotic activity, since natural stable isotope abundances of *T. longicaudata* from various sediments consistently reflect the utilization of methane-derived carbon (Vafeiadou et al. 2014; Sahraean et al. 2017).

3.2 Small-Scale Horizontal Distribution Patterns

At scales of mm to cm (microscale), meiobenthos of intertidal flats often show aggregated distribution patterns with patch sizes in the order of a few cm in diameter (Findlay 1981, 1982; Decho and Fleeger 1988; Blanchard 1990; Moens et al. 1999a; Pinckney et al. 2003; Boldina et al. 2014; Fig. 5.6). Such clustered distribution patterns may have multiple causes, but the aggregate distribution of food sources is undoubtedly one of, if not the, most important. Microphytobenthos, for instance, exhibits aggregate distribution patterns with very similar patch sizes as meiofauna

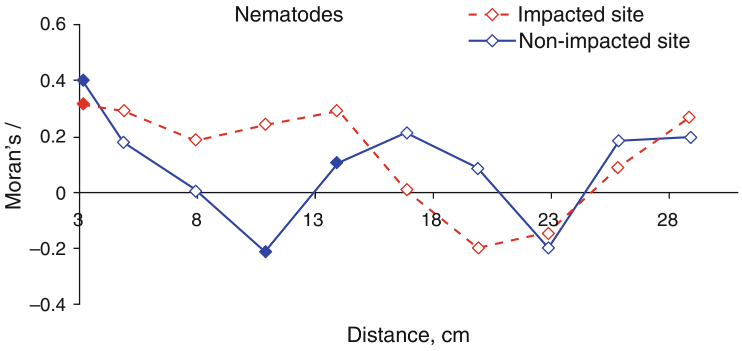

Fig. 5.6 Omnidirectional spatial autocorrelogram using 10 equidistant classes for nematode densities at a mudflat site impacted by clam digging and at an unimpacted reference site. Moran's *I* is a measure of similarity (here, in nematode density). The correlogram shows strong aggregation for the non-impacted site and attenuated aggregation (only significant autocorrelation in distance class 1) for the disturbed site. Significant values are represented by solid symbols; non-significant values are represented by empty symbols. From Boldina et al. (2014), with permission from Elsevier.

(Blanchard 1990; Pinckney and Sandulli 1990; Guarini et al. 1998; Seuront and Spilmont 2002; Murphy et al. 2008), due to, among other factors, sediment heterogeneity and grazing, both of which may be caused, at least in part, by macrobenthic activity, and to topographic irregularities (Montagna et al. 1983; Decho and Fleeger 1988; Sun et al. 1993; Reise 2002; Braeckman et al. 2011b). Microalgal patchiness tends to be higher in siltier relative to sandy sediments, pointing to a close link between food source distribution and sediment type (Sandulli and Pinckney 1999). The spatial correlation between patches of MPB and of meiobenthos suggests that both are structured by a common driver, or are causally related. Microphytobenthos may thus play a role in structuring meiofaunal small-scale spatial distribution and/or vice versa (Montagna et al. 1983; Decho and Fleeger 1988; Blanchard 1990). Small-scale patches of food, disturbance and biotic interactions create microhabitats in space and time, which harbor distinct communities in different successional stages, thus allowing many different species to coexist at very small scales (e.g., Gallucci et al. 2008). Nematodes and copepods thus exhibit a characteristic patchiness and patch size, but patch size can become attenuated in nematodes by disturbance such as mudflat clam digging, while it remains largely unaffected in the more motile harpacticoid copepods (Boldina et al. 2014; Fig. 5.6).

In addition to food patchiness, microtopographic irregularities, generated by waves and currents (see Chap. 8), or by the activity of macro-/megafauna, may contribute substantially to meiobenthic patchiness (Sun et al. 1993; Reise 2002). Meiobenthos can, for instance, accumulate in depressions or around biogenic structures due to the aggregation of food sources and/or to the reduction in hydrodynamics (Findlay 1981; DePatra and Levin 1989; Sun et al. 1993). In contrast, disturbance due to bioturbation and/or predation can locally reduce meiofauna densities (Ólafsson and Elmgren 1991; Schratzberger and Warwick 1999; Danovaro et al.

2007). The combined results of all these small-scale drivers cause a dynamic mosaic of patches (Gallucci et al. 2008), which is typically more pronouced in muddy sediments, whereas in more exposed sediments, hydrodynamics are a homogenizing factor that overrides part of this small-scale patchiness (Boeckner et al. 2009; Gingold et al. 2010).

3.3 Vertical Distribution Patterns

In addition to the horizontal patchiness in meiofaunal spatial distribution described above, meiofauna abundances also show vertical variability in the sediment. These vertical patterns are generally related to oxygen gradients, to the distribution of food, to hydrodynamics and to biological interactions (see Sect. 5.2). Hydrodynamics in turn affect oxygen gradients and food distribution in a dynamic way related to the tides. Hence, while the main vertical distribution patterns in intertidal flats are fairly general, they often exhibit significant shifts over the course of a tidal cycle.

First of all, it is important to state that abundances of meiofauna in muddy sediments exhibit much more marked depth profiles than those in coarser sediments (Moens et al. 2013; Wetzel et al. 2001; Steyaert et al. 2003). Approximately three-quarters of the nematodes, and virtually all of the harpacticoid copepods, are confined to the upper 2 cm in muddy tidal flat sediments, whereas in sandier sediments, nematode abundances can be much more evenly distributed over a depth of several cm, and even down to 50 cm or more on reflective beaches (Renaud-Debyser 1963). These depth profiles resemble the vertical profiles of oxygen and redox potential in the upper centimeters of sediment, although free oxygen in muddy sediments is usually confined to an even thinner upper layer than that where nematodes abound. Perhaps more important to many meiofauna than the mere concentration of freely available oxygen, is the presence of sulfide ions, generated in the underlying reduced sediment layer (Gray 1981). Sulfide ions are toxic to most aerobic species, and especially to harpacticoid copepods (Wetzel et al. 2001), although exceptions exist, perhaps using quiescence to survive periods of elevated sulfide concentrations (Vopel et al. 1996). Together with the presumed comparatively higher trophic dependence of copepods on microphytobenthos (MPB) (see Sects. 4.1 and 4.2), this may explain a second general observation: harpacticoid copepods usually exhibit steeper vertical profiles than nematodes (Wetzel et al. 2001). The smoother vertical profile of nematodes may also be due to their generally greater tolerance of extended periods of anoxia, as well as of elevated sulfide levels (see below). Nevertheless, the redox potential discontinuity (RPD) layer marks the lower limit of the depth distribution of many species.

The redox potential discontinuity (RPD) lies deeper in coarser sediment, whereas in finer sediments it can be restricted to the first centimeters or even millimeters. Although the RPD layer represents an ecological barrier, many nematode species tolerate hypoxic or anoxic conditions and occur below the RPD layer (Fenchel and Riedl 1970; Ott and Schiemer 1973). These species show adaptations that allow them to survive or even thrive in anoxic environments. For instance, the elongation of the body, typical of some species living in the deeper layers, is probably related to the increase in the ratio of body surface area to body volume, which facilitates the epidermal absorption of oxygen (Jensen 1986; Soetaert et al. 2002) as well as of dissolved organic matter as an additional food source (Schiemer et al. 1990; Soetaert et al. 2009). In addition, an elongated body may increase mobility, facilitating short 'oxygen replenishing' excursions from the anoxic to the oxic layer (Fonseca et al. 2007; Gallucci et al. 2008; Vanreusel et al. 2010). Physiological adaptations, such as the presence of elemental sulphur granules accumulated in the epidermis, have also been observed in some nematode species (Thiermann et al. 2000). Such elemental inclusions in the epidermis may temporarily reduce the concentrations and toxic effect of H_2S, while also providing an energy resource for later oxidation under oxic conditions (Thiermann et al. 2000).

At the Molenplaat tidal flat in the Schelde Estuary, SW Netherlands, variation in sediment granulometry controlled nematode abundance and assemblage composition in the upper sediment layers (2–3 cm). Beneath that depth, nematode assemblages were very similar, irrespective of sediment granulometry, suggesting that other environmental features determine nematode assemblage abundance and composition (Steyaert et al. 2003; Fig. 5.7). Given that even at the sandiest site on this tidal flat, free oxygen is usually confined to the uppermost centimetre of sediment (Herman et al. 2001), and the position of the RPD layer is no deeper than at 2–3 cm, it is plausible that the deeper-living nematofauna is shaped by its tolerance to hypoxia and related biogeochemical conditions. In the sandy sediment, a clear vertical segregation of nematode species occurred, with a surface-dwelling assemblage dominated by large predatory nematodes (mainly *Enoploides longispiculosus*) and a deeper-living (beneath 2 cm) assemblage dominated by deposit feeding and epistrate feeding species (Fig. 5.7, site 3) (see Sect. 4.1 for explanation on nematode feeding types). Species interactions (mainly predator-prey) are believed to cause this segregation, which is—moreover—dynamic over the course of the tidal cycle (see Sect. 5.2). In the siltiest sediments, a large majority of nematode species were confined to the upper 1.5 cm of sediment, with a sharp decline in both density and diversity deeper down (Fig. 5.7, site 1). Such a pattern is reminiscent of typical oxygen/sulphide dominated depth distributions (Steyaert et al. 2003). At intermediate conditions of hydrodynamics and sediment granulometry, an intermediate vertical pattern of nematode assemblage diversity and composition was obtained (Fig. 5.7, site 2).

The vertical oxygen concentration gradient in intertidal sediments is profoundly influenced by currents and tides, but at the same time modified by other meio- and macrobenthic organisms through processes such as the construction of tubes, bioturbation etc., which alter patch-scale hydrodynamics and physical-chemical gradients of the sediment (e.g., Callaway 2006, and see Chaps. 2, 3, and 10). These processes and structures transport oxygen deeper into the sediment, thereby producing a three-dimensional mosaic of oxygenated and sulfuric microhabitats (Reise 1981; Wetzel et al. 1995; Tita et al. 2000).

Nematode vertical distribution may also be controlled by the interstitial water drainage and by abrupt changes in abiotic conditions during sediment emersion at low tide. Many nematodes are sensitive to low sediment water content (Jansson

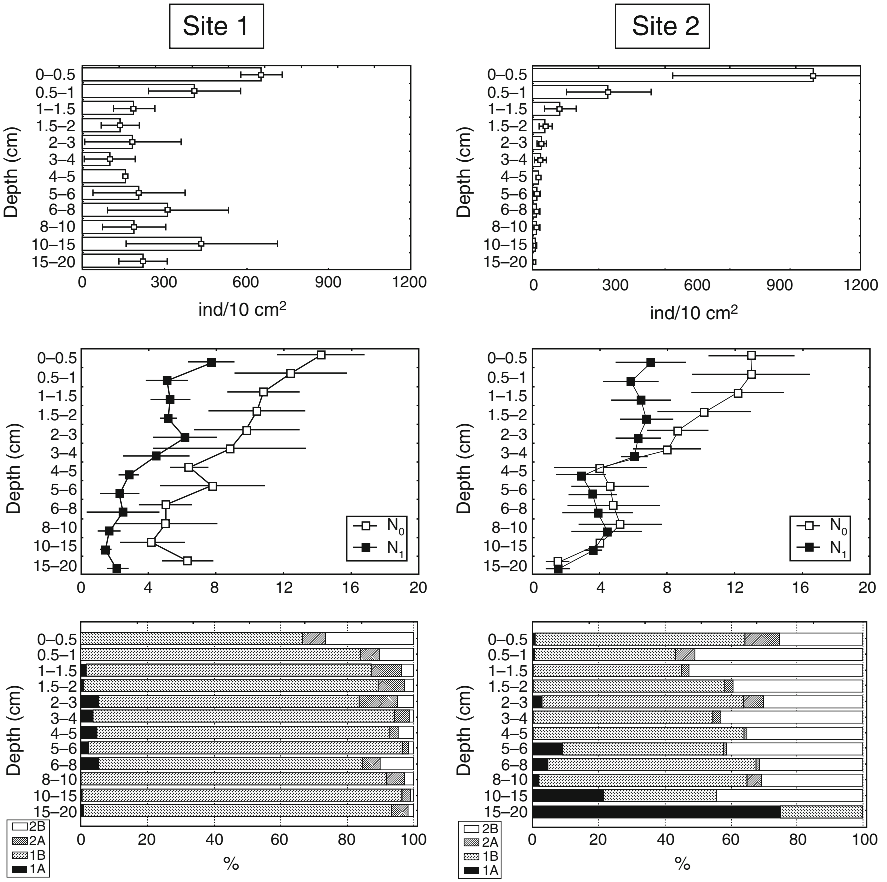

Fig. 5.7 Abundance, species diversity (expressed as richness (N_0) and the exponent of the Shannon-Wiener diversity (N_1) and feeding-type composition of nematode assemblages at three stations on the Molenplaat tidal flat in the Schelde Estuary. Site 1 is a muddy sediment, site 3 a fine to medium sandy sediment devoid of silt, and site 2 has intermediate hydrodynamic and granulometric characteristics. From Steyaert et al. (2003), with permission from Elsevier.

1968; Gallucci et al. 2005), and migrate to deeper layers during low tide, returning to the surface as the rising tide re-establishes more favourable sediment conditions (McLachlan et al. 1977; Steyaert et al. 2001). Still other species migrate upwards during low tide and downwards during submersion (Steyaert et al. 2001; Maria et al. 2012). This counter-intuitive behaviour may present several advantages: increased diatom production and biomass accumulate at the sediment surface during tidal exposure (Guarini et al. 1997), resulting in high food availability to upward-migrating grazers, as well as a reduced predation risk if predatory nematodes (e.g. *Enoploides longispiculosus*) are among the downward-migrating species (Gallucci et al. 2005).

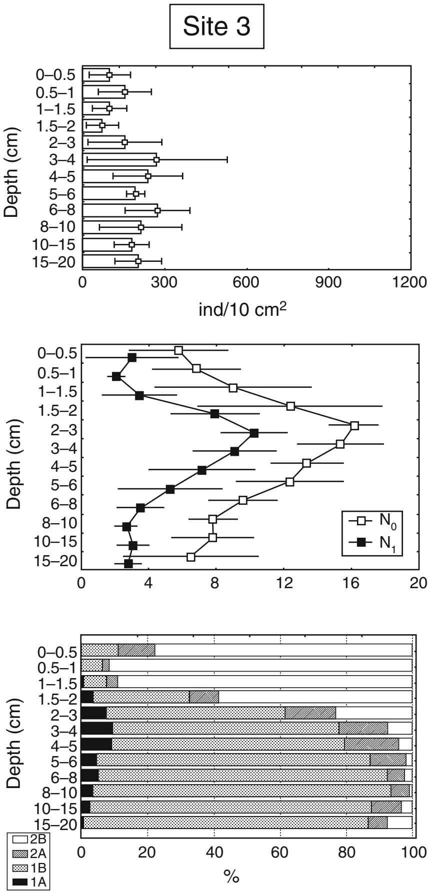

Fig. 5.7 (continued)

Stochastic factors may also induce nematode vertical migrations. For example, heavy rainfall on exposed mudflats may cause rapid, considerable changes in salinity, stimulating the downward migration of more osmotically-sensitive species (Steyaert et al. 2001). The same result may be observed in response to strong currents or waves. On the other hand, the upward migration of opportunistic nematode species, such as *Sabatieria* sp., may be triggered by the deposition of a phytoplankton bloom on the sedment surface (Franco et al. 2008).

3.4 Temporal Variability in Meiofauna Communities

Mudflat meiofaunal assemblages can exhibit temporal fluctuations in abundance and/or community composition on scales of hours to years (Coull 1986; Eskin and

Coull 1987; Steyaert et al. 2001; Nicholas 2001; Maria et al. 2012), although some studies have found a lack of any clear temporal pattern (Warwick and Buchanan 1971; Juario 1975). Most studies on marine meiofauna assemblages have focused on seasonal fluctuations (McIntyre and Murison 1973; Gourbault et al. 1998; Nicholas and Hodda 1999; Nicholas 2001; Albuquerque et al. 2007; Liu et al. 2008; Venekey et al. 2014). Long-term (i.e. year-to-year) (Coull 1985, 1986; Eskin and Coull 1987; Li et al. 1996; Riera et al. 2011) and very short-term (i.e. hours) (Boaden and Platt 1971; Steyaert et al. 2001) variation have received only limited attention.

3.4.1 Climatic Factors

Among the main causes of seasonal variation in meiofauna assemblages are climatic factors such as temperature, precipitation and their impacts on salinity, and factors related to food availability. Temperature can affect meiofauna abundances directly, e.g. by dehydration, and indirectly, e.g. by its effects on the growth and abundance of food items such as bacteria and diatoms (Harris 1972a, b), and/or by affecting the depth of the RPD layer in sediments (Dye 1983). Temperature can also affect interspecific interactions such as predation and competition (Moens et al. 2000; De Meester et al. 2015b). Although a considerable number of studies have investigated effects of temperature on aspects of the life cycle of nematodes and harpacticoid copepods, such studies usually incubate test organisms under different constant temperature regimes. Effects of temperature fluctuations have only rarely been considered, even though benthic organisms in intertidal sediments often experience large temperature variation on a tidal or daily basis, especially in the most superficial sediments.

De Meester et al. (2015b) compared the fitness of three cryptic species of the nematode *Litoditis spp.* in monospecific cultures as well as in mixed culture, under a constant temperature of 20 °C and a fluctuating temperature regime with daily temperature variations between 15 and 25 °C. Although temperature regime had no significant effect on the fitness of any of the three species in monospecific culture, it did affect interspecific interactions. Vafeiadou et al. (2018) subjected a temperate and a tropical intertidal meiofauna community to two elevated-temperature regimes, one a constant elevated temperature, the other a regime with daily fluctuations, comprising a few hours of (very) high temperature. Both regimes affected the temperate meiofauna assemblage, while the tropical assemblage was only affected by the fluctuating temperature regime. Different meiofauna taxa exhibited somewhat different responses to the imposed temperature regimes.

Other climatic factors such as precipitation can also cause temporal fluctuations in meiofauna assemblages at both seasonal and very short time scales. Seasonal nematode density may, for instance, be affected by rain cycles (Venekey et al. 2014). On a completely different time scale, short episodes of heavy rainfall, such as a strong shower during low-tide exposure, may cause vertical migrations of nematodes in sediments (Steyaert et al. 2001).

Precipitation can in turn affect salinity. Salinity fluctuations can generally be linked with seasonal cycles of precipitation (Paranhos and Mayr 1993). However, in intertidal habitats, and particularly so in sandier sediments, there can also be considerable short-term variability in salinity, both in direct relation to the tides [e.g. because of the higher specific density of more saline water, bottom-water layers and interstitial water tend to have slightly higher salinities (Kaiser et al. 2011)], and indirectly through episodic events such as the above-mentioned heavy rainfall during low-tide exposure (Steyaert et al. 2001).

3.4.2 Food Availability and Predation

Food availability is a major driver of temporal variation in nematode assemblages (Heip et al. 1985; Moens et al. 2013). Because microphytobenthos and settling phytoplankton, as well as the bacteria growing on these carbon sources, often exhibit pronounced seasonal peaks in productivity, food availability for meiofauna can have clear seasonal patterns, and the abundances of total meiofauna and/or of specific taxonomic or functional groups may follow a similar pattern (e.g. Austen and Warwick 1995; Kendall et al. 1995; Li et al. 1996; Ólafsson and Elmgren 1997). If food availability in the form of MPB and/or deposited phytoplankton is a major driver of temporal variability in meiofauna abundance in tidal flats, one might expect generally more pronounced seasonal patterns in muddy sediments, where both the build-up of MPB and the accumulation of deposited suspended matter are much stronger than in sandier sediments.

Interestingly, while there is relatively limited evidence for a stronger seasonality in meiofauna communities on muddy compared to sandy sediments, a higher year-to-year variability of meiofauna and nematode communities in finer sediments has indeed been observed (Coull 1985, 1986; Eskin and Coull 1987; Sahraean and Moens 2018). These longer-term studies have suggested that assemblages in finer sediments are largely controlled by biological interactions—both bottom-up and top-down—whereas those in sandier sediments are predominantly determined by hydrodynamics. Top-down controls include predation by ‘macrofauna’. For instance, Coull (1985, 1986) found no recurrent patterns other than seasonal ones in an 11-year study on the abundances of meiofauna higher taxa in two intertidal sites, a muddy and a sandy one. However, the between-year variability observed in the muddy site was much larger and generally well-correlated with that in the abundance of juvenile spot, a fish species known to prey on harpacticoid copepods and perhaps other meiofauna (Smith and Coull 1987). In turn, Li et al. (1996) found a significant correlation in fortnightly and monthly variability in nematode biomass with the abundance of mainly deposit-feeding macrobenthos; this effect was selective, in that it mostly affected large-sized predatory and omnivorous nematodes, whereas other feeding types varied more with proxies of primary productivity.

4 Trophic and Functional Ecology

4.1 Trophic Diversity of Meiofauna

At the higher-taxon level, marine nematodes can consume a wide array of resources, including prokaryotes, auto/mixo- and heterotrophic protists, and various benthic invertebrates, including other nematodes (Moens and Vincx 1997; Moens et al. 2004). Consumption of some potential food sources, like fungi—known to be eaten by many terrestrial and some freshwater nematodes—and dissolved organic matter, has hitherto been poorly documented (Moens et al. 2004). Essentially the same range of food sources can be consumed by harpacticoid copepods (Hicks and Coull 1983). Despite this wide range of trophic sources, there seems to be an (admittedly inconclusive) consensus that benthic and/or deposited planktonic microalgae are a major food source for a majority of mudflat copepods (Buffan-Dubau et al. 1996; Buffan-Dubau and Carman 2000; Cnudde et al. 2015), although debate remains as to whether most species obtain microalgal carbon directly or indirectly (see Sect. 4.2). Nevertheless, anecdotal observations exist of harpacticoid copepods feeding on flagellates, ciliates (Rieper 1985; Reiss and Schmid-Araya 2011), nematodes (Lehman and Reid 1992) or even on their own offspring (Dahms and Qian 2006).

Because of the paucity of adequate species-level information on feeding behaviour and resources of a majority of meiobenthos species, nematologists have traditionally assigned species to feeding types or guilds based on mouth morphology and, to a lesser extent, pharyngeal musculature, using a feeding-type classification proposed by Wieser as early as 1953 (Fig. 5.8). Wieser distinguished no more than four feeding types, with a primary subdivision between nematodes with and without ‘buccal armature’, each of these two groups then further being subdivided in two. Buccal armature refers to the presence of a tooth or teeth, onchia, denticles, mandibles or other sclerotised structures. In Wieser’s (1953) classification, nematodes without a buccal armature are labeled deposit feeders; the size of the buccal cavity is then suggested to reflect the degree of feeding selectivity. Thus, marine nematodes without a buccal armature and with only a tiny mouth opening are considered selective deposit feeders, whereas nematodes with larger buccal cavities are termed non-selective deposit feeders. The logic behind this distinction is that a sediment matrix contains many more inedible than edible particles. Nematodes with a spacious mouth may benefit from a foraging strategy in which they display only limited selectivity, as they are capable of ingesting sufficient amounts of particles to deal with a substantial proportion of inedible material. Moreover, they are able to locate feeding spots where suitable food is plentiful, and may thus limit ingestion of inedible particles by choosing optimal feeding patches (Moens et al. 2006).

Nematodes with very small buccal cavities, by contrast, should avoid uptake of non-nutritious particles, since they are limited in the amount of particles they can process. While this mouth-size-based distinction between selective and non-selective deposit feeders looks arbitrary, the relative abundances of these two groups indeed often behave differently (e.g. Thistle et al. 1995; Vincx 1989; Smol et al. 1991),

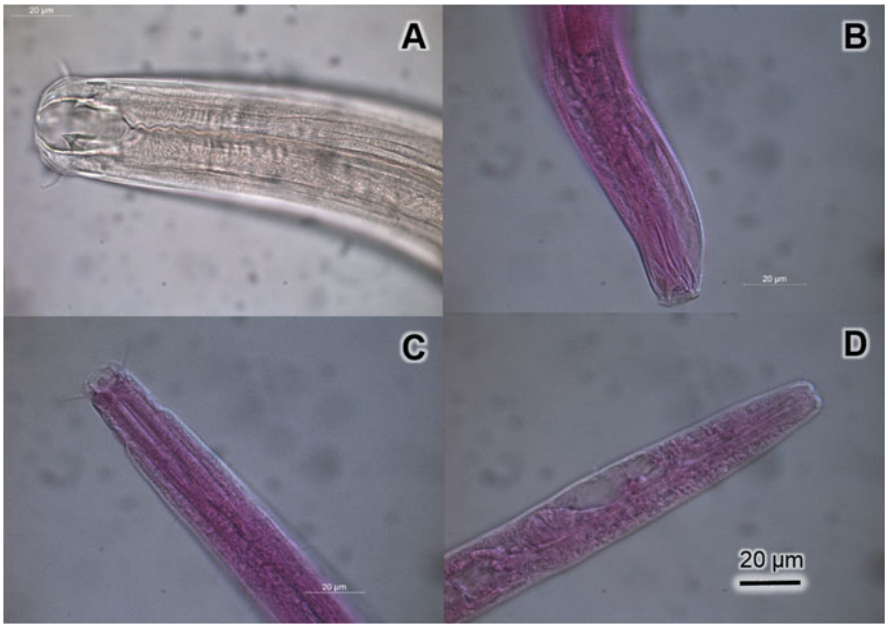

Fig. 5.8 Illustrations of the four feeding types of Wieser (1953), based on mouth morphology. (**a**) *Oncholaimus* sp. is a predator/omnivore with a spacious buccal cavity with two prominent teeth. (**b**) *Ptycholaimellus* sp. is an epistrate feeder with a relatively small buccal cavity and a tooth to crack or puncture microalgal cells. (**c**) *Daptonema* sp. is a non-selective deposit feeder with a spacious mouth opening without any 'buccal armature' like teeth. (**d**) *Terschellingia* sp. is a selective deposit-feeder with a tiny, unarmed buccal cavity. All four genera shown here are common inhabitants of mudflats. Scale bar = 20 μm for all photos, courtesy of Tania Campinas Bezerra.

indicating they have at least partly different ecological requirements. However, selective feeding is probably the rule rather than the exception in most nematodes (Moens et al. 2004) and harpacticoid copepods. For example, harpacticoid copepods and nematodes are able to discriminate between different diatom or bacteria species, sizes or growth phases (Lee et al. 1977; Van den Berghe and Bergmans 1981; Rieper 1982; Moens et al. 1999b, 2014; Azovsky et al. 2005; De Troch et al. 2006, 2012).

The other two guilds in Wieser's (1953) feeding-type classification bear sclerotized structures like teeth, onchia, denticles or cuticular ridges in their stoma with which they can pierce, crack, or rupture prey items. Epistratum feeders can scrape bacteria or microalgae from a substratum, such as a sand grain, using a partly evertible tooth, or use that same tooth to puncture or crack food cells which they will then empty by sucking movements of their muscular pharynx (Jensen 1982; Moens and Vincx 1997). Predators or omnivores have larger mouth openings with more prominent teeth, onchia, and/or jaw-like mandibles that can pierce, tear or 'harpoon' and ingest a prey (often invertebrates) (Moens and Vincx 1997; Fonseca and Gallucci 2008). Some predators use a largely hollow dorsal tooth, on the top of which opens a glandular outlet, and observations suggest that such nematodes pierce their prey to inject paralyzing or lethal secretions (Moens and Vincx 1997).

Several alternative feeding-guild classifications have more recently been proposed—the one by Moens and Vincx (1997) being based on actual observations of the feeding behaviour of living nematodes—but the ease of trophically classifying nematodes based entirely on a few easily observable morphological characters remains attractive to many researchers. However, an important limitation of Wieser's (1953) and other feeding-type classifications is that they counter-intuitively funnel the high marine nematode species diversity into a very limited trophic diversity. Equally problematic from a modeling and an ecosystem functioning point of view, is that *the proposed feeding guilds mostly reflect a way of feeding, rather than delineating resource use* (Moens et al. 2004). For instance, both non-selective deposit feeders and epistrate feeders may to a large extent graze on the same benthic microalgae, but in a different manner. Predators/omnivores may be highly flexible feeders that can switch to predation on heterotrophic protists (Hamels et al. 2001) or even to herbivory (Franco et al. 2008; Moens et al. 2014) or bacterivory (Moens et al. 1999c), depending on resource availability (Fig. 5.9). The feeding-guild classifications often draw an all- too rigorous picture of nematodes as belonging in a single box with one feeding ecology label on top. In reality, a majority of mudflat nematodes may be flexible feeders that can switch between different feeding

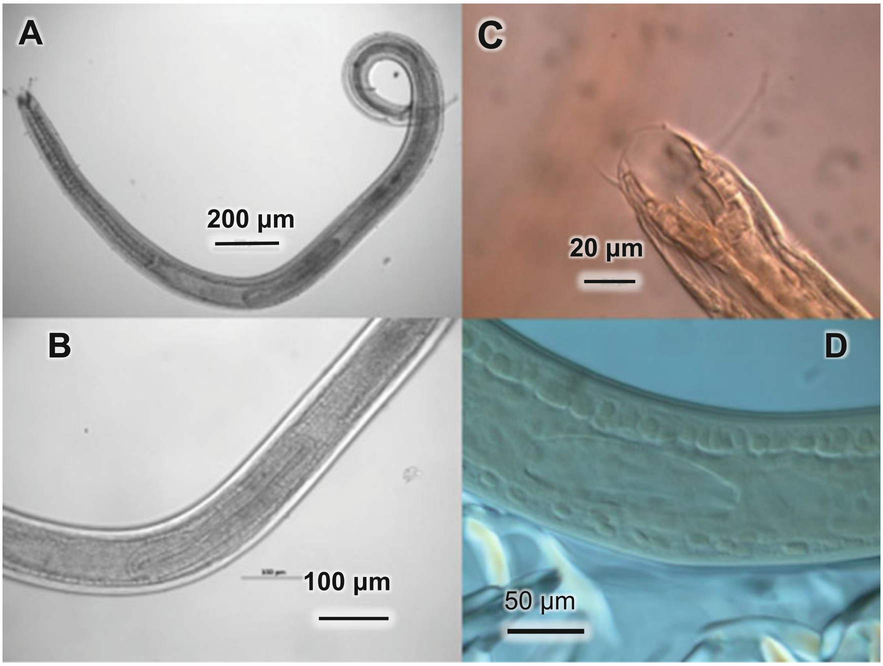

Fig. 5.9 The predatory/omnivorous (*sensu* Wieser 1953) or predatory (Moens and Vincx 1997) nematode *Enoploides longispiculosus*. (**a**) Adult male with fairly intact prey nematode in the midgut; (**b**) midgut section of the same specimen; (**c**) close-up of the head region, including mouth with teeth and jaw-like structures; (**d**) detail of midgut section with diatom cell ingested whole. Photos courtesy of Tania Campinas Bezerra.

strategies and resources, depending on availability (Moens et al. 2004) and/or on competitive interactions with other consumers. It is nevertheless important to note that some general trends about the abundance of each feeding type in different marine habitats exist, indicating that the proposed feeding types are not entirely meaningless groupings (Moens et al. 2013).

In harpacticoid copepods, clear links between the morphology of the mouth parts and the mode of feeding or resource types used have not been established. Hence, no similar feeding type classifications as in nematodes exist. Harpacticoid copepods are more commonly classified 'functionally' on the basis of their body shape and size into phytal, epibenthic and the usually more slender mesopsammic or interstitial forms (Noodt 1971) (Fig. 5.10).

In conclusion, our knowledge concerning the feeding ecology of meiobenthos is still very much a mixture of generalizations at the level of higher taxa and/or feeding guilds, and of anecdotal information for selected species. A comprehensive overview of which species consume which resources is largely lacking, and this is all the more true when it comes to quantitative information on feeding rates, a knowledge gap which hampers accurate inclusion of meiofauna in benthic food web models. Moreover, when qualitative and/or quantitative information is available for particular species, it is usually restricted to a limited set of experimental data, and can therefore not be readily extrapolated or generalized (Moens et al. 2006). Another consequence

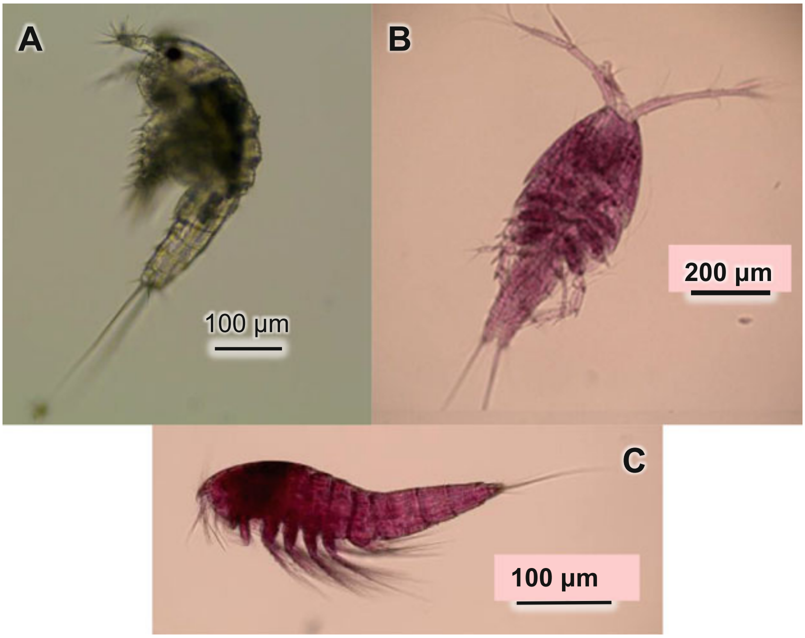

Fig. 5.10 Examples of 'typical' body shapes of benthic harpacticoid copepods. (**a**) the (epi)benthic *Microarthidion littorale*; (**b**) the epibenthic *Tisbe furcata*; (**c**) the interstitial/mesopsammic *Ectinosoma dentatum*. Photos courtesy of Thibaud Mascart and Marleen De Troch.

of our lack of species-level knowledge on meiobenthos feeding habits, is that the importance of resource selectivity as a structuring factor for the often species-rich communities remains a matter of debate. From the above, it is clear that meiofaunal trophic ecology is a pressing research need in the field of marine biology as a whole, and in mudflat ecology in particular.

4.2 Resource Utilization and Trophic Position

4.2.1 Microphytobenthos

Several studies using natural stable isotope ratios of carbon and nitrogen, sometimes complemented with fatty acid profiles, have provided compelling evidence that the main basal carbon source fueling nematodes and harpacticoid copepods on intertidal flats is microphytobenthos (MPB). This pattern is more pronounced in sediments with higher sand content (Moens et al. 2002, 2005a; Rzeznik-Orignac et al. 2008; Cnudde et al. 2015). Despite a MPB biomass which is easily one order of magnitude higher in muddy sediments, primary productivity may be very comparable in silty and in more sandy sediments (Middelburg et al. 2000; Herman et al. 2001). The latter, then, have a much higher turnover rate, mainly as a consequence of hydrodynamics and more efficient grazing by macrofauna (Herman et al. 2001). Nematodes and some harpacticoid copepods in sandy intertidal sediments can have almost purely MPB-based isotopic signatures, whereas those of mudflats typically have some—albeit limited—influence of deposited phytoplankton, a trend which becomes more pronounced as mudflats are more sheltered or have features, such as the presence of vegetation, that enhance deposition of suspended particulate organic matter (Moens et al. 2002, 2005a; Cnudde et al. 2015). Nevertheless, meiobenthos from sandy sediments may also utilize freshly settled phytoplankton to a significant extent (Maria et al. 2011; Evrard et al. 2012), even though a comparative study on a sandy beach found a systematic preference for microphytobenthos over deposited phytoplankton across Nematoda, Harpacticoida and Turbellaria (Maria et al. 2011).

While MPB is undoubtedly a crucial carbon source for many mudflat meiofauna (Moens et al. 2005a; Rzeznik-Orignac et al. 2008), debate remains as to the pathways by which MPB carbon is transferred to meiofauna. For example, only a fraction of the most abundant mudflat nematode and harpacticoid copepod species at the Paulina tidal flat in the Schelde estuary, SW Netherlands, have stable N isotope ratios that convincingly reflect herbivory and hence direct grazing on MPB (Moens et al. 2005a, 2014; Cnudde et al. 2015). Others have δ^{15}N values which are intermediate between primary and secondary consumers, suggesting they are either omnivorous (i.e. feeding on resources belonging to different trophic levels) or more generalist consumers, and a substantial portion of nematodes are secondary consumers (i.e. predators) (Moens et al. 2005a). The latter seem to be more prominent in sandy than in muddy sediments, which agrees well with the generally higher prominence of large-bodied, supposedly predatory or omnivorous nematodes in sandy compared to muddy sediments (Moens et al. 2013; see also Sect. 5.2).

A higher-than-expected trophic level fractionation of stable N isotopes between MPB and supposedly diatom-feeding nematodes and harpacticoid copepods may indicate that part of the MPB carbon flows to meiofauna through a trophic intermediate (Moens et al. 2014; Cnudde et al. 2015), such as bacteria or heterotrophic protists. Prokaryotes are the principal decomposers of organic matter in most aquatic sediments (Mostajir et al. 2011), yet transfer of prokaryotic biomass up the food chain may generally be limited on mudflats (Van Oevelen et al. 2006c). An in situ pulse-chase experiment on a mudflat demonstrated that a nematode-dominated meiobenthos community grazed *ca*. 3% of bacterial carbon production, while bacterial biomass in turn accommodated no more than 6% of the nematodes' carbon requirements (Van Oevelen et al. 2006a, b). Nevertheless, specific nematode and copepod species may thrive on bacteria as their main food (see below, this section).

Based on the high abundances of meiofauna in intertidal sediments and on their generally fast biomass turnover when compared to most macrofauna (Kuipers et al. 1981; Coull 1999), as well as on grazing rate estimates from radiotracer or other feeding experiments (Montagna and Yoon 1991; Montagna 1995; Rzeznik-Orignac et al. 2003), it has been repeatedly argued that meiofauna are important in benthic carbon flows. By contrast, several more recent tracer experiments using stable isotopes suggest that nematodes process only negligible fractions of MPB and of freshly-settled phytoplankton (Middelburg et al. 2000; Van Oevelen et al. 2006c; Urban-Malinga and Moens 2006; Franco et al. 2008). There is clearly an important challenge in reconciling these seemingly conflicting results, and in improving approaches for obtaining reliable estimates of the metabolic activity of meiofauna under field conditions (see e.g. Braeckman et al. 2013).

4.2.2 Bacteria

Harpacticoid copepods may complement their algal diets with bacteria (Dahms et al. 2007; Cnudde et al. 2015), some of which may be obtained from the copepod's own fecal pellets as part of a sort of gardening process (De Troch et al. 2009, and see Chap. 4). However, in an experimental study on four mudflat copepod species, Cnudde et al. (2013c) concluded that bacterial uptake was mostly through co-ingestion of cells that were attached to other food particles like diatoms; in a follow-up study with two of these four copepod species, the same authors demonstrated that bacteria in their own right represent a low-quality food for harpacticoids (Cnudde et al. 2013a). Nevertheless, natural stable isotope and fatty acid signatures of some species, particularly the slender and small interstitial species living in more sandy sediments, indicate an important contribution of bacteria to their nutrition (Cnudde et al. 2015).

While strictly or mainly bacterivorous nematodes and harpacticoid copepods in intertidal habitats are often prominently present in organically (particularly with vascular plant or macroalgal litter) enriched habitats such as salt marshes (Van den

Berghe and Bergmans 1981; Warwick 1987), the importance of bacteria as a food source to most truly benthic species inhabiting bare tidal flat sediments remains to be established. A variety of nematode and copepod species are capable of feeding on bacteria, either purposely or through accidental co-ingestion with other food particles, but whether and to what extent they depend on bacterial carbon remains to be assessed.

Bacterial-feeding meiofauna can significantly shape bacterial communities through selective grazing, influencing the relative abundances of the different community members (De Mesel et al. 2004, 2006). Such effects are species-specific (De Mesel et al. 2004) as well as diversity-dependent (De Mesel et al. 2006) (Fig. 5.11).

Other intricate meiofauna-bacteria interactions include ecto- and endosymbioses, which have been well-documented for a few marine nematode species (Polz et al. 2000; Bayer et al. 2009), but also the presence of a diverse gut microflora (Derycke et al. 2016). The sum of gut microflora, symbionts, and (remnants of) ingested bacteria is the microbiome of an organism, and these microbiomes can be highly

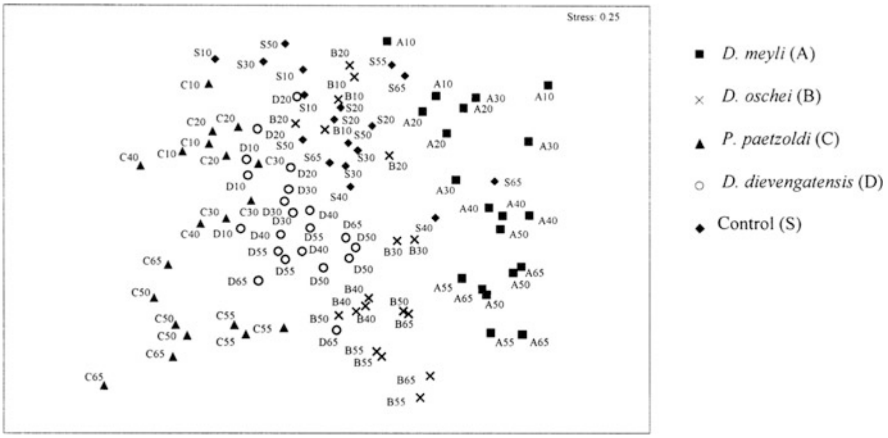

Fig. 5.11 Non-metric multidimensional scaling ordination (nMDS) of the bacterial communities developing in microcosms, to which different bacterivorous nematode species have been added. Letters and symbols refer to the inoculated nematode species: *Diplolaimelloides meyli*, *Diplolaimelloides oschei* and *Diplolaimella dievengatensis* belong to the family Monhysteridae, order Monhysterida, while *Panagrolaimus paetzoldi* belongs to the Panagrolaimidae, order Rhabditida. Numbers refer to the duration (in days) of the experimental incubation. The closer two samples are in the ordination plot, the more similar their bacterial communities. Results show that while control samples without nematodes loosely cluster near the top of the ordination plot, without any clear pattern, all nematode treatments display a bacterial succession with time of incubation, leading to communities that differ increasingly from the initial inoculum to the end of the experiment. In addition, the very limited overlap between nematode treatments demonstrates that each nematode species has its own, species-specific impact on the bacterial community composition. This experiment illustrates that nematodes affect bacterial community structure and do so in a species-specific manner, even for very closely related species (the three Monhysteridae), suggesting that functional redundancy among species is limited. Figure from De Mesel et al. (2004), with permission from Wiley Publishers.

species-specific in marine nematodes (Derycke et al. 2016). Nevertheless, Schuelke et al. (2018) did not find consistent differences in microbiomes among nematodes belonging to the different feeding types discussed in Sect. 4.1.

A special trophic relationship between meiofauna and prokaryotes is the use of methane-derived carbon by specific nematodes [e.g. *Terschellingia longicaudata* (Vafeiadou et al. 2014)] and harpacticoid copepods [e.g. members of the family Cletodidae (Cnudde et al. 2015)] from intertidal and shallow subtidal sediments. While such relationships have previously been established in nematode species from specific habitats such as methane seeps (Van Gaever et al. 2009), mangroves (Bouillon et al. 2008), seagrass beds (Vafeiadou et al. 2014), and sediments of saltmarshes (Cnudde et al. 2015), they also occur in mudflats (Moens et al. 2011). *Terschellingia longicaudata*, for instance, is found in nearly all of these habitats, and its natural stable isotope signatures of carbon and nitrogen consistently mirror the use of chemoautotrophic bacteria that utilize methane as a carbon source (Moens et al. 2011; Vafeiadou et al. 2014) (Fig. 5.12). It remains unclear whether such relations reflect selective grazing on chemoautotrophic bacteria, the presence of chemoautotrophic symbionts (such as sulphide oxidizing bacteria in *Astomonema* and *Parastomonema* spp. (Austen et al. 1993; Musat et al. 2007; Tchesunov et al. 2012), or yet another type of meiofauna-bacteria interaction.

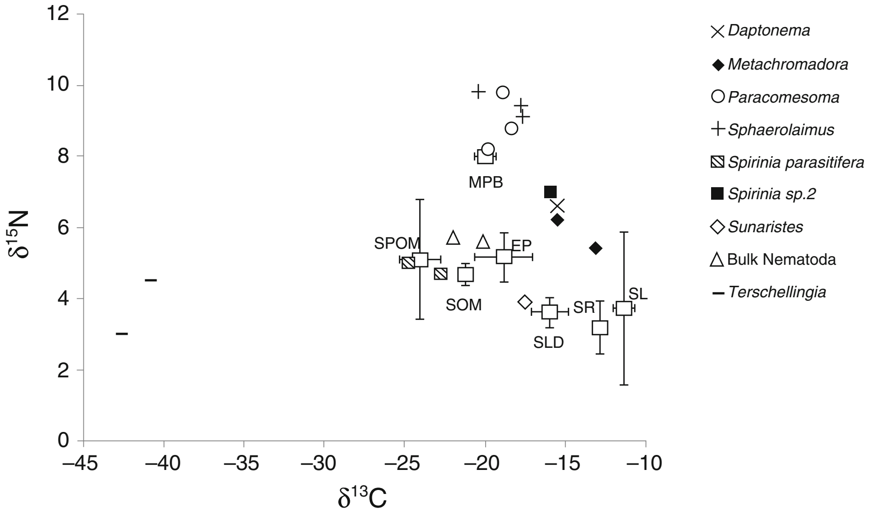

Fig. 5.12 Dual stable isotope plot of total nematodes, of a range of nematode genera, and of the canuellid copepod genus *Sunaristes* from a tidal mudflat in the Mira Estuary, SW Portugal. Note the strongly depleted δ^{13}C and—to a lesser extent—δ^{15}N values of *Terschellingia longicaudata*, which are indicative of this species' dependence on methane-derived carbon (chemoautotrophic pathways). Figure from Vafeiadou et al. (2014), open access.

4.3 Functional Roles of Meiofauna in Mudflat Sediments

4.3.1 Cryptobioturbation

Trophic structure and diversity (Sects. 4.1 and 4.2) are but two characteristics that may influence the roles of meiofauna in the functioning of marine sedimentary ecosystems such as mudflats. Other aspects, such as the motility and (micro)bioturbation capacity of meiofaunal organisms also come into play.

In more sandy sediments, many harpacticoid copepod and nematode species may most easily move through the interstitial spaces, thus leaving no or only a very limited impact on the porosity, structure or other features of the sediment. Other harpacticoid copepod species, and particularly those in muddy tidal flat sediments, live epibenthically and/or are confined to the upper 1 cm of the sediment. By contrast, larger nematode species are common in sandy as well as in muddy sediments, where they burrow and vertically migrate in sediments, activities which probably reduce predation by macrofauna (Leduc and Probert 2009) and can be collectively referred to as micro- or cryptobioturbation (Giere 2009). Cryptobioturbation has been shown to enhance oxygen and nutrient cycling and, in turn, the mineralization of detritus (Alkemade et al. 1992b; Schratzberger and Ingels 2018). Cryptobioturbation of the very top layers of sediments by various meiofauna, from harpacticoid copepods and nematodes to unicellular foraminiferans, was first brought to light in a landmark paper by Cullen (1973), visualizing the loosening effect of meiobenthic activity on the surface layer of sediment. Indeed, the movements of meiofauna increase sediment porosity, while other activities such as feeding and mucus production (see below) lead to particle fragmentation (Aller and Aller 1992) and a modified sediment structure (Cullen 1973; Gerlach 1978), respectively.

Cryptobioturbation is now well-recognized as a process with consequences for the fluxes of oxygen and nutrients, which in turn impact microbial populations and hence key ecosystem functions such as organic matter decomposition, nutrient regeneration, and more generally biogeochemical cycles. Nevertheless, whether and to what degree this process is quantitatively important in mudflat sediments remains under debate. Cryptobioturbation by meiofauna (particularly nematodes, juvenile bivalves and polychaetes) can more than double solute transport rates in marine muds; 20–40% of this increase can be attributed to an increased sediment porosity, the remainder probably to biologically-induced fluid motion and three-dimensional diffusion (Aller and Aller 1992). Indirectly, cryptobioturbation enhances aerobic decomposition and associated processes, such as nitrification (e.g., Alkemade et al. 1992b; Rysgaard et al. 2000; Bonaglia et al. 2014). The mineralization rate of dead *Spartina anglica* leaves, for instance, increased by up to 300% in the presence of bacterial-feeding monhysterid nematodes (Findlay and Tenore 1982; Alkemade et al. 1992a).

Although the process of cryptobioturbation and its consequences are well-recognized by meiobenthologists, it appears to be a comparatively recent insight among geologists, who after documenting the occurrence of cryptobioturbation in

Pliocene sediments, pose the question ' *. . .how pervasively altered are other sediments presently assumed to lack animal influence and how far into the geological record does this influence extend?*' (Löhr and Kennedy 2015).

4.3.2 EPS Production

A microcosm experiment with bacterial-feeding nematodes, bacteria and diatoms demonstrated that nematodes may also enhance the production of extracellular polymeric substances (EPS; i.e. mucus composed of colloidal carbohydrates and proteins) by stimulating bacterial and/or diatom population growth (Hubas et al. 2010), perhaps as a result of the release from nitrogen limitation of these microorganisms through the enhanced cycling of nitrogen by the nematodes' excretion of ammonium (Hubas et al. 2010; Gaudes et al. 2013). An enhanced EPS production, particularly by MPB, improves sediment stability on intertidal mudflats (Lucas et al. 2000; Widdows and Brinsley 2002), which in turn may affect a number of other organisms [e.g. the settlement of larvae of macrobenthos (Van Colen et al. 2009)] and ecosystem processes (Herman et al. 2001; Widdows and Brinsley 2002, and see Chaps. 2, 8, 10). Recently, a natural nematode assemblage from an intertidal flat was also demonstrated to significantly stimulate the productivity and affect the species composition of an artificial 4-species MPB biofilm, whereas an opposite impact was observed on the productivity of a monospecies biofilm (D'Hondt et al. 2018). This suggests that both trophic and non-trophic mechanisms may be at play, and that generalizations about the effects of meiofauna on MPB biofilms and their associated ecosystem functions will be difficult to make.

In addition to microbioturbation, the caudal and/or oesophageal glands of many nematode species produce sticky mucus secretions (Riemann and Schrage 1978) that can facilitate nematode attachment (or that of their eggs) to sediment or algal surfaces and that may serve as a trap for bacteria, microalgae and detritus (mucus-trap-hypothesis; Riemann and Schrage 1978; Warwick 1981), which in turn can serve as food (i.e. gardening), as producers of dissolved organic matter (Riemann and Helmke 2002) or, in the case of detritus, as a component of temporary or permanent tubes in which nematodes may reside (Nehring 1991; Nehring et al. 1990). Tube-building also occurs in a variety of harpacticoid copepods, and may affect the interactions between different species of meiobenthos (Chandler and Fleeger 1987). In addition, laboratory experiments have demonstrated that the bacteria that colonize nematode tracks covered with mucus are not just a random subset of bacteria from the surrounding sediment (Moens et al. 2005b) (Fig. 5.13); hence, mucus secretion may be yet another way—in addition to selective grazing and N cycling—through which meiofauna can affect microbial community composition and diversity (De Mesel et al. 2004, 2006).

The roles of meiofauna in sediment stabilization/erosion are conjugated with those of the other living mudflat components (Fig. 5.14). As is emphasized in Chaps. 2, 4, 8, and 10, sediment stability is a crucial determinant of mudflat ecology, so the importance of this function cannot be underestimated.

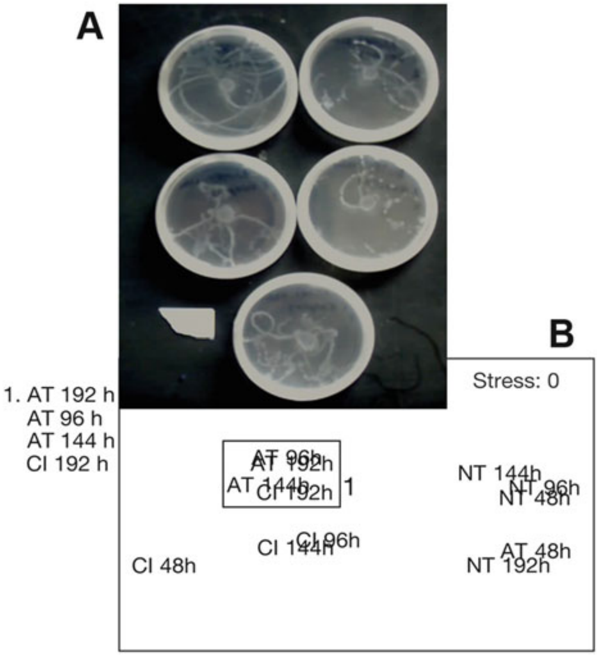

Fig. 5.13 (**a**) Nematodes and bacteria have been inoculated in the centre of Petri dishes with an agar medium. The tracks where nematodes have been crawling on or in the agar are clearly visible by the bacterial growth on the mucus left behind by the moving nematodes. Photo coutesy Giovanni dos Santos. (**b**) Multidimensional scaling (MDS) of bacterial community composition (based on presence/absence data) in inocula (centre of the dishes), artificial tracks and nematode tracks after 48, 96, 144 and 192 h. Example of a treatment with the nematode *Adoncholaimus fuscus* and a bacterial inoculum derived from a fine-sandy sediment at the Paulina tidal flat, SW Netherlands. From Moens et al. (2005b), with permission from Inter-Research.

4.3.3 Fecal Pellets

In planktonic food webs, calanoid copepods channel approximately a third of ingested carbon to their fecal pellets, and an additional fraction to dispersed amorphous particles lacking the peritrophic membrane characteristic of copepod fecal pellets (Turner 2002; Olesen et al. 2005). The pellets and amorphous particles are colonized and decomposed by bacteria, which in turn are consumed by heterotrophic protists, thus shunting back part of the 'lost' organic matter to the food web. The fecal pellets are bacterial 'hot spots' in terms of activity and abundance (Jacobsen and Azam 1984; Thor et al. 2003). As such, copepod fecal pellets and their subsequent bacterial degradation contribute significantly to the energy flow and nutrient cycling in pelagic ecosystems. A similar process of fecal pellet recycling may occur in the benthos, where the fecal pellets of benthic copepods are rich in internal and external bacteria (De Troch et al. 2010; Cnudde et al. 2013b) (Fig. 5.15) and can even be grazed by harpacticoids (De Troch et al. 2009; Møller et al. 2011). Some nematodes

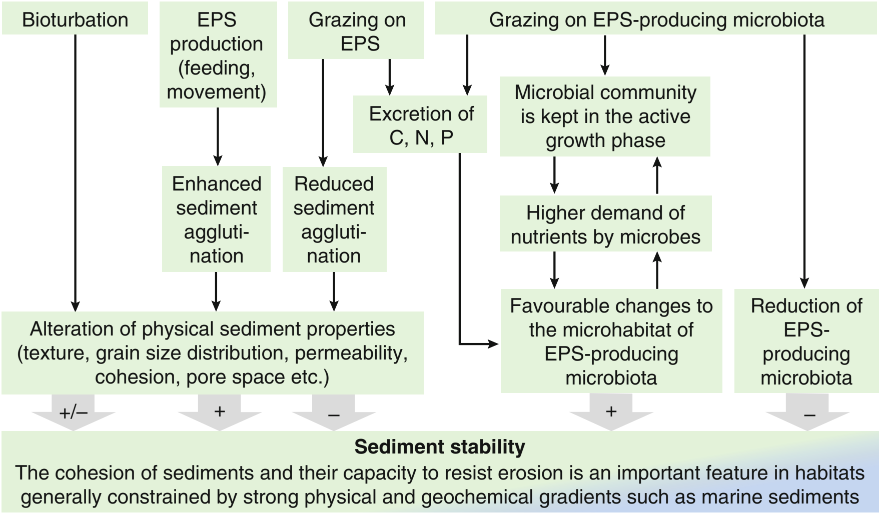

Fig. 5.14 Conceptual diagram recapitulating meiofauna-mediated effects on sediment stability. *EPS* extracellular polymeric substances, *C* carbon, *N* nitrogen, *P* phosphorous. Arrows are not indicative of effect size. '+' indicates stabilising effect, '−' indicates destabilising effect. From Schratzberger and Ingels (2018).

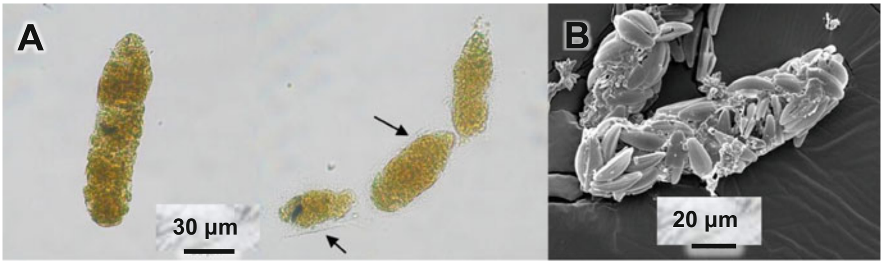

Fig. 5.15 Harpacticoid fecal pellets obtained after feeding diatoms to harpacticoids in the laboratory: (**a**) light microscopic image of fecal pellets from the harpacticoid *Paramphiascella fulvofasciata*, enclosed by a peritrophic membrane (arrows) (De Troch et al. 2009), and (**b**) SEM image of fecal pellets from *Platychelipus littoralis* (with permission, Cnudde 2014).

also produce fecal pellets, but these disintegrate more readily (Moens unpubl.). However, both copepod and nematode faeces may enrich the sediment in particulate and dissolved organic matter, and may thus affect microbial activity and community composition (Cnudde et al. 2013b).

4.3.4 Functional Diversity

Species composition and diversity play a crucial role in ecosystem functioning (e.g., Cardinale et al. 2012). Marine meiofauna can be very diverse at a local scale, and typically comprise multiple species from each trophic or functional group (see above). Theoretically, such ‘confunctional’ species might share the same function and hence be interchangeable or functionally redundant, but empirical evidence suggests only limited functional overlap (De Mesel et al. 2004, 2006; Dos Santos 2009; Gingold et al. 2013). Laboratory experiments at low species diversity indicate that species contribute idiosyncratically to ecosystem functioning as a consequence of intricate species interactions (see Sect. 5.1), but microcosm experiments with higher numbers of nematode species (up to 25) indicated that nematode species richness has a positive influence on microbial activity (Dos Santos 2009).

4.4 Functional Roles of Meiofauna in Mudflat Sediments: The Case of N Cycling

4.4.1 N Sources and Cycling

Faunal effects on solute fluxes, MPB biofilms and particle reworking in mudflats can significantly influence key ecosystem services. In macrotidal coastal areas, intertidal sediments can cover huge surface areas, and are sites of intense primary production and nutrient cycling. The discovery of denitrification under oxic conditions in intertidal sediments (Gao et al. 2010, 2012) underscores the importance of these zones in coastal N cycling and their buffering role (Burgin and Hamilton 2007; Gruber and Galloway 2008). Human activities have caused a sharp build-up of fixed nitrogen (N) in the environment (Leach et al. 2012), a substantial share of which enters coasts and estuaries, leading to a tenfold increase of coastal N levels over the past century (Galloway et al. 2004; Paerl 2006). This in turn can cause severe eutrophication (Rabalais et al. 2009), shifts in community composition and hypoxia (Conley et al. 2009). Coastal areas, however, also act as buffer zones (Burgin and Hamilton 2007; Gruber and Galloway 2008), as they are sites of intense N respiration processes such as denitrification, which may counter the increased N load (Galloway et al. 2004; Marchant et al. 2014). It has been estimated that denitrification in coastal shelf sediments accounts for up to 44% of total global denitrification (Seitzinger et al. 2006).

Nitrogen cycling in intertidal sediments is driven by a diverse assemblage of mostly heterotrophic microorganisms (Kjellin et al. 2007). Retention or removal of N from the sediment is mainly controlled by the rates of three processes: denitrification (DNF) and anaerobic ammonium oxidation (*anammox*, AMX) remove N from the sediment, whereas dissimilatory nitrate reduction to ammonium (DNRA) preserves reactive N in the system (Brandes et al. 2007). DNF is a NO_3^- reduction process whereby NO_3^- is reduced to the gaseous compounds nitrous oxide (N_2O) or dinitrogen (N_2), while AMX is the anaerobic oxidation of NH_4^+ to N_2 by reduction of NO_2^- (Herbert 1999). When DNRA processes exceed DNF, eutrophication is enhanced (Burgin and Hamilton 2007). In light-replete intertidal and adjacent shallow subtidal coastal sediments, the presence of phototrophic biofilms may impact N cycling through changes in oxygen levels and competition for nutrients (Porubsky et al. 2009).

4.4.2 Meiofaunal Modulation of N Cycling

In coastal food chains, benthic meiofauna not only provide key links between primary producers and higher trophic levels (Gee 1989; Coull 1990; Danovaro et al. 2007), but may also play an important role in N cycling. Bonaglia et al. (2014) found that an increase in meiofaunal abundance led to stimulation of DNF, and attributed this to meiofaunal bioturbation. Stock et al. (2014) observed that intertidal benthic copepods stimulate DNRA and negatively impact DNF, and suggested this is mediated by copepod excretion products. The observed differences may be caused by different contexts, but are most likely also due to the fact that meiofauna can affect the N cycle through different mechanisms. First, by analogy with macrofauna, bioturbation could enhance transport of nutrients and oxygen into the sediment and thus stimulate coupled nitrification-DNF (Bonaglia et al. 2014; Stock et al. 2014). Second, meiofauna excretion can potentially impact the N cycle. Copepod excretions contain high amounts of labile carbon (Frangoulis et al. 2005), which can stimulate DNRA over DNF and AMX (Bonaglia et al. 2014; Stock et al. 2014). Nematode excretions contain N mostly as NH_4^+ and dissolved organic N (Ferris et al. 1998), which may stimulate nitrifiers and denitrifiers (Bonaglia et al. 2014). In addition, as mentioned above, nematodes often leave mucus trails which can affect microbial community composition and biofilm formation (De Mesel et al. 2004; Moens et al. 2005b; Hubas et al. 2010). Third, meiofauna can also directly or indirectly impact the N cycle via grazing on bacteria and MPB, respectively. Meiofaunal grazing rates may on average amount to 1% of MPB and bacterial biomass per hour (Montagna 1995). Perhaps more importantly, nematodes can affect bacterial community composition even at low grazing pressure (De Mesel et al. 2004). Bacterivory may thus influence microbial community composition and may stimulate bacterial activity (De Mesel et al. 2003, 2004, 2006; Näslund et al. 2010). This in turn could also impact the N cycle.

5 Interactions Among Meiofauna and Among Meio- and Macrofauna

5.1 Competition, Facilitation and Inhibition Among Meiofauna

As mentioned previously (Sect. 4.3.4), laboratory experiments on the effects of bacterivorous nematodes on organic matter decomposition demonstrate that—at least at low species diversity—both species richness and species composition affect ecosystem functioning, but in a largely unpredictable way (De Mesel et al. 2006; De Meester et al. 2016). Such idiosyncratic diversity-ecosystem functioning relationships are largely a consequence of horizontal species interactions, including resource and interference competition *sensu lato*, and facilitation (Fig. 5.16). The rhabditid nematode *Litoditis marina*, for instance, facilitates population growth of Monhysteridae in microcosms where bacterial densities exceed optimal conditions for the Monhysteridae (Dos Santos et al. 2009). Many Rhabditidae are extreme colonizers which abound only under highly-enriched conditions (Bongers and Ferris 1999), characterised by explosive bacterial growth, whereas Monhysteridae enter somewhat later in the succession of decomposition-associated bacterivores. The rapid population growth rate and high per-capita grazing of *L. marina* suppress bacterial abudances in microcosms, thus creating conditions which are better suited for the Monhysteridae (Dos Santos et al. 2009). Facilitative interactions have also been observed among cryptic species of *L. marina* (this morphospecies is actually a complex of multiple cryptic species, local

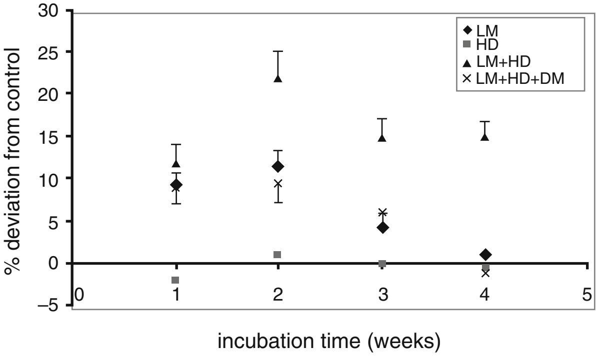

Fig. 5.16 Effects of single species and of combinations of species of bacterivorous nematodes on the decomposition rate of macroalgal (*Fucus vesiculosus*) detritus in a microcosm experiment, expressed as % deviation from a control treatment without nematodes. *LM Litoditis marina*, *HD Halomonhystera disjuncta*, *DM Diplolaimelloides meyli*. Treatments LM and HD contained a single nematode species, treatment LM + HD contained two, and treatment LM + HD + DM three nematode species. *Litoditis marina* has a generation time of 4 days and produces several hundred progeny per female. It also has high grazing rates on bacteria. However, its populations start to collapse after 2–3 weeks in microcosms. As a consequence, it already had a strong impact on decomposition rate after 1 week of incubation, an effect which decreased from the third week onwards. *Halomonhystera disjuncta* and *Diplolaimelloides meyli* are confamiliar species belonging to the Monhysteridae. Their generation times are 2.5–4.5 times longer than that of *L. marina*, and they produce *ca.* one-third the number of progeny of that species. However, they can maintain high population densities for several months in microcosms. *Halomonhystera disjuncta* did not reproduce in the monospecific treatment, but did reproduce at high rates in the presence of *L. marina*, as a consequence of facilitation by *L. marina*, and resulting in an additive effect on algal decomposition from the second week of incubation onwards. Addition of *D. meyli* eliminated the effect of *H. disjuncta* on decomposition, because both monhysterid species strongly competed with each other, resulting in very low monhysterid abundances in the three-species treatment. These results demonstrate intricate species interactions which very much depend on the exact combination of species used; they also show that such interaction effects can have significant repercussions for ecosystem functioning. Data from Moens and Quintelier (unpubl.).

co-existence of several cryptic species being the rule rather than the exception) (De Meester et al. 2015a, b).

Competitive interactions among meiofauna are probably the dominant meiofaunal relations. Resource competition among harpacticoid species has not been demonstrated directly, but evidence for resource and/or habitat partitioning among harpacticoid copepod species exists (Pace and Carman 1996; Guisande et al. 2002; De Troch et al. 2003, 2005; Evrard et al. 2012). Van den Berghe and Bergmans (1981) suggested that the differential exploitation of photoautotrophs and bacteria among some co-occurring *Tisbe* sibling species can drive coexistence. Moreover, interference competition among some species of harpacticoid copepods exists (see below).

Competitive interactions have been well-studied in the same cryptic species complex of *Litoditis marina* (De Meester et al. 2011, 2015a, b) and among Monhysteridae (De Mesel et al. 2006; Dos Santos et al. 2009; Dos Santos and Moens 2011). In the former, competitive loops or 'rock-paper-scissor' dynamics exist, where species A is competitively stronger than species B, species B can outcompete species C, and species C in turn is competitively superior to species A. Depending on the precise combination of species and on the presence of dispersal opportunities, this may lead to a competitively intransitive network where all species can co-exist in a kind of dynamic mosaic (De Meester et al. 2015a; De Meester 2016). In the absence of dispersal options, many combinations lead to the complete exclusion of one or more species (De Meester et al. 2011). In Monhysteridae, asymmetric competition is the rule rather than the exception. Competition for food and space cannot explain the observations of the microcosm experiments, hence the precise mechanism of competition remains unknown (De Mesel et al. 2006; Dos Santos et al. 2009; Dos Santos and Moens 2011). It is possible that monhysterid nematodes use allelopathy or some other type of inhibitory interactions with closely-related species.

Interference competition and facilitation have also been observed among burrowing species of tidal flat harpacticoid copepods. The tube structures generated by the abundant *Pseudostenhelia wellsi* facilitated colonization by two other species, yet inhibited that of a fourth species in the assemblage (Chandler and Fleeger 1987). The observed interactions and underlying mechanisms were highly species-specific, rendering generalizations about how one species will affect the colonization by others problematic. Such predictions would likely become even more problematic if priority effects were taken into account. Priority effects occur when a species obtains a competitive advantage from the timing of its arrival in a certain habitat patch; early-arriving species may even monopolize resources (De Meester et al. 2002). To our knowledge, priority effects have not been studied in meiofauna assemblages. Nonetheless, the order of arrivals in habitat patches is not a purely deterministic process, but is likely heavily affected by chance. Given the highly species-specific nature of interactions among meiofauna, and the stochasticity of dispersal and colonization processes, predictions about the species composition of meiofauna in novel habitat patches are bound to fail, yet certain more general predictions about the diversity and composition at higher taxonomic levels (from family upwards) may be possible (Gallucci et al. 2008).

5.2 Predation Among Meiofauna

Predation can shift competitive (dis)equilibria among meiofaunal species. Dos Santos and Moens (2011) demonstrated that the predacious nematode *Enoploides longispiculosus* stabilized coexistence between two mutually-competing congeneric Monhysteridae by preying on both, albeit with a preference for the competitively inferior species. Intuitively, one would then expect that the sum of competition by a dominant competitor, and of predation, would lead to the exclusion of the weaker competitor. However, when the preferred prey became rare, and because the predator selected only adults and larger juveniles, most of the predation was directed towards the dominant competitor, alleviating competitive pressure on the weaker competitor and resulting in more balanced abundances among the two competing Monhysteridae (Dos Santos and Moens 2011).

Predation is a very common interaction among meiofauna. Nematode communities typically comprise several predacious or omnivorous species. Particularly in the more sandy sediments, their proportional abundances may be high, and they may exert strong top-down control on both total abundances and community composition of their (mostly nematode) prey (Moens et al. 2000; Gallucci et al. 2005) (Fig. 5.17). The typically higher abundance of predacious nematodes in sandy sediments may reflect the greater difficulty of finding and catching prey invertebrates in muddy compared to sandy sediments (Gallucci et al. 2005) (Fig. 5.18).

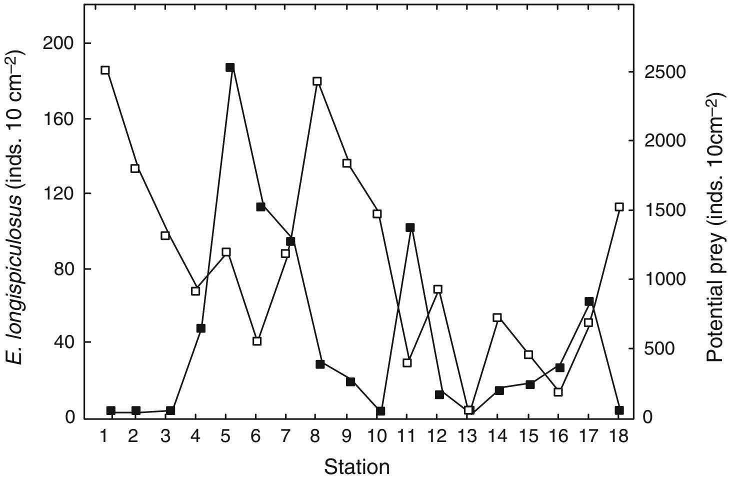

Fig. 5.17 Abundances of the predacious nematode *Enoploides longispiculosus* (closed symbols) and of other nematodes, which are potential prey for *E. longispiculosus* (open symbols) across 18 sampling stations at the Paulina intertidal flat in the Schelde Estuary, SW Netherlands. There was a inverse correlation (Pearson R $= -0.76$, $p < 0.001$) between both, suggesting that abundances of other nematodes may be top-down controlled by predatory species. New figure using data from Gallucci et al. (2005).

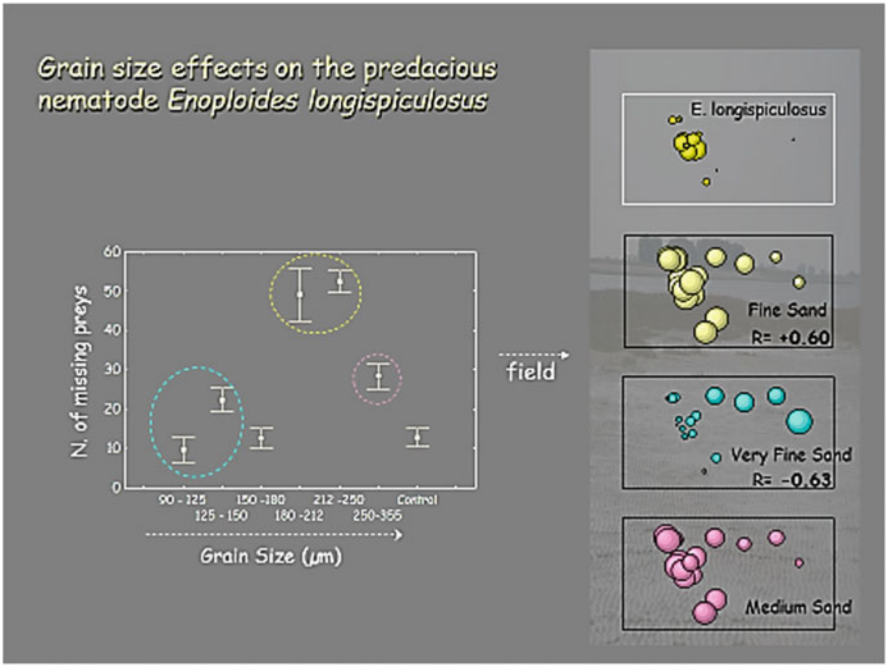

Fig. 5.18 Grain size effects on the abundance and predation rate of the predatory nematode *Enoploides longispiculosus*. Left panel: results of a predation experiment in closed microcosms (reported as number of missing prey individuals after a 24-h inoculation with *E. longispiculosus*), demonstrating highest predation rates in fine sandy sediments with grain sizes of 180–250 µm and near absence of predation in finer and coarser sediments. Right panel: bubble plots of *E. longispiculosus* abundance (top) and proportions of very fine, fine and medium sand, based on data of 18 sampling sites at the Paulina tidal flat in the Schelde Estuary, SW Netherlands. The abundance of *E. longispiculosus* is positively related to the fine sand fraction and negatively to the very find sand (and mud) fraction. New figure using data from Gallucci et al. (2005).

Other predacious meiofauna, such as turbellarians (Martens and Schockaert 1986), (some) tardigrades (Sanchez-Moreno et al. 2008) and harpacticoid copepods (Kennedy 1994; Seifried and Durbaum 2000), as well as Foraminifera (Dupuy et al. 2010), nematophagous fungi (Moens unpubl.) and predacious as well as deposit-feeding macrofauna (see below), may further add to such top-down controls. Predacious turbellarians and tardigrades also tend to be more abundant in sandier sediments (Martens and Schockaert 1986; Higgins and Thiel 1988), whereas predacious Foraminifera have hitherto mostly been documented from silty sediments (Dupuy et al. 2010).

Predation among meiofauna may not only have significant top-down effects on the abundances and composition of the local prey assemblages, it may also affect their vertical distribution patterns within the sediment (Steyaert et al. 2001; Maria et al. 2012, 2018). In medium sandy sediments in the Schelde Estuary (SW Netherlands), for instance, the predacious *Enoploides longispiculosus* is one of the dominant nematode species in the upper 2 cm (Steyaert et al. 2001; Gallucci et al. 2005). Over the course of a tidal cycle, this species migrates to the surface at high tide, and repositions itself about 1 cm deeper when exposed during low tide (Steyaert et al. 2001), perhaps avoiding the dessication of the surficial layer of these permeable sediments (Gallucci et al. 2005). Interestingly, some of its most abundant prey nematode species display an opposite vertical migration behaviour (Steyaert et al. 2001), allowing them to feed at the surface during low tide, where their preferred food source, i.e. epipelic diatoms, are then most abundant, while at the same time avoiding heavy predation pressure by *Enoploides* (Gallucci et al. 2005). It is plausible that such predator-prey interactions contribute in many ways to abundances and composition of meiofaunal assemblages, but such impacts are likely more prominent in the more sandy sediments (see also Maria et al. 2012).

It should be noted that a substantial proportion of meiofaunal-sized organisms are not actually meiofauna, but rather inactive stages of planktonic organisms (52% by number in a coastal lagoon of the North Adriatic). These organisms are collectively referred to as *inactive temporary meiobenthos* (Pati et al. 1999). They constitute an easily-accessed and potentially major food source; although assimilated by some benthic macrofauna (Karlson and Viitasalo-Frösen 2009), it is not yet known to what extent they are preyed upon by meiofauna. Similarly, settling larvae of a variety of macrobenthic species fall within the meiofauna size range, and can be preyed upon by permanent members of the meiofauna (Watzin 1985, see Sect. 5.3). It is clear that predation by, and on, meiofauna is common and quantitatively significant, yet its real importance as a structuring factor in benthic communities requires considerably more research effort.

PCR-based techniques may contribute to the elucidation of yet unknown or unquantified meiobenthic trophic relationships. Recent advances in the technique, using prey-taxon-specific primers, have allowed workers to identify species-level trophic relationships, despite the high predator-sequence ‘noise’ in the data. A combination of ecosystem-level diagnostic PCR, as well as next-generation sequencing (NGS) for detailed analyses of specific relations, offers a promising future for the investigation of meiofaunal trophic relationships (Maghsoud et al. 2014).

5.3 Macrofauna: Meiofauna Interactions

Through direct targeting, indiscriminate scavenging, or incidental uptake, mudflat meiofauna are potential prey to a variety of endo-, epi- and hyperbenthic macrofauna, from juvenile and adult fish, birds and crustaceans (e.g. Schratzberger and Warwick 1999; Carpentier et al. 2014), to predatory and deposit-feeding polychaetes and even suspension feeders that can intercept resuspended meiofauna from the water column (Coull 1999). Macrofauna can reduce the abundance of meiofauna through predation and disturbance (e.g. Hedqvist-Johnson and Andre 1991; Aarnio et al. 1998). It has been estimated that more than 75% of total metazoan meiofaunal production is transferred to higher trophic levels through macrofaunal predation on meiofauna (Danovaro et al. 2007).

Important though it may be, predation is but one of the mechanisms through which macrofauna can affect meiobenthic communities. Other interactions include competition (both resource and interference competition) and facilitation. Bioturbation and bio-irrigation by macrobenthos (Meysman et al. 2006; Schratzberger and Warwick 1999) alter the vertical distribution of organic matter (Graf 1989; Levin et al. 1997; Braeckman et al. 2011a) and the distribution and fluxes of oxygen and toxic metabolites in sediments (Kristensen and Kostka 2005). In addition to affecting direct transport of solids and solutes, these macrofaunal activities also stimulate biogeochemical processes along their burrow walls (Mermillod-Blondin et al. 2004), which may alter and/or stimulate the microbial community (Kristensen and Kostka 2005). Burrows, tubes (e.g., polychaete tubes) and other physical structures can provide shelter from predation (Zühlke et al. 1998), but macrofaunal activity such as bioturbation may also create interference competition (Austen and Widdicombe 1998; Schratzberger and Warwick 1999) as well as direct competition for shared food resources (Ólafsson et al. 1993; Braeckman et al. 2011a, b).

Despite these predation- and disturbance-related negative effects on meiofaunal populations and communities, macrofauna may also enhance meiofaunal abundance and diversity (Ólafsson et al. 1990; Austen et al. 1998). For example, in situations where macrobenthos activities affect food availability, meiofauna abundance and diversity may increase, and/or vertical distribution in the sediment may shift (Warwick et al. 1986; Austen and Widdicombe 1998; Austen et al. 1998; Dashfield et al. 2008; Braeckman et al. 2011a, b).

The outcome of macrofauna-meiofauna interactions on meiobenthic community structure and abundance is context-dependent. For example, macrofaunal impacts on meiobenthic communities are likely more prominent in sheltered muddy sediments than in exposed tidal flats with more permeable sandy sediments, where meiofauna may be more structured by hydrodynamic forces (Coull 1985, 1986; Warwick et al. 1997; Vanaverbeke et al. 2011). The very few studies that have investigated long-term dynamics of meiofaunal abundance, biomass and/or community composition, have concluded that the abundance of macrofauna (deposit-feeding macrobenthos in one study, fish feeding in the benthic boundary layer in another) was the principal driver of the between-year meiofaunal variation, particularly in muddy sediments (Coull 1985, 1986, Li et al. 1996; see Sect. 3.4.2).

Most of the meiofauna-macrofauna interactions considered to this point have been macrofauna-dominated, i.e. top-down, especially with respect to predation. It is all too easy to forget that the early life stages of benthic macrofauna are in the same size range as adult meiofauna, opening a myriad of additional possibilities for macrofauna-meiofauna interaction. The effect of sediment-dwelling meiofauna on co-occurring macrofaunal early life stages has been reported to be large enough to significantly structure the macrobenthic community (Watzin 1983). This is obviously an effect of major importance for our understanding of macrobenthic recruitment and community structure, but it has received only very limited attention (Watzin 1983, 1985) and is just another example of the unrecognized importance of meiofauna in the mudflat ecosystem, and in the marine ecosystem as a whole.

6 Conclusion: The Future of Mudflat Meiofauna Research

Given the little we know about mudflat meiobenthology, it is tempting to positively spin this knowledge chasm by saying that the future holds enormous research potential. Despite our feeble understanding of the basic biology and ecology of meiofauna, it is likely that such research will be prioritized toward 'hot' topics such as the effects of a warming, acidifying biosphere (Meadows et al. 2015; Zeppilli et al. 2015), which appear to affect muddy-sediment meiofauna communities more than those in sandier sediments (Ingels et al. 2018), and harpacticoid copepods in particular (Sarmento et al. 2017). As with all branches of ecology, the danger is in focusing too narrowly on 'problem-solving', rather than on basic understanding of the system, without which the most important problems cannot be solved in any event. On the other hand, we cannot wait until we have understood the system completely, because the pressing environmental problems will have all snowballed by then. Mudflat meiobenthology is definitely a discipline in which researchers have 'miles to go before [they] sleep' (Frost 1923).

References

Aarnio K, Bonsdorff E, Norkko A (1998) Role of *Halicryptus spinulosus* (Priapulida) in structuring meiofauna and settling macrofauna. Mar Ecol Prog Ser 163:145–153

Albuquerque EF, Pinto APB, Perez AQ, Veloso VG (2007) Spatial and temporal changes in interstitial meiofauna on a sandy ocean beach of South America. Braz J Oceanogr 55:121–131

Alkemade R, Wielemaker A, Hemminga MA (1992a) Stimulation of decomposition of *Spartina anglica* leaves by the bacterivorous marine nematode *Diplolaimelloides bruciei* (Monhysteridae). J Exp Mar Biol Ecol 159:267–278

Alkemade R, Wielemaker A, de Jong SA, Sandee AJJ (1992b) Experimental evidence for the role of bioturbation by the marine nematode *Diplolaimella dievengatensis* in stimulating the mineralization of *Spartina anglica* detritus. Mar Ecol Prog Ser 90:149–155

Aller RC, Aller JY (1992) Meiofauna and solute transport in marine muds. Limnol Oceanogr 37:1018–1033

Armonies W, Hellwig M (1986) Quantitative extraction of living meiofauna from marine and brackish muddy sediments. Mar Ecol Prog Ser 29:37–43

Armonies W, Reise K (2000) Faunal diversity across a sandy shore. Mar Ecol Prog Ser 196:49–57

Austen MC, Warwick RM (1995) Effects of manipulation of food-supply on estuarine meiobenthos. Hydrobiologia 311:175–184

Austen MC, Widdicombe S (1998) Experimental evidence of effects of the heart urchin *Brissopsis lyrifera* on associated subtidal meiobenthic nematode communities. J Exp Mar Biol Ecol 222:219–238

Austen MC, Warwick RM, Ryan KP (1993) *Astomonema southwardorum* sp. nov. a gutless nematode dominant in a methane seep area in the North Sea. J Mar Biol Assoc UK 73:627–634

Austen MC, Widdicombe S, Villano-Pitacco N (1998) Effects of biological disturbance on diversity and structure of meiobenthic nematode communities. Mar Ecol Prog Ser 174:233–246

Azovsky AI, Saburova MA, Chertoprud ES, Polikarpov IG (2005) Selective feeding of littoral harpacticoids on diatom algae: hungry gourmands? Mar Biol 148:327–337

Baermann G (1917) Eine einfache Methode zur Auffindung von *Ankylostomum*- (Nematoden)-Larven in Erdproben. Geneeskundig Laboratorium Feestbundel, Weltevreden Batavia, pp 41–47

Barnett BE (1980) A physico-chemical method for the extraction of marine and estuarine benthos from clays and resistant muds. J Mar Biol Assoc U K 60:255

Bayer C, Heindl NR, Rinke C, Lucker S, Ott JA, Bulgheresi S (2009) Molecular characterization of the symbionts associated with marine nematodes of the genus *Robbea*. Environ Microbiol Rep 1:136–144

Bedino JH (2003) Embalming chemistry: glutaraldehyde versus formaldehyde. Champ Expand Enc Mortu Pract 649:2614–2632

Beknazarova M, Millsteed S, Robertson G, Whiley H, Ross K (2017) Validation of DESS as a DNA preservation method for the detection of *Strongyloides* spp. in canine feces. Int J Environ Res Public Health 14:e624

Bernhard JM, Ostermann DR, Williams DS, Blanks JK (2006) Comparison of two methods to identify live benthic Foraminifera: a test between Rose Bengal and CellTracker Green with implications for stable isotope paleoreconstructions. Paleoceanography 21:1–8

Blanchard GF (1990) Overlapping microscale dispersion patterns of meiofauna and microphytobenthos. Mar Ecol Prog Ser 68:101–111

Boaden PJS, Platt HM (1971) Daily migration patterns in an intertidal meiobenthic community. Thalass Jugosl 7:1–12

Boeckner MJ, Sharma J, Proctor HC (2009) Revisiting the meiofauna paradox: dispersal and colonization of nematodes and other meiofaunal organisms in low- and high-energy environments. Hydrobiologia 624:91–106

Boldina I, Beninger PG, Le Coz M (2014) Effect of long-term mechanical perturbation on intertidal soft-bottom meiofunal community spatial structure. J Sea Res 85:85–91

Bonaglia S, Nascimento FJA, Bartoli M, Klawonn I, Bruchert V (2014) Meiofauna increases bacterial denitrification in marine sediments. Nat Commun 5:e5133

Bongers T, Ferris H (1999) Nematode community structure as a bioindicator in environmental monitoring. Trends Ecol Evol 14:224–228

Bouillon S, Connolly RM, Lee SY (2008) Organic matter exchange and cycling in mangrove ecosystems: recent insights from stable isotope studies. J Sea Res 59:44–58

Braeckman U, Provoost P, Moens T, Soetaert K, Middelburg JJ, Vincx M, Vanaverbeke J (2011a) Biological vs. physical mixing effects on benthic food web dynamics. PLoS One 6:e18078

Braeckman U, Van Colen C, Soetaert K, Vincx M, Vanaverbeke J (2011b) Contrasting macrobenthic activities differentially affect nematode density and diversity in a shallow subtidal marine sediment. Mar Ecol Prog Ser 422:179–191

Braeckman U, Vanaverbeke J, Vincx M, Van Oevelen D, Soetaert K (2013) Meiofauna metabolism in suboxic sediments: currently overestimated. PLoS One 8:e59289

Brandes JA, Devol AH, Deutsch C (2007) New developments in the marine nitrogen cycle. Chem Rev 107:577–589

Buffan-Dubau E, Carman KR (2000) Diel feeding behaviour of meiofauna and their relationships with microalgal resources. Limnol Oceanogr 45:381–395

Buffan-Dubau E, deWit R, Castel J (1996) Feeding selectivity of the harpacticoid copepod *Canuella perplexa* in benthic muddy environments demonstrated by HPLC analyses of chlorin and carotenoid pigments. Mar Ecol Prog Ser 137:71–82

Burgess B (2001) An improved protocol for separating meiofauna from sediments using colloidal silica sols. Mar Ecol Prog Ser 214:161–165

Burgin AJ, Hamilton SK (2007) Have we overemphasized the role of denitrification in aquatic ecosystems? A review of nitrate removal pathways. Front Ecol Environ 5:89–96

Callaway R (2006) Tube worms promote community change. Mar Ecol Prog Ser 308:49–60

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S (2012) Biodiversity loss and its impact on humanity. Nature 486:59–67

Carpentier A, Como S, Dupuy C, Lefrancois C, Feunteun E (2014) Feeding ecology of *Liza* spp. in a tidal flat: evidence of the importance of primary production (biofilm) and associated meiofauna. J Sea Res 92:86–91

Caulle C, Koho KA, Mojtahid M, Reichart GJ, Jorissen FJ (2014) Live (Rose Bengal stained) foraminiferal faunas from the northern Arabian Sea: faunal succession within and below the OMZ. Biogeosciences 11:1155–1175

Chandler GT, Fleeger JW (1987) Facilitative and inhibitory interactions among estuarine meiobenthic harpacticoid copepods. Ecology 68:1906–1919

Cleven EJ (1999) An improved method for taking cores in sandy sediments. Arch Hydrobiol 147:65–72

Cnudde C (2014) Trophic ecology of intertidal harpacticoid copepods, with emphasis on their interactions with bacteria. PhD thesis, Ghent University, 209 p

Cnudde C, Clavano CJS, Moens T, Willems A, De Troch M (2013a) Structural and functional patterns of active bacterial communities during aging of harpacticoid copepod fecal pellets. Aquat Microb Ecol 71:25–42

Cnudde C, Moens T, Hoste B, Willems A, De Troch M (2013b) Limited feeding on bacteria by two intertidal benthic copepod species as revealed by trophic biomarkers. Environ Microbiol Rep 5:301–309

Cnudde C, Moens T, Willems A, De Troch M (2013c) Substrate-dependent bacterivory by intertidal benthic copepods. Mar Biol 160:327–341

Cnudde C, Moens T, Werbrouck E, Lepoint G, Van Gansbeke D, De Troch M (2015) Trophodynamics of estuarine intertidal harpacticoid copepods based on stable isotope composition and fatty acid profiles. Mar Ecol Prog Ser 524:225–239

Commito JA, Tita G (2002) Differential dispersal rates in an intertidal meiofauna assemblage. J Exp Mar Biol Ecol 268:237–256

Conley DJ, Paerl HW, Howarth RW, Boesch DF, Seitzinger SP, Havens KE, Lancelot C, Likens GE (2009) Ecology controlling eutrophication: nitrogen and phosphorus. Science 323:1014–1015

Connell JH (1978) Diversity in tropical rain forests and coral reefs – high diversity of trees and corals is maintained only in a non-equilibrium state. Science 199:1302–1310

Couch CA (1988) A procedure for extracting large numbers of debris-free, living nematodes from muddy marine sediments. Trans Am Microsc Soc 107:96–100

Coull BC (1985) Long-term variability of estuarine meiobenthos: an 11 year study. Mar Ecol Prog Ser 24:205–218

Coull BC (1986) Long-term variability of meiobenthos: value, synopsis, hypothesis generation and predictive modelling. Hydrobiologia 142:271–279

Coull BC (1990) Are members of the meiofauna food for higher trophic levels? Trans Am Microsc Soc 109:233–246

Coull BC (1999) Role of meiofauna in estuarine soft-bottom habitats. Aust J Ecol 24:327–343

Coull BC, Chandler GT (1992) Pollution and meiofauna: field, laboratory, and mesocosm studies. Oceanogr Mar Biol Annu Rev 30:191–271

Creer S, Deiner K, Frey S, Porazinska D, Taberlet P, Thomas WK, Potter C, Bik HM (2016) The ecologist's field guide to sequence-based identification of biodiversity. Methods Ecol Evol 7:1008–1018

Cullen DJ (1973) Bioturbation of superficial marine sediments by interstitial meiobenthos. Nature 242:323–324

D'Hondt A-S, Stock W, Blommaert L, Moens T, Sabbe K (2018) Nematodes stimulate biomass accumulation in a multispecies diatom biofilm. Mar Environ Res. https://doi.org/10.1016/j.marenvres.2018.06.005

Dahms H-U, Qian P-Y (2006) Kin recognition during intraspecific predation by *Harpacticus* sp. (Copepoda: Harpacticoida). Zool Stud 45:395–403

Dahms H-U, Harder T, Qian P-Y (2007) Selective attraction and reproductive performance of a harpacticoid copepod in a response to biofilms. J Exp Mar Biol Ecol 341:228–238

Danovaro R, Scopa M, Gambi C, Fraschetti S (2007) Trophic importance of subtidal metazoan meiofauna: evidence from in situ exclusion experiments on soft and rocky substrates. Mar Biol 152:339–350

Dashfield SL, Somerfield PJ, Widdicombe S, Austen MC, Nimmo M (2008) Impacts of ocean acidification and burrowing urchins on within-sediment pH profiles and subtidal nematode communities. J Exp Mar Biol Ecol 365:46–52

de Jonge VN, Bouwman LA (1977) A simple density separation technique for quantitative isolation of meiobenthos using the colloidal silica Ludox-TM. Mar Biol 42:143–148

De Ley P, Mundo-Ocampo M (2004) The cultivation of nematodes. In: Chen ZX, Chen SY, Dickson DW (eds) Nematology: advances and perspectives, vol 1. Tsinghua University Press, Tsinghua, China, pp 541–619

De Meester N (2016) Unravelling coexistence of cryptic *Litoditis marina* species. PhD thesis, Ghent University, Belgium, 322 p

De Meester L, Gomez A, Okamura B, Schwenk K (2002) The monopolization hypothesis and the dispersal-gene flow paradox in aquatic organisms. Acta Oecol Intern J Ecol 23:121–135

De Meester N, Derycke S, Bonte D, Moens T (2011) Salinity effects on the coexistence of cryptic species: a case study on marine nematodes. Mar Biol 158:2717–2726

De Meester N, Derycke S, Rigaux A, Moens T (2015a) Active dispersal is differentially affected by inter- and intraspecific competition in closely related nematode species. Oikos 124:561–570

De Meester N, Dos Santos GAP, Rigaux A, Valdez Y, Derycke S, Moens T (2015b) Daily temperature fluctuations alter interactions between closely related species of marine nematodes. PLoS One 10:e0131625

De Meester N, Gingold R, Rigaux A, Derycke S, Moens T (2016) Cryptic diversity and ecosystem functioning: a complex tale of differential effects on decomposition. Oecologia 182:559–571

De Mesel I, Derycke S, Swings J, Vincx M, Moens T (2003) Influence of bacterivorous nematodes on the decomposition of cordgrass. J Exp Mar Biol Ecol 296:227–242

De Mesel I, Derycke S, Moens T, Van der Gucht K, Vincx M, Swings J (2004) Top-down impact of bacterivorous nematodes on the bacterial community structure: a microcosm study. Environ Microbiol 6:733–744

De Mesel I, Derycke S, Swings J, Vincx M, Moens T (2006) Role of nematodes in decomposition processes: does within-trophic group diversity matter? Mar Ecol Prog Ser 321:157–166

De Troch M, Fiers F, Vincx M (2003) Niche segregation and habitat specialisation of harpacticoid copepods in a tropical seagrass bed. Mar Biol 142:345–355

De Troch M, Steinarsdóttir MB, Chepurnov V, Ólafsson E (2005) Grazing on diatoms by harpacticoid copepods: species-specific density-dependent uptake and microbial gardening. Aquat Microb Ecol 39:135–144

De Troch M, Chepurnov V, Gheerardyn H, Vanreusel A, Olafsson E (2006) Is diatom size selection by harpacticoid copepods related to grazer body size? J Exp Mar Biol Ecol 332:1–11

De Troch M, Cnudde C, Vyverman W, Vanreusel A (2009) Increased production of faecal pellets by the benthic harpacticoid *Paramphiascella fulvofasciata*: importance of the food source. Mar Biol 156:469–477

De Troch M, Cnudde C, Willems A, Moens T, Vanreusel A (2010) Bacterial colonization on faecal pellets of harpacticoid copepods and on their diatom food. Microb Ecol 60:581–591

De Troch M, Vergaerde I, Cnudde C, Vanormelingen P, Vincx M (2012) The taste of diatoms: the role of diatom growth phase characteristics and associated bacteria for grazing by the harpacticoid copepod *Microarthridion littorale*. Aquat Microb Ecol 67:47–58

Decho AW, Fleeger JW (1988) Microscale dispersion of meiobenthic copepods in response to food-resource patchiness. J Exp Mar Biol Ecol 118:229–243

DePatra KD, Levin LA (1989) Evidence of the passive deposition of meiofauna into fiddler crab burrows. J Exp Mar Biol Ecol 125:173–192

Derycke S, De Meester N, Rigaux A, Creer S, Bik H, Thomas WK, Moens T (2016) Coexisting species of the *Litoditis marina* complex (Nematoda) show differential resource use and have distinct microbiomes with high intraspecific variability. Mol Ecol 25:2093–2110

Dos Santos GAP (2009) Top-down and bottom-up controls on populations and assemblages of marine nematodes, and their effects on benthic ecosystem functioning: an experimental approach. PhD thesis, Ghent University, Belgium, 252 p

Dos Santos GAP, Moens T (2011) Populations of two prey nematodes and their interaction are controlled by a predatory nematode. Mar Ecol Prog Ser 427:117–131

Dos Santos GAP, Derycke S, Fonsêca-Genevois VG, Coelho L, Correia MTS, Moens T (2009) Interactions among bacterial-feeding nematode species at different levels of food availability. Mar Biol 156:629–640

Du Y, Xu K, Lei Y (2009) Simultaneous enumeration of diatom, protozoa and meiobenthos from marine sediments using Ludox-QPS method. Chin J Oceanol Limnol 27:775–783

Dupuy C, Rossignol L, Geslin E, Pascal P-Y (2010) Predation of mudflat meio-macrofaunal metazoans by a calcareous foraminifer, *Ammonia tepida* (Cushman, 1926). J Foraminifer Res 40:305–312

Dye A (1983) Oxygen consumption by sediments in a southern African mangrove swamp. Estuar Coast Shelf Sci 17:473–478

Eskin RA, Coull BC (1987) Seasonal and three-year variability of meiobenthic nematode populations at two estuarine sites. Mar Ecol Prog Ser 41:295–303

Evrard V, Huettel M, Cook PLM, Soetaert K, Heip CHR, Middelburg JJ (2012) Importance of phytodetritus and microphytobenthos for heterotrophs in a shallow subtidal sandy sediment. Mar Ecol Prog Ser 455:13–31

Fan Q-H, France S, Green O, Gunawardana D, Ho W, Kumarasinghe L, et al (2016) Guide to delivering phytosanitary diagnostic services. International Plant Protection Convention, FAO

Fenchel T, Riedl RJ (1970) The sulfide system: a new biotic community underneath the oxidized layer of marine sand bottoms. Mar Biol 7:255–268

Ferris H, Venette RC, van der Meulen HR, Lau SS (1998) Nitrogen mineralization by bacterial-feeding nematodes: verification and measurement. Plant Soil 203:159–171

Findlay SEG (1981) Small-scale spatial distribution of meiofauna on a mud- and sandflat. Estuar Coast Shelf Sci 12:471–484

Findlay SEG (1982) Influence of sampling scale on apparent distribution of meiofauna on a sandflat. Estuaries 5:322–324

Findlay S, Tenore KR (1982) Effect of a free-living marine nematode (*Diplolaimella chitwoodi*) on detrital carbon mineralization. Mar Ecol Prog Ser 8:161–166

Folk RL, Andrews PB, Lewis DW (1970) Detrital sedimentary rock classification and nomenclature for use in New Zealand. NZ J Geol Geophys 13:937–968

Fonseca G, Gallucci F (2008) Direct evidence of predation in deep-sea nematodes: the case of *Pontonema* sp. Cah Biol Mar 49:295–297

Fonseca G, Muthumbi A, Vanreusel A (2007) Species richness of the genus *Molgolaimus* (Nematoda) from local to ocean scale along continental slopes. Mar Ecol 28:446–459

Fonseca VG, Sinniger F, Gaspar JM, Quince C, Creer S, Power DM, Peck LS, Clark MS (2017) Revealing higher than expected diversity in Antarctic sediments: a metabarcoding approach. Sci Rep 7:6094

Franco MA, Soetaert K, Costa MJ, Vincx M, Vanaverbeke J (2008) Uptake of phytodetritus by meiobenthos using C-13 labelled diatoms and *Phaeocystis* in two contrasting sediments from the North Sea. J Exp Mar Biol Ecol 362:1–8

Frangoulis C, Christou ED, Hecq JH (2005) Comparison of marine copepod outfluxes: nature, rate, fate and role in the carbon and nitrogen cycles. Adv Mar Biol 47:253–309

Frost R (1923) Stopping by woods on a snowy evening. In: Lathem EC (ed) The poetry of Robert Frost. Henry Holt, New York

Galloway JN, Dentener FJ, Capone DG, Boyer EW, Howarth RW, Seitzinger SP et al (2004) Nitrogen cycles: past, presence, and future. Biogeochemistry 70:153–226

Gallucci F, Steyaert M, Moens T (2005) Can field distributions of marine predacious nematodes be explained by sediment constraints on their foraging success? Mar Ecol Prog Ser 304:167–178

Gallucci F, Moens T, Vanreusel A, Fonseca G (2008) Active colonization of disturbed sediments by deep-sea nematodes: evidence for the patch mosaic model. Mar Ecol Prog Ser 367:173–183

Gao H, Schreiber F, Collins G, Jensen MM, Kostka JE, Lavik G et al (2010) Aerobic denitrification in permeable Wadden Sea sediments. ISME J 4:417–426

Gao H, Matyka M, Liu B, Khalili A, Kostka JE, Collins G et al (2012) Intensive and extensive nitrogen loss from intertidal permeable sediments of the Wadden Sea. Limnol Oceanogr 57:185–198

Garraffoni ARS, Alcantara FC, Checon HH (2017) Evaluating the anesthetization and fixation efficacy of "soft" and "hard" freshwater benthic meiofauna: what is the best method for specimen reservation? Limnology 18:209–218

Gaudes A, Muñoz I, Moens T (2013) Bottom-up effects on freshwater bacterivorous nematode populations: a microcosm approach. Hydrobiologia 707:159–172

Gee JM (1989) An ecological and economic review of meiofauna as food for fish. Zool J Linnean Soc 96:243–261

Gerlach SA (1978) Food-chain relationships in subtidal silty sand marine sediments and role of meiofauna in stimulating bacterial productivity. Oecologia 33:55–69

Gheskiere T, Hoste E, Vanaverbeke J, Vincx M, Degraer S (2004) Horizontal zonation patterns and feeding structure of marine nematode assemblages on a macrotidal, ultra-dissipative sandy beach (De Panne, Belgium). J Sea Res 52:221–226

Giere O (2009) Meiobenthology: the microscopic motile fauna of aquatic sediments, 2nd edn. Springer, Berlin, 527 p

Gingold R, Mundo-Ocampo M, Holovachov O, Rocha-Olivares A (2010) The role of habitat heterogeneity in structuring the community of intertidal free-living marine nematodes. Mar Biol 157:1741–1753

Gingold R, Moens T, Rocha Olivares A (2013) Assessing the response of nematode communities to climate change driven warming: a microcosm experiment. PLoS One 8:e66653

Gourbault N, Warwick RM, Hellequet M-N (1998) Spatial and temporal variability in the composition and structure of meiobenthic assemblages (especially nematodes) in tropical beaches (Guadeloupe, FWI). Cah Biol Mar 39:29–39

Graf G (1989) Benthic pelagic coupling in a deep-sea benthic community. Nature 341:437–439

Gray JS (1981) The ecology of marine sediments. An introduction to the structure and function of benthic communities. Cambridge studies in modern biology, vol 2. Cambridge University Press, Cambridge, 185 p

Gray NF (1984) Ecology of nematophagous fungi: comparison of the soil sprinkling method with the Baermann funnel technique in the isolation of endoparasites. Soil Biol Biochem 16:81–83

Grego M, Stachowitsch M, De Troch M, Riede B (2013) CellTracker Green labelling vs. rose bengal staining: CTG wins by points in distinguishing living from dead anoxia-impacted copepods and nematodes. Biogeosciences 10:4565–4575

Grime JP (1973) Competitive exclusion in herbaceous vegetation. Nature 242:344–347

Gruber N, Galloway JN (2008) An Earth-system perspective of the global nitrogen cycle. Nature 451:293–296

Guarini JM, Blanchard GF, Gros P, Harrison SJ (1997) Modelling the mud surface temperature on intertidal flats to investigate the spatio-temporal dynamics of the benthic microalgal photosynthetic capacity. Mar Ecol Prog Ser 153:25–36

Guarini JM, Blanchard GF, Bacher C, Gros P, Riera P, Richard P et al (1998) Dynamics of spatial patterns of microphytobenthic biomass: inferences from a geostatistical analysis of two comprehensive surveys in Marennes-Oléron Bay (France). Mar Ecol Prog Ser 166:131–141

Guisande C, Maneiro I, Riveiro I, Barreiro A, Pazos Y (2002) Estimation of copepod trophic niche in the field using amino acids and marker pigments. Mar Ecol Prog Ser 239:147–156

Hamels I, Moens T, Muylaert K, Vyverman W (2001) Trophic interactions between ciliates and nematodes from an intertidal flat. Aquat Microb Ecol 26:61–72

Harris RP (1972a) The distribution and ecology of the interstitial meiofauna of a sandy beach at Whitsand Bay, East Cornwall. J Mar Biol Assoc UK 52:1–18

Harris RP (1972b) Seasonal changes in population density and vertical distribution of harpacticoid copepods on an intertidal sand beach. J Mar Biol Assoc UK 52:493–505

Hedqvist-Johnson K, Andre C (1991) The impact of the brown shrimp *Crangon crangon* L on soft-bottom meiofauna – An experimental approach. Ophelia 34:41–49

Heiner I, Neuhaus B (2007) Loricifera from the deep sea at the Galapagos Spreading Center, with a description of *Spinoloricus turbatio* gen. et sp. nov. (Nanaloricidae). Helgol Mar Res 61:167–182

Heip C, Smol N, Hautekiet W (1974) Rapid method of extracting meiobenthic nematodes and copepods from mud and detritus. Mar Biol 28:79–81

Heip C, Vincx M, Vranken G (1985) The ecology of marine nematodes. Oceanogr Mar Biol Annu Rev 23:399–489

Herbert RA (1999) Nitrogen cycling in coastal marine sediments. FEMS Microbiol Rev 23:563–590

Herman PMJ, Middelburg JJ, Heip CHR (2001) Benthic community structure and sediment processes on an intertidal flat: results from ECOFLAT project. Cont Shelf Res 21:2055–2071

Hicks GRF, Coull BC (1983) The ecology of marine meiobenthic harpacticoid copepods. Oceanogr Mar Biol 21:67–175

Higgins RP, Thiel H (1988) Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, DC

Hubas C, Sachidhanandam C, Rybarczyk H, Lubarsky HV, Rigaux A, Moens T, Paterson DM (2010) Bacterivorous nematodes stimulate microbial growth and exopolymer production in marine sediment microcosms. Mar Ecol Prog Ser 419:85–94

Hulings NC, Gray JS (1971) A manual for the study of meiofauna. Smithsonian contributions to zoology, vol 78. Smithsonian Institution Press, Washington, DC

Ingels J, dos Santos G, Hicks A, Valdes Vazquez Y, Neres PF, Pontes LP et al (2018) Short-term CO_2 exposure and temperature rise effects on metazoan meiofauna and free-living nematodes in sandy and muddy sediments: results from a flume experiment. J Exp Mar Biol Ecol 502:211–226

Jacobsen TR, Azam F (1984) Role of bacteria in copepod fecal pellet decomposition: colonization, growth rates and mineralization. Bull Mar Sci 35:495–502

Jansson BO (1968) Quantitative and experimental studies of the interstitial fauna in four Swedish sandy beaches. Ophelia 5:1–71

Jensen P (1982) Diatom-feeding behaviour of the free-living marine nematode *Chromadorita tenuis*. Nematologica 28:71–76

Jensen P (1986) Nematode fauna in the sulphide-rich brine seep and adjacent bottoms of the East Flower Garden, NW Gulf of Mexico. IV. Ecological aspects. Mar Biol 92:489–503

Joint IR, Gee JM, Warwick RM (1982) Determination of fine-scale vertical distribution of microbes and meiofauna in an intertidal sediment. Mar Biol 72:157–164

Juario JV (1975) Nematode species composition and seasonal fluctuation of a sublittoral meiofauna community in the German Bight. Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven 15:283–337

Kaiser MJ, Attrill MJ, Jennings S, Thomas DN, Barnes DKA (2011) Marine ecology: processes, systems, and impacts, 2nd edn. Oxford University Press, Oxford

Karlson AML, Viitasalo-Frösen S (2009) Assimilation of C-14-labelled zooplankton benthic eggs by macrobenthos. J Plankton Res 31:459–463

Kendall MA, Davey JT, Widdicombe S (1995) The response of two estuarine benthic communities to the quantity and quality of food. Hydrobiologia 311:207–214

Kennedy AD (1994) Predation within meiofaunal communities – Description and results of a rapid-freezing method of investigation. Mar Ecol Prog Ser 114:71–79

Kjellin J, Hallin S, Wörman A (2007) Spatial variations in denitrification activity in wetland sediments explained by hydrology and denitrifying community structure. Water Res 41:4710–4720

Kristensen E, Kostka JE (2005) Macrofaunal burrows and irrigation in marine sediment: microbiological and biogeochemical interactions. In: Kristensen E, Haese RR, Kostka JE (eds) Interactions between macro- and microorganisms in marine sediments. Coastal and estuarine studies, vol 60. American Geophysical Union, New York, pp 125–157

Kuipers BR, de Wilde PAWJ, Creutzberg F (1981) Energy flow in a tidal flat ecosystem. Mar Ecol Prog Ser 5:215–221

Lampadariou N, Ingels J, Schratzberger M, Thistle D (2018) “Meiofauna research approaching 2020: knowledge gaps and new avenues”, an introduction to the special meiofauna issue resulting from I₆IMCo, the 16th International Meiofauna Conference. J Exp Mar Biol Ecol 502:1–3

Leach AM, Galloway J, Bleeker A, Kitzes J (2012) A nitrogen footprint model to help consumers understand their role in nitrogen losses to the environment. Environ Dev 1:40–66

Leduc D, Probert PK (2009) The effect of bacterivorous nematodes on detritus incorporation by macrofaunal detritivores: a study using stable isotope and fatty acid analyses. J Exp Mar Biol Ecol 371:130–139

Leduc D, Probert P, Nodder S (2010) Influence of mesh size and core penetration on estimates of deep-sea nematode abundance, biomass, and diversity. Deep Sea Res I 57:1354–1362

Lee JJ, Tietjen JH, Mastropaolo C, Rubin H (1977) Food quality and the heterogeneous spatial distribution of meiofauna. Helgoländer Meeresun 30:272–282

Lehman PS, Reid JW (1992) *Phyllognathopus viguieri* (Crustacea: Harpacticoida), a predaceous copepod of phytoparasitic, entomopathogenic, and free-living nematodes. Proc Soil Crop Sci Soc FL 52:78–82

Levin L, Blair N, DeMaster D, Plaia G, Fornes W, Martin C, Thomas C (1997) Rapid subduction of organic matter by maldanid polychaetes on the North Carolina slope. J Mar Res 55:595–611

Li J, Vincx M, Herman PMJ (1996) A model of nematode dynamics in the Westerschelde estuary. Ecol Model 90:271–284

Liu X-S, Xu W-Z, Cheung SG, Shin PK (2008) Subtropical meiobenthic nematode communities in Victoria Harbour, Hong Kong. Mar Pollut Bull 56:1491–1497

Löhr SC, Kennedy MJ (2015) Micro-trace fossils reveal pervasive reworking of Pliocene sapropels by low-oxygen-adapted benthic meiofauna. Nat Commun:6. https://doi.org/10.1038/ncomms7589

Lucas CH, Widdows J, Brinsley MD, Salkeld PN, Herman PMJ (2000) Benthic-pelagic exchange of microalgae at a tidal flat. 1. Pigment analysis. Mar Ecol Prog Ser 196:59–73

Maghsoud H, Weiss A, Smith JPS, Litvaitis MK, Fegley SR (2014) Diagnostic PCR can be used to illuminate meiofaunal diets and trophic relationships. Invertebr Biol 133:121–127

Mangubhai S, Greenwood JG (2004) A simple practical method for bulk and rapid extraction of free-living nematodes from marine and estuarine sediments. Hydrobiologia 522:343–347

Marchant HK, Lavik G, Holtappels M, Kuypers MMM (2014) The fate of nitrate in intertidal permeable sediments. PLoS One 9:e104517

Maria TF, De Troch M, Vanaverbeke J, Esteves AM, Vanreusel A (2011) Use of benthic vs planktonic organic matter by sandy-beach organisms: a food tracing experiment with C-13 labelled diatoms. J Exp Mar Biol Ecol 407:309–314

Maria TF, Vanaverbeke J, Esteves AM, De Troch M, Vanreusel A (2012) The importance of biological interactions for the vertical distribution of nematodes in a temperate ultra-dissipative sandy beach. Estuar Coast Shelf Sci 97:114–126

Maria TF, Paiva P, Vanreusel A, Esteves AM (2013a) The relationship between sandy beach nematodes and environmental characteristics in two Brazilian sandy beaches (Guanabara Bay, Rio de Janeiro). An Acad Bras Cienc 85:257–270

Maria TF, Vanaverbeke J, Gingold R, Esteves AM, Vanreusel A (2013b) Tidal exposure or microhabitats: what determines sandy-beach nematode zonation? A case study of a macrotidal ridge-and-runnel sandy beach in Belgium. Mar Ecol 34:207–217

Maria TF, Silva MG, Souza TP, Vanaverbeke J, Vanreusel A, Esteves AM (2018) Is the vertical distribution of meiofauna similar in two contrasting microhabitats? A case study of a macrotidal sandy beach. J Exp Mar Biol Ecol 502:39–51

Martens PM, Schockaert ER (1986) The importance of turbellarians in the marine meiobenthos – A review. Hydrobiologia 132:295–303

Materatski P, Moens T, Vafeiadou A-M, Ribeiro R, Adão H (2015) A comparative analysis of benthic nematode assemblages before habitat loss and during the early recovery of *Zostera noltii* seagrass beds. Estuar Coast Shelf Sci 167:256–268

McIntyre A, Murison D (1973) The meiofauna of a flatfish nursery ground. J Mar Biol Assoc U K 53:93–118

McLachlan A, Erasmus T, Furstenberg JP (1977) Migration of sandy beach meiofauna. Afr Zool 12:257–277

Meadows AS, Ingels J, Widdicombe S, Hale R, Rundle SD (2015) Effects of elevated CO_2 and temperature on an intertidal meiobenthic community. J Exp Mar Biol Ecol 469:44–56

Mermillod-Blondin F, Rosenberg R, Francois-Carcaillet F, Norling K, Mauclaire L (2004) Influence of bioturbation by three benthic infaunal species on microbial communities and biogeochemical processes in marine sediment. Aquat Microb Ecol 36:271–284

Meysman FJR, Middelburg JJ, Heip CHR (2006) Bioturbation: a fresh look at Darwin's last idea. Trends Ecol Evol 21:688–695

Middelburg JJ, Barranguet C, Boschker HTS, Herman PMJ, Moens T, Heip CHR (2000) The fate of intertidal microphytobenthos carbon: an *in situ* ^{13}C labelling study. Limnol Oceanogr 45:1224–1234

Moens T, Vincx M (1997) Observations on the feeding ecology of estuarine nematodes. J Mar Biol Assoc U K 77:211–227

Moens T, Van Gansbeke D, Vincx M (1999a) Linking estuarine nematodes to their suspected food. A case study from the Westerschelde Estuary (south-west Netherlands). J Mar Biol Assoc UK 79:1017–1027

Moens T, Verbeeck L, de Maeyer A, Swings J, Vincx M (1999b) Selective attraction of marine bacterivorous nematodes to their bacterial food. Mar Ecol Prog Ser 176:165–178

Moens T, Verbeeck L, Vincx M (1999c) Feeding biology of a predatory and a facultatively predatory nematode (*Enoploides longispiculosus* and *Adoncholaimus fuscus*). Mar Biol 134:585–593

Moens T, Herman PMJ, Verbeeck L, Steyaert M, Vincx M (2000) Predation rates and prey selectivity in two predacious estuarine nematodes. Mar Ecol Prog Ser 205:185–193

Moens T, Luyten C, Middelburg JJ, Herman PMJ, Vincx M (2002) Tracing organic matter sources of estuarine tidal flat nematodes with stable carbon isotopes. Mar Ecol Prog Ser 234:127–137

Moens T, Yeates GW, De Ley P (2004) Use of carbon and energy sources by nematodes. Nematol Monogr Perspect 2:529–545

Moens T, Bouillon S, Gallucci F (2005a) Dual stable isotope abundances unravel trophic position of estuarine nematodes. J Mar Biol Assoc UK 85:1401–1407

Moens T, Dos Santos GAP, Thompson F, Swings J, Fonsêca-Genevois V, Vincx M et al (2005b) Do nematode mucus secretions affect bacterial growth? Aquat Microb Ecol 40:77–83

Moens T, Bergtold M, Traunspurger W (2006) Chapter 6. Feeding ecology of free-living benthic nematodes. In: Eyualem A, Andrássy I, Traunspurger W (eds) Freshwater nematodes: ecology and taxonomy. CAB International Publishing, Cambridge, pp 105–131

Moens T, Moodley L, Steyaert M, Van Colen C, Van Oevelen D, Boschker HT S, et al (2011) The structure and functional roles of tidal flat meiobenthos. In: Heip C, Laane R (eds) Aspects of coastal research in contribution to LOICZ in The Netherlands and Flanders (2002-2010). LOICZ Research and Studies, vol 38, pp 171–184

Moens T, Braeckman U, Derycke S, Fonseca G, Gallucci F, Gingold R, Guilini K, Ingels J, Leduc D, Vanaverbeke J, Van Colen C, Vanreusel A, Vincx M (2013) Ecology of free-living marine nematodes. In: Schmidt-Rhaesa A (ed) Handbook of zoology. Gastrotricha, cycloneuralia and gnathifera, vol 2. Nematoda. De Gruyter, Berlin, pp 109–152

Moens T, Vafeiadou AM, De Geyter E, Vanormelingen P, Sabbe K, De Troch M (2014) Diatom feeding across trophic guilds in tidal flat nematodes, and the importance of diatom cell size. J Sea Res 92:125–133

Møller EF, Borg CMA, Jónasdóttir SH, Satapoomin S, Jaspers C, Nielsen TG (2011) Production and fate of copepod fecal pellets across the Southern Indian Ocean. Mar Biol 158:677–688

Montagna PA (1995) Rates of metazoan meiofaunal microbivory: a review. Vie et Milieu 45:1–9

Montagna PA, Yoon WB (1991) The effect of freshwater inflow on meiofaunal consumption of sediment bacteria and microphytobenthos in San Antonio Bay, Texas, U.S.A. Estuar Coast Shelf Sci 33:529–547

Montagna PA, Coull BC, Herring TL, Dudley BW (1983) The relationship between abundances of meiofauna and their suspected microbial food (diatoms and bacteria). Estuar Coast Shelf Sci 17:381–394

Montagna PA, Baguley JG, Hsiang C-Y, Reuscher MG (2017) Comparison of sampling methods for deep-sea infauna. Limnol Oceanogr Methods 15:166–183

Montagnes DJS, Lynn DH (1993) A quantitative protargol stain (QPS) for ciliates and other protists. In: Kemp PF, Sherr BF, Sherr EB, Cole JJ (eds) Handbook of methods in aquatic microbial ecology. Lewis Publishers, Boca Raton, FL, pp 229–240

Moreno M, Ferrero TJ, Gallizia I, Vezzulli L, Albertelli G, Fabiano M (2008a) An assessment of the spatial heterogeneity of environmental disturbance within an enclosed harbour through the analysis of meiofauna and nematode assemblages. Estuar Coast Shelf Sci 77:565–576

Moreno M, Vezzulli L, Marin V, Laconi P, Albertelli G, Fabiano M (2008b) The use of meiofauna diversity as an indicator of pollution in harbours. J Mar Sci 65:1428–1435

Mostajir B, Amblard C, Buffan-Dubau E, De Wit R, Lensi R, Simé-Ngando T (2011) Chapter 13. Microbial food webs in aquatic and terrestrial ecosystems. In: Bertrand J-C, Caumette P, Lebaron P, Matheron R, Normand P, Simé-Ngando T (eds) Environmental microbiology: fundamentals and applications. Springer, pp 485–509

Murphy RJ, Tolhurst TJ, Chapman MG, Underwood AJ (2008) Spatial variation of chlorophyll on estuarine mudflats determined by field-based remote sensing. Mar Ecol Prog Ser 365:45–55

Murray JW, Bowser SS (2000) Mortality, protoplasm decay rate, and reliability of staining techniques to recognize ‘living’ foraminifera: a review. J Foraminifer Res 30:66–70

Musat N, Giere O, Gieseke A, Thiermann F, Amann R, Dubilier N (2007) Molecular and morphological characterization of the association between bacterial endosymbionts and the marine nematode *Astomonema* sp. from the Bahamas. Environ Microbiol 9:1345–1353

Nascimento FJA, Naslund J, Elmgren R (2012) Meiofauna enhances organic matter mineralization in soft sediment ecosystems. Limnol Oceanogr 57:338–346

Näslund J, Nascimento FJ, Gunnarsson JS (2010) Meiofauna reduces bacterial mineralization of naphthalene in marine sediment. ISME J 4:1421–1430

Nehring S (1991) Der Röhrenbau: eine neuentdeckte, erfolgreiche Lebensweise bei den Nematoden. Mikokosmos 80:134–138

Nehring S, Jensen P, Lorenzen S (1990) Tube-dwelling nematodes: tube construction and possible ecological effects on sediment-water interfaces. Mar Ecol Prog Ser 64:123–128

Nicholas WL (2001) Seasonal variations in nematode assemblages on an Australian temperate ocean beach: the effect of heavy seas and unusually high tides. Hydrobiologia 464:17–26

Nicholas W, Hodda M (1999) The free-living nematodes of a temperate, high energy, sandy beach: faunal composition and variation over space and time. Hydrobiologia 394:113–127

Noodt W (1971) Ecology of the copepoda. In: Hulings NC (ed) Proceedings of the first international conference on Meiofauna, Tunis, 1969. Smithsonian contributions to zoology, vol 76, pp 97–102

Ólafsson E, Elmgren R (1991) Effects of biological disturbance by benthic amphipods Monoporeia affinis on meiobenthic community structure: a laboratory approach. Mar Ecol Prog Ser 74:99–107

Ólafsson E, Elmgren R (1997) Seasonal dynamics of sublittoral meiobenthos in relation to seasonality in a coastal marine ecosystem. Oecologia 67:157–168

Ólafsson E, Moore GC, Bett BJ (1990) The impact of *Melinna palmata* Grube, a tube-building polychaete, on meiofaunal community structure in a soft-bottom subtidal habitat. Estuar Coast Shelf Sci 31:883–893

Ólafsson E, Elmgren R, Papakosta O (1993) Effects of the deposit-feeding benthic bivalve *Macoma balthica* on meiobenthos. Oecologia 93:457–462

Olesen M, Strake S, Andrushaitis A (2005) Egestion of non-pellet-bound fecal material from the copepod *Acartia tonsa*: implication for vertical flux and degradation. Mar Ecol Prog Ser 293:131–142

Ott JA, Schiemer F (1973) Respiration and anaerobiosis of free living nematodes from marine and limnic sediments. Neth J Sea Res 7:233–243

Pace MC, Carman KR (1996) Interspecific differences among meiobenthic copepods in the use of microalgal food resources. Mar Ecol Prog Ser 143:77–86

Paerl HW (2006) Assessing and managing nutrient-enhanced eutrophication in estuarine and coastal waters: interactive effects of human and climatic perturbations. Ecol Eng 26:40–54

Paranhos R, Mayr LM (1993) Seasonal patterns of temperature and salinity in Guanabara Bay, Brazil. Fresenius Environ Bull 2:647–652

Pati AC, Belmonte G, Ceccherelli VU, Boero F (1999) The inactive temporary component: an unexplored fraction of meiobenthos. Mar Biol 134:419–427

Pfannkuche O, Thiel H (1988) Chapter 9. Sample processing. In: Higgins RP, Thiel H (eds) Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, DC, pp 134–145

Pinckney J, Sandulli R (1990) Spatial autocorrelation analysis of meiofaunal and microalgal populations on an intertidal sandflat – Scale linkage between consumers and resources. Estuar Coast Shelf Sci 30:341–353

Pinckney JL, Carman KR, Lumsden SE, Hymel SN (2003) Microalgal-meiofaunal trophic relationships in muddy intertidal estuarine sediments. Aquat Microb Ecol 31:99–108

Polz MF, Ott JA, Bright M, Cavanaugh CM (2000) When bacteria hitch a ride. ASM News 66:531–539

Porubsky WP, Weston NB, Joye SB (2009) Benthic metabolism and the fate of dissolved inorganic nitrogen in intertidal sediments. Estuar Coast Shelf Sci 83:392–402

Rabalais NN, Turner RE, Díaz RJ, Justic D (2009) Global change and eutrophication of coastal waters. ICES J Mar Sci 66:1528–1537

Reise K (1981) High abundance of small zoobenthos around biogenic structures in tidal sediments of the Wadden Sea. Helgoländer Meeresun 34:413–425

Reise K (2002) Sediment mediated species interactions in coastal waters. J Sea Res 48:127–141

Reiss J, Schmid-Araya JM (2011) Feeding response of a benthic copepod to ciliate prey type, prey concentration and habitat complexity. Freshw Biol 56:1519–1530

Remane A (1934) Die Brackwasserfauna. Verhandlungen der Deutschen Zoologischen Gesellschaft, Greifswald, pp 34–74

Renaud-Debyser J (1963) Recherches écologiques sur la faune interstitielle des sables. Bassin d'Arcachon, île de Bimini, Bahamas. Vie et Milieu, Suppl 15:1–157

Riemann F, Helmke E (2002) Symbiotic relations of sediment-agglutinating nematodes and bacteria in detrital habitats: the enzyme-sharing concept. Mar Ecol 23:93–113

Riemann F, Schrage M (1978) The mucus-trap hypothesis on feeding of aquatic nematodes and implications for biodegradation and sediment texture. Oecologia 34:75–88

Rieper M (1982) Feeding preferences of marine harpacticoid copepods for various species of bacteria. Mar Ecol Prog Ser 7:303–307

Rieper M (1985) Some lower food web organisms in the nutrition of marine harpacticoid copepods: an experimental study. Helgoländer Meeresun 39:357–366

Riera R, Monterroso O, Rodríguez M, Ramos E, Sacramento A (2011) Six-year study of meiofaunal dynamics in fish farms in Tenerife (Canary Islands, NE Atlantic Ocean). Aquat Ecol 45:221–229

Rohal M, Thistle D, Easton Erin E (2018) Extraction of metazoan meiofauna from muddy deep-sea samples: operator and taxon effects on efficiency. J Exp Mar Biol Ecol 502:105–110

Rysgaard S, Christensen PB, Sørensen MV, Funch P, Berg P (2000) Marine meiofauna, carbon and nitrogen mineralization in sandy and soft sediments of Disko Bay, West Greenland. Aquat Microb Ecol 21:59–71

Rzeznik-Orignac J, Fichet D, Boucher G (2003) Spatio-temporal structure of the nematode assemblages of the Brouage mudflat (Marennes-Oleron, France). Estuar Coast Shelf Sci 58:77–88

Rzeznik-Orignac J, Fichet D, Boucher G (2004) Extracting massive numbers of nematodes from muddy marine deposits: efficiency and selectivity. Nematology 6:605–616

Rzeznik-Orignac J, Boucher G, Fichet D, Richard P (2008) Stable isotope analysis of food source and trophic position of intertidal nematodes and copepods. Mar Ecol Prog Ser 359:145–150

Sahraean N, Moens T (2018) Year-to-year variability in beach nematode assemblage structure and biodiversity along the northern coast of the Strait of Hormuz, Persian Gulf (submitted)

Sahraean N, Campinas Bezerra T, Ejlali Khanaghah K, Mosallanejad H, Van Ranst E, Moens T (2017) Effects of pollution on nematode assemblage structure and diversity on beaches of the Northern Persian Gulf. Hydrobiologia 799:349–369

Sanchez-Moreno S, Ferris H, Guil N (2008) Role of tardigrades in the suppressive service of a soil food web. Agric Ecosyst Environ 124:187–192

Sandulli R, Pinckney J (1999) Patch sizes and spatial patterns of meiobenthic copepods and benthic microalgae in sandy sediments: a microscale approach. J Sea Res 41:179–187

Sarmento VC, Santos PJP, Hale R, Ingels J, Widdicombe S (2017) Effects of elevated CO_2 and temperature on an intertidal harpacticoid copepod community. ICES J Mar Sci 74:1159–1169

Schiemer F, Novak R, Ott J (1990) Metabolic studies on thiobiotic free-living nematodes and their symbiotic microorganisms. Mar Biol 106:129–137

Schratzberger M, Ingels J (2018) Meiofauna matters: the roles of meiofauna in benthic ecosystems. J Exp Mar Biol Ecol 502:12–25

Schratzberger M, Warwick RM (1999) Impact of predation and sediment disturbance by *Carcinus maenas* (L.) on free-living nematode community structure. J Exp Mar Biol Ecol 235:255–271

Schratzberger M, Gee JM, Rees HL, Boyd SE, Wall CM (2000) The structure and taxonomic composition of sublittoral meiofauna assemblages as an indicator of the status of marine environments. J Mar Biol Assoc UK 80:969–980

Schratzberger M, Lampadariou N, Somerfield PJ, Vandepitte L, Vanden Berghe E (2009) The impact of seabed disturbance on nematode communities: linking field and laboratory observations. Mar Biol 156:709–724

Schuelke T, Pereira TJ, Hardy SM, Bik HM (2018) Nematode-associated microbial taxa do not correlate with host phylogeny, geographic region or feeding morphology in marine sediment habitats. Mol Ecol 27:1930–1951

Schwinghamer P (1981) Extraction of living meiofauna from marine sediments by centrifugation in a silica sol-sorbitol mixture. Can J Fish Aquat Sci 38:476–478

Seifried S, Durbaum J (2000) First clear case of predation in marine Copepoda Harpacticoida. J Nat Hist 34:1595–1618

Seitzinger S, Harrison JA, Böhlke JK, Bouwman AF, Lowrance R, Peterson B, Tobias C, Van Drecht G (2006) Denitrification across landscapes and waterscapes: a synthesis. Ecol Appl 16:2064–2090

Seuront L, Spilmont N (2002) Self-organized criticality in intertidal microphytobenthos patch patterns. Phys A Stat Mech Appl 313:513–539

Smith LD, Coull BC (1987) Juvenile spot (Pisces) and grass shrimp predation on meiobenthos in muddy and sandy substrata. J Exp Mar Biol Ecol 105:123–136

Smol N, Huys R, Vincx M (1991) A 4-years' analysis of the meiofauna community of a dumping site for TiO_2-waste off the Dutch coast. Chem Ecol 5:197–215

Soetaert K, Vincx M, Wittoeck J, Tulkens M, Van Gansbeke D (1994) Spatial patterns of Westerschelde meiobenthos. Estuar Coast Shelf Sci 39:367–388

Soetaert K, Vincx M, Wittoeck J, Tulkens M (1995) Meiobenthic distribution and nematode community structure in 5 European estuaries. Hydrobiologia 311:185–206

Soetaert K, Muthumbi AW, Heip C (2002) Size and shape of ocean margin nematodes: morphological diversity and depth-related patterns. Mar Ecol Prog Ser 242:195–204

Soetaert K, Franco M, Lampadariou N, Muthumbi A, Steyaert M, Vandepitte L, van den Berghe E, Vanaverbeke J (2009) Factors affecting nematode biomass, length and width from the shelf to the deep sea. Mar Ecol Prog Ser 392:123–132

Somerfield P, Warwick RM, Moens T (2005) Chapter 6. Meiofauna techniques. In: Eleftheriou A, McIntyre A (eds) Methods for the study of marine benthos, 3rd edn. Blackwell Science, Oxford, pp 229–272

Steyaert M, Herman PMJ, Moens T, Widdows J, Vincx M (2001) Tidal migration of nematodes on an estuarine tidal flat (The Molenplaat, Schelde Estuary, SW Netherlands). Mar Ecol Prog Ser 224:299–304

Steyaert M, Vanaverbeke J, Vanreusel A, Barranguet C, Lucas M, Vincx M (2003) The importance of fine-scale, vertical profiles in characterizing nematode community structure. Estuar Coast Shelf Sci 58:353–366

Stock W, Heylen K, Sabbe K, Willems A, De Troch M (2014) Interactions between benthic copepods, bacteria and diatoms promote nitrogen retention in intertidal marine sediments. PLoS One 9:e111001

Sun B, Fleeger JW, Carney RS (1993) Sediment microtopography and the small-scale spatial distribution of meiofauna. J Exp Mar Biol Ecol 167:73–90

Svensson JR, Lindegarth M, Siccha M, Lenz M, Molis M, Wahl M, Pavia H (2010) Maximum species richness at intermediate frequencies of disturbance: consistency among levels of productivity. Ecology 88:830–838

Tchesunov AV, Ingels J, Popova EV (2012) Marine free-living nematodes associated with symbiotic bacteria in deep-sea canyons of north-east Atlantic Ocean. J Mar Biol Assoc UK 92:1257–1271

Thiel H, Thistle D, Wilson GD (1975) Ultrasonic treatment of sediment samples for more efficient sorting of meiofauna. Limnol Oceanogr 20:472–473

Thiermann F, Vismann B, Giere O (2000) Sulphide tolerance of the marine nematode *Oncholaimus campylocercoides* – A result of internal sulphur formation? Mar Ecol Prog Ser 193:251–259

Thistle D, Lambshead PJD, Sherman KM (1995) Nematode tail-shape groups respond to environmental differences in the deep sea. Vie et Milieu 45:107–115

Thor P, Dam HG, Rogers DR (2003) Fate of organic carbon released from decomposing copepod fecal pellets in relation to bacterial production and ectoenzymatic activity. Aquat Microb Ecol 33:279–288

Tita G, Vincx M, Desrosiers G (1999) Size spectra, body width and morphotypes of intertidal nematodes: an ecological interpretation. J Mar Biol Assoc UK 79:1007–1015

Tita G, Desrosiers G, Vincx M, Nozais C (2000) Predation and sediment disturbance effects of the intertidal polychaete *Nereis virens* (Sars) on associated meiofaunal assemblages. J Exp Mar Biol Ecol 243:261–282

Turner JT (2002) Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. Aquat Microb Ecol 27:57–102

Uhlig G, Thiel H, Gray JS (1973) Quantitative separation of meiofauna – Comparison of methods. Helgoländer Meeresun 25:173–195

Urban-Malinga B, Moens T (2006) Fate of organic matter in Arctic intertidal sediments: is utilisation by meiofauna important? J Sea Res 56:239–248

Vafeiadou A-M, Materatski P, Adão H, De Troch M, Moens T (2014) Resource utilization and trophic position of nematodes harpacticoid copepods in and adjacent to *Zostera noltii* beds. Biogeosciences 11:4001–4014

Vafeiadou A-M, Bretaña BL, Van Colen C, Wu X, Dos Santos GAP, Moens T (2018) Climate change-induced temperature effects to intertidal tropical and temperate meiobenthic communities (submitted)

Van Colen C, Montserrat F, Verbist K, Vincx M, Steyaert M, Vanaverbeke J, Herman PMJ, Degraer S, Ysebaert T (2009) Tidal flat nematode responses to hypoxia and subsequent macrofauna-mediated alterations of sediment properties. Mar Ecol Prog Ser 381:189–197

Van den Berghe W, Bergmans M (1981) Differential food preferences in 3 co-occurring species of *Tisbe* (Copepoda, Harpacticoida). Mar Ecol Prog Ser 4:213–219

Van Gaever S, Moodley L, Pasotti F, Houtekamer M, Middelburg JJ, Danovaro R, Vanreusel A (2009) Trophic specialisation of metazoan meiofauna at the Håkon Mosby Mud Volcano: fatty acid biomarker isotope evidence. Mar Biol 156:1289–1296

Van Oevelen D, Middelburg JJ, Soetaert K, Moodley L (2006a) The fate of bacterial carbon in an intertidal sediment: modeling an in situ isotope tracer experiment. Limnol Oceanogr 51:1302–1314

Van Oevelen D, Moodley L, Soetaert K, Middelburg JJ (2006b) The trophic significance of bacterial carbon in a marine intertidal sediment: results of an in situ stable isotope labeling study. Limnol Oceanogr 51:2349–2359

Van Oevelen D, Soetaert K, Middelburg JJ, Herman PMJ, Moodley L, Hamels I, Moens T, Heip C (2006c) Quantifying intertidal food webs, using biomass, tracer and carbon isotope data. J Mar Res 64:453–482

Vanaverbeke J, Merckx B, Degraer S, Vincx M (2011) Sediment-related distribution patterns of nematodes and macrofauna: two sides of the benthic coin? Mar Environ Res 71:31–40

Vanreusel A, De Groote A, Gollner S, Bright M (2010) Ecology and biogeography of free-living nematodes associated with chemosynthetic environments in the deep sea: a review. PLoS One 5: e12449

Venekey V, Santos PJP, Fonsêca-Genevois VG (2014) The influence of tidal and rainfall cycles on intertidal nematodes: a case study in a tropical sandy beach. Braz J Oceanogr 62:247–256

Viglierchio DR, Schmitt RV (1983) On the methodology of nematode extraction from field samples – Baermann funnel modifications. J Nematol 15:438–444

Vincx M (1989) Free-living marine nematodes from the southern bight of the North Sea. Academiae Analecta, Klasse Wetenschappen 51:39–70

Vincx M (1996) Meiofauna in marine and freshwater sediments. In: Hall GS (ed) Methods for the examination of organismal diversity in soils and sediments. IUBS, UNESCO. CAB International, New York, pp 187–195

Vopel K, Dehmlow J, Arlt G (1996) Vertical distribution of *Cletocamptus confluens* (Copepoda, Harpacticoida) in relation to oxygen and sulphide microprofiles of a brackish water sulphuretum. Mar Ecol Prog Ser 141:129–137

Vranken G, Herman PMJ, Vincx M, Heip C (1986) A re-evaluation of marine nematode productivity. Hydrobiologia 135:193–196

Walton WR (1952) Techniques for recognition of living foraminifera. Contr Cush Found Foram Res 3:56–60

Warwick RM (1981) Survival strategies of meiofauna. In: Jones NV, Wolff WJ (eds) Feeding and survival strategies of estuarine organisms. Plenum Press, New York, pp 39–52

Warwick RM (1987) Meiofauna: their role in marine detrital systems. In: Moriarty DJW, Pullin RSV (eds) Detritus and microbial ecology in aquaculture, ICLARM Conference Proceedings, vol 14. International Center for Living Aquatic Resources Management, Manila, pp 282–295

Warwick RM, Buchanan J (1971) The meiofauna off the coast of Northumberland. II. Seasonal stability of the nematode population. J Mar Biol Assoc UK 51:355–362

Warwick RM, Gee JM (1984) Community structure of estuarine meiobenthos. Mar Ecol Prog Ser 18:97–111

Warwick RM, Gee JM, Berge JA, Ambrose W (1986) Effects of the feeding activity of the polychaete *Streblosoma bairdi* (Malmgren) on meiofaunal abundance and community structure. Sarsia 71:11–16

Warwick RM, McEvoy AJ, Thrush SF (1997) The influence of *Atrina zelandica* Gray on meiobenthic nematode diversity and community structure. J Exp Mar Biol Ecol 214:231–247

Watzin MC (1983) The effects of meiofauna on settling macrofauna: meiofauna may structure macrofaunal communlties. Oecologia 59:163–166

Watzin MC (1985) Interactions among temporary and permanent meiofauna: observations on the feeding and behaviour of selected taxa. Biol Bull Mar Biol Lab Woods Hole 169:397–416

Wetzel MA, Jensen P, Giere O (1995) Oxygen/sulfide rexime and nematode fauna associated with Arenicola marina burrows: new insights in the thiobios case. Mar Biol 124:301–312

Wetzel MA, Fleeger JW, Powers SP (2001) Effects of hypoxia and anoxia on meiofauna: a review with new data from the Gulf of Mexico. Coas Estuar Sci 58:165–184

Widdows J, Brinsley M (2002) Impact of biotic and abiotic processes on sediment dynamics and the consequences to the structure and functioning of the intertidal zone. J Sea Res 48:143–156

Wieser W (1953) Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. Arkiv für Zoologie 4:439–484

Wieser W (1960) Benthic studies in Buzzards Bay. 2. The meiofauna. Limnol Oceanogr 5:121–137

Wiltshire KH, Blackburn J, Paterson DM (1997) The cryolander: a new method for in situ sampling of unconsolidated sediments minimising the distortion of sediment fabric. J Sediment Res 67:980–984

Xu K, Du Y, Lei Y, Dai R (2010) A practical method of Ludox density gradient centrifugation combined with protargol staining for extracting and estimating ciliates in marine sediments. Eur J Protistol 46:263–270

Yoder M, Tandingan De Ley I, King IW, Mundo-Ocampo M, Mann J, Blaxter M, Poiras L, De Ley P (2006) DESS: a versatile solution for preserving morphology and extractable DNA of nematodes. Nematology 8:367–376

Zeppilli D, Sarrazin J, Leduc D, Martinez Arbizu P, Fontaneto D, Fontanier C, Gooday AJ, Kristensen RM, Ivanenko VN, Sørensen MV, Vanreusel A, Thébault J, Mea M, Allio N, Andro T, Arvigo A, Castrec J, Danielo M, Foulon V, Fumeron R, Hermabessiere L, Hulot V, James T, Langonne-Augen R, Le Bot T, Long M, Mahabror D, Morel Q, Pantalos M, Pouplard E, Raimondeau L, Rio-Cabello A, Seite S, Traisnel G, Urvoy K, Van Der Stegen T, Wey M, Fernandes D (2015) Is the meiofauna a good indicator for climate change and anthropogenic impacts? Mar Biodivers 45:505–535

Zühlke R, Blome D, van Bernem KH, Dittmann S (1998) Effects of the tube-building polychaete *Lanice conchilega* (Pallas) on benthic macrofauna and nematodes in an intertidal sandflat. Senckenberg Marit 29:131–138

Chapter 6
The Upper Living Levels: Invertebrate Macrofauna

Carl Van Colen

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Abstract Mudflats provide a suitable habitat for a functionally diverse invertebrate macrofauna community that can cope with the high variability in sediment physico-chemical conditions associated with the tidal regime. The most common macrofaunal taxonomic groups are annelids, molluscs and crustaceans. Macrofauna are usually the link from primary producers, meiofauna, and detritus to higher trophic levels like wading birds and epibenthic fish that forage in mudflats. Behavioral activities related to macrofauna feeding, burrowing and respiration alter biogeochemistry and mudflat sediment dynamics and are thus of paramount importance for the cycling of energy and matter in mudflats from estuaries, mangroves and coastal lagoons. Variability in abiotic and biotic interactions structures macrofauna communities in space and time and hence defines the influence macrofauna has on the diversity and functioning of the wider ecosystem through direct and indirect interactions.

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1 Introduction

Technically, invertebrate benthic macrofauna are defined as benthic invertebrates that live in or on the bottom substrate of a water body and that are retained on a sieve with a mesh size of 0.5 or 1 mm after the sediment passed through. This operational mesh-size convention can however vary and the relatively small size of many macrofauna in organically enriched mudflat sediments has prompted mudflat ecologists to often use 300–500 μm mesh-sized sieves to collect macrofauna; others refer to macrofauna as being those readily visible with the naked eye, such as gastropods and bivalves.

Benthic macrofauna are divided into two categories depending on their habitat: infauna (or endofauna) live in the sediment and epifauna lives on top of the sediment or attached to other fauna, like mussels. Categorisation into epi- or infauna can, however, be challenging, as some species like tubeworms live between both realms (here the term 'hemibenthic' has been used—Le Pennec et al. 1995), and infaunal species are often well-connected to the water column. Mudflats harbor relatively low taxonomic diversity of macrofauna, compared to other coastal soft-sediment habitats, but, in contrast, population biomass is often high. The accessibility of mudflats during low tide, together with the relatively sedentary life habit, tractable size and generally fast response time of macrofauna species to environmental change has facilitated empirical testing of the mechanisms that govern distribution of macrofauna in space and time, and the impact macrofauna has on other biotic and abiotic properties of the mudflat habitat.

1.1 Overview of Mudflat Macrofaunal Groups

Annelids (polychaetes and oligochaetes), molluscs (bivalves and gastropods) and amphipods generally comprise the majority of macrofauna species that inhabit mudflat sediments, with annelids typically outnumbering the other taxonomic groups, whereas molluscs often form the majority of the biomass (Ysebaert et al. 2003). Other groups that are frequently encountered are mud shrimps, crabs, nemerteans, isopods, chironomid larvae, and sessile epifauna such as ascidians and barnacles attached to (dead) shells or occasional rocks. A wide array of diverse biological and functional traits characterises mudflat macrofauna. Due to this high functional diversity, macrofauna communities modulate many ecosystem processes at different spatial scales, thereby influencing overall ecosystem functioning. For example, macrofauna plays an important role in benthic remineralisation processes, both directly as an important component in the mudflat food web (Sect. 3.1), and indirectly through its structuring role on the sediment community via e.g. bioturbation and bio-irrigation activities (Sect. 3.2).

1.2 The Epifaunal vs Infaunal Life Habit

Due to their different locations, epifaunal and infaunal macrobenthic animals face very different environmental conditions. While infauna are always surrounded by moist sediment, epifauna have developed hard exoskeletons such as shells (molluscs) and carapaces (crustaceans), which modulate heat exchange and help to cope with desiccation and variability in external osmolarity during low tide. On the other hand, mudflat infauna face low oxygen and high hydrogen sulphide concentrations, except in the upper few mm of sediment (see Chaps. 2 and 3), and deeper when burrows facilitate water flow into the sediment. Many infauna have specialized adaptations which maintain aerobic respiration at low oxygen concentrations (e.g. Giere 2006 and references therein). Hemoglobin in the blood (responsible for the bright red coloration of e.g. oligochaetes and capitellid polychaetes) facilitates transportation of oxygen, while ventilation of burrows through active pumping of oxygen-rich seawater (bio-irrigation; Sect. 3.2) also allows infauna to oxygenate their habitat. Furthermore, infaunal species have often developed sophisticated feeding apparatuses like robust elongated antennae (e.g. *Corophium volutator*) or long siphons (e.g. *Limecola balthica*, *Scrobicularia plana*), allowing them to reach out across the mud to graze on deposited organic matter and/or intercept plankton from the water column (Sect. 3.1).

1.3 Sampling Procedures

Collection of sediment through coring is the most commonly-used technique to sample infauna. Although most mudflat infauna live in the upper 10–15 cm of sediment at all times, burrowing depth generally varies with size, season (deeper in winter), and in the presence of predators (e.g. Esselink and Zwarts 1989; Flynn and Smee 2010). Some species, such as the subsurface polychaete feeder *Heteromastus filiformis* and the lugworm *Arenicola marina* also occur abundantly in deeper layers. Once the specific spatial lags are known (see Chap. 15), sampling of surfaces of 70–180 cm^2 to a depth of 15 cm is usually adequate to quantitatively collect macrofauna, although core properties might differ depending on the species of interest. Infauna is typically extracted from the sediment through wet-sieving or sieving after fixation, over a 300 μm–1 mm mesh. In addition, specific sampling devices have been used for the targeted collection of lugworms (i.e. bait pump, see Chap. 13), cockles and hard clams (i.e. hand raking, e.g. Peterson et al. 1983; Kaiser et al. 2001, and see Chap. 13).

Remote sensing techniques have been used to determine distribution and surface coverage of dense aggregations of tidal flat sessile epifauna in a non-destructive manner, e.g. mussel beds (e.g. Nieuwhof et al. 2015) and tube-building polychaetes (Alves 2017). Quadrats of 0.25–0.5 m^2 are commonly used to estimate density of these aggregations (e.g. Alves et al. 2017). Similarly, densities of faecal mounds at the sediment surface have been quantified and used as proxies for densities of deep-living macrofauna (e.g. Cadee 1979; Reise et al. 2001; Boldina and Beninger 2014). Epifauna are typically collected through coring, as well as beam trawling during ebbing tides (De Smet et al. 2015), or collection of dispersing fauna by fyke- and block nets (e.g. Hampel et al. 2004). Due to spatial aggregation at multiple scales, the question of sampling strategy is crucial. An overview of this aspect, as well as of the quantitative treatment of such data, is presented in Chap. 15.

2 Spatio-Temporal Dynamics

Mudflat macrofauna density and distribution display great variability in space and time (e.g. Kraan et al. 2009) as a result of biological and physical effects that play at multiple scales. In addition to the natural interplay of biotic and abiotic interactions, human impacts such as fishing disturbance, trampling and pollution have influenced macrofauna distribution at different spatial and temporal scales (e.g. Essink 2003; Rossi et al. 2007; Boldina and Beninger 2013, 2014; Beninger and Boldina 2014).

2.1 Spatial Distribution: Intertidal Zonation and Small-Scale Patchiness

The macrofauna species occurring on mudflats generally have a wide geographical range and are rarely strictly confined to mudflats. Some of the most dominant mudflat species can be found in sandier sediments or below the low water mark (Ysebaert et al. 2000), although generally in lower abundances, compared to mudflats (Fig. 6.1). Despite the strong gradients in, e.g., pore water salinity, temperature, and oxygen related to sediment organic loading and associated with temporal fluctuations in inundation regime and climate, mudflats thus provide a suitable habitat for some macrofauna species.

Spatial variability in macrofauna community structure occurs in mudflats, but distribution patterns depend on variability in site-specific abiotic and biotic conditions. Zonation patterns are often related to the hydrodynamic regime, sediment type and sediment transport processes (van der Wal et al. 2008), dynamics in food supply (especially microphytobenthos, MPB—Guarini et al. 1998; Seuront and Spilmont 2002; Murphy et al. 2008; Chapman et al. 2010) and epifaunal predation pressure. For example, shifts in the deposit-feeder community toward a lower dietary dependency on benthic microalgal carbon and a deeper living position were found to correspond to a gradient of coarsening of the sediment and greater exposure to hydrodynamic stress, with distance from the high water mark, in an estuarine mudflat in the Netherlands (Van Colen et al. 2010a). Sediment resuspension in the low intertidal seems thus to impede a surficial living habit, whereas the high standing

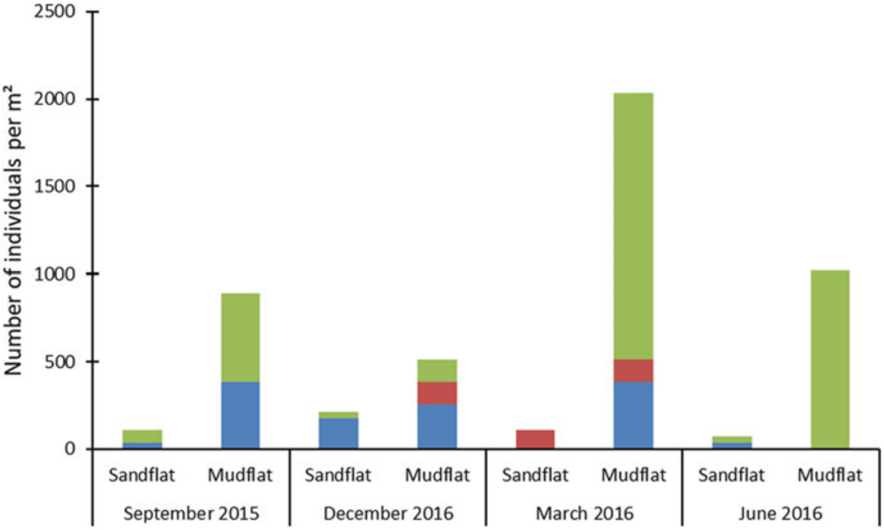

Fig. 6.1 Average density of the polychaetes *Hediste diversicolor* (blue), and *Heteromastus filiformis* (red), and the gasteropod *Peringia (= Hydrobia) ulvae* (green) in the mudflat and sandflat of Paulinapolder, Westerschelde estuary (SW the Netherlands) during four sampling campaigns. Error bars are 95% confidence intervals. Data: S. Mestdagh, University of Ghent.

stock of benthic microalgae in muddy sediments (Van de Koppel et al. 2001) likely supports the dominance of surface deposit-feeders in the high intertidal community. A comparison of mollusc distributions at different mudflats in NW Europe showed that maximum densities for the mudsnail *Peringia (Hydrobia) ulvae*—an important grazer on benthic microalgae—are generally found at the highest tidal levels (Bocher et al. 2007).

Hydrodynamics also determine zonation patterns of surficial living suspension feeders, like the edible cockle *Cerastoderma edule*, that typically concentrate in the areas where bottom shear stress is relatively low, and submersion time is sufficient to feed long enough to meet energetic requirements. Such conditions are often present in the mid-intertidal area of mudflats (Herman et al. 2001). Biotic interactions can also determine the zonation of macrofauna. For example, Flach (1992) demonstrated that densities of a typical high-intertidal species, the mud shrimp (actually an amphipod) *Corophium volutator*, increase in lower intertidal areas where the lugworm *Arenicola marina* and *Cerastoderma edule* were locally removed, whereas transplantation of both species into the high intertidal decreased mud shrimp numbers in that zone. Furthermore, long-term monitoring in the Dutch Wadden Sea showed that the upper limit of *Corophium volutator* distribution is determined by the duration of inundation with upward and downward migration in periods with higher and lower-than-average water levels, respectively (Beukema and Flach 1995), illustrating the role of abiotic factors in setting the upper intertidal limit of this species.

Macrofauna distribution on a mudflat can also be life-stage dependent. Well-known examples include post-settlement dispersal events of clams (e.g. Hunt 2004), like the Baltic tellin *Limecola (Macoma) balthica* that uses active dispersal through byssal thread drifting during high tide to migrate from the settling area in the low intertidal to the high intertidal (Hiddink et al. 2002a). This process is thought to reduce high predation pressure from brown shrimps *Cragnon cragnon* (Hiddink et al. 2002b, c) in the low intertidal. Furthermore, sediment stabilization by microphytobenthos (see Chaps. 2, 8, 10) in the high intertidal might facilitate recruitment and growth for juvenile *L. balthica* that rely predominantly on benthic microalgae for their diet (Van Colen et al. 2010b). Other frequently-encountered mudflat macrofauna species that display water column dispersal are *Hediste* spp. (Aberson et al. 2011), *Corophium volutator* (De Backer et al. 2010) and *Peringia ulvae* (Armonies and Hartke 1995). Dispersal of these species is not confined to the juvenile recruits, and swimming activity can be restricted, e.g. to nocturnal spring tide periods for *Corophium volutator* (Drolet and Barbeau 2009a).

In addition to the macrofauna zonation patterns related to larger-scale environmental structuring, distinct small-scale patchiness is prevalent in mudflats (Boldina and Beninger 2013, 2014; Beninger and Boldina 2014). Habitat heterogeneity (e.g. sediment composition—Huxham and Richards 2003), modulated by biotic interactions and associated with local perturbations, biogenic habitat structuring features and local interactions of spatial self-organisation, e.g. diatom-sediment-benthos feedbacks (see Chap. 8), are some of the common mechanisms that govern small-scale distribution of macrofauna. For example, eutrophication-induced drifting algal mats that deposit on tidal flats represent a local resource subsidy for macrofaunal consumers. However, effects may vary from positive to negative depending on mat thickness. In an 8-week study, Green and Fong (2016) empirically demonstrated that thin mats of 0.5 cm yield a higher diversity of macrofauna by supporting surface feeding and burrowing detritivores as compared to thicker mats (1.5 and 4 cm) that created anoxia and promoted pore water sulphide conditions under which capitellid polychaetes thrived. Interactions between the frequency of such perturbations and subsequent recovery processes will ultimately generate small-scale patchiness. The creation of feeding pits and mounds by callianassid shrimps, shore crabs and rays are other examples of biotic perturbations that create local heterogeneity in the community via physical disturbance and sediment resuspension, direct consumption of macrofaunal prey, or indirect mechanisms such as the entrapment of food in the pits. Effects on the macrofauna community depend on disturbance—recovery dynamics, but generalization is difficult as responses are species-specific and may differ between life stages (e.g. Zajac 2004). Furthermore, rates of pit creation, infilling and recolonization by fauna can be rapid in less-muddy tidal flats (e.g. Thrush et al. 1991), so that distribution patterns of long-lived macrofauna can be smoothed out.

In general, mudflat surface features are a structuring agent of macrofauna community small-scale distribution. Anibal et al. (2007) showed that the epifaunal community in the Ria Formosa tidal lagoon was more diverse and had higher biomass in local depressions of the mudflat, compared to adjacent elevated areas that have less deposition of organic matter, experience stronger currents during high tide and are longer exposed to wind and solar radiation during low tide. Another example is the aggregated distribution of *Corophium volutator* in tide pools in the Bay of Fundy, Canada (Drolet and Barbeau 2009b). Particularly patches of living biogenic structures like mussel beds, tube-building polychaete reefs, seagrass meadows or tussocks of marsh plants can considerably alter local topography in a bare mudflat via their influence on fine sediment dynamics (e.g. Bouma et al. 2009). These aggregations are also prime examples of ecosystem engineers that go on to affect macrofauna indirectly through the modulation of resources (see Chap. 10).

2.2 Seasonal and Interannual Dynamics

Strong interannual fluctuations in invertebrate macrofauna are commonplace for individual species; however, the total macrobenthic biomass fluctuation is less pronounced (Beukema et al. 1993). Macrofauna species are generally present throughout the year, although distinct seasonal differences in population abundance, size classes and biomass related to population demographics (i.e. recruitment and mortality) occur. Ysebaert (2000) studied seasonal dynamics for some of the most common macrofauna infaunal species in temperate estuarine mudflats on a monthly basis between March 1993 and August 1994. He found a general pattern of an increase in abundance during the period of temperature rise in late spring and early summer, followed by a decrease towards winter that can either occur rather rapidly or more gradually, depending on the species and mudflat. Rising temperatures do trigger spawning but moments of peak abundances differed between species (Fig. 6.2). In contrast to relatively sedentary species (e.g. *Limecola balthica*, *Heteromastus filiformis*), temporal population dynamics in *Hediste diversicolor* differed more between nearby locations (Fig. 6.2), illustrating the role of dispersal processes in regulating the rise and fall of local population abundances for mobile species. In general, patterns in biomass resembled the seasonal pattern in abundance, indicating that biomass variability mainly relates to recruitment and successive disappearance of the newly-settled individuals, except in mudflats where biomass of larger long-lived species like cockles and clams are more dominant than the influence of juvenile growth.

Several juvenile cohorts can be present during the season of recruitment for some species (e.g. Barbeau et al. 2009) and recruitment success can differ between years (see e.g. *Scobicularia plana* in Fig. 6.2). Another example is the lower recruitment of typical mudflat bivalve species such as *Limecola balthica*, *Cerastoderma edule*, and blue mussel *Mytilus edulis* after mild winters. Based on a 30-year data series, Beukema and Dekker (2014) demonstrated that this trend was inversely related to the density of shore crabs *Carcinus maenas* and *Cragnon cragnon* in the period preceding recruitment, since abundances of both epibenthic predators were higher in springs after mild winters. In addition to predation by crustaceans and wading birds (see Chaps. 8 and 12), natural winter mortality and episodic extreme weather conditions such as heat waves and floods (e.g. Grilo et al. 2011) or infections by parasites (see Chap. 9) are some of the mechanisms that can govern decreases in

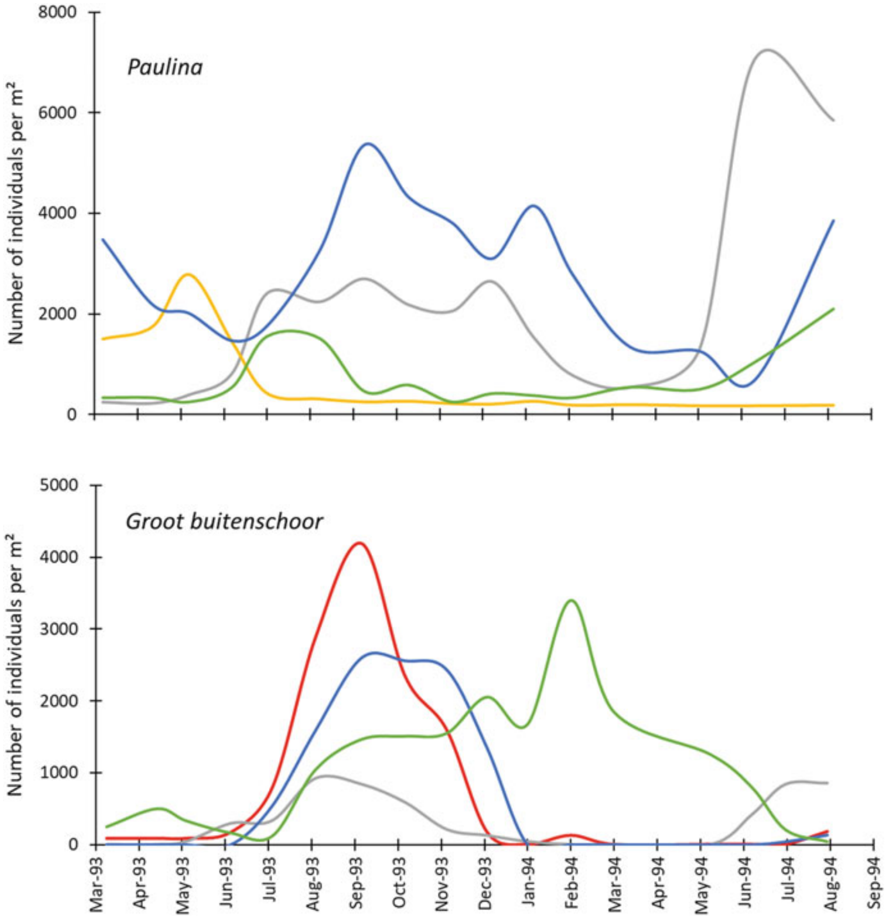

Fig. 6.2 Monthly variation in abundance of *Scrobicularia plana* (yellow), *Limecola balthica* (grey), *Hediste diversicolor* (green), *Corophium volutator* (red), and *Heteromastus filiformis* (blue) on two mudflats (Paulina and Groot Buitenschoor) in the Westerschelde estuary, SW the Netherlands. After Ysebaert (2000).

population abundances at seasonal and shorter time scales (Beukema et al. 1993; Zwarts and Wanink 1993). Mortality related to food shortage seems unlikely, given the flexible reliance on highly-abundant sources of dead and live organic matter in mudflat sediments (Sect. 3.1). Rather, short-term enhancement in food nutritional value has been related to the stimulation of population growth during several periods of the year (Rossi et al. 2001 and references therein).

3 Trophic and Functional Ecology

3.1 Resource Utilization and Trophic Position

A variety of trophic guilds can be found in mudflat macrofauna communities, including herbivore grazers, suspension feeders, predators, scavengers, and deposit feeders. Although some motile predators may greatly impact ‘easy target’ adult macrofauna during high tides (e.g. Yap 1977), in general, mudflat macrofauna is chiefly composed of deposit feeders (e.g. Van Colen et al. 2010a) that obtain their nutritional intake from the organic fraction of the sediment, including microbial organisms that provide essential proteins, fatty acids and vitamins. Reconstruction of carbon pathways, stable isotope signatures and tracer data confirms that deposition of detritus from the water column and subsequent assimilation and respiration by bacteria dominates the mudflat infaunal foodweb, but also that detritivory of macrofauna can be negligible due to high selective feeding on microphytobenthos and pelagic primary production (Van Oevelen et al. 2006). Based on food labeling studies and the natural abundance of stable isotope ratios of carbon and nitrogen, Herman et al. (2000) confirmed the importance of microphytobenthos as a food source for surface deposit feeders and the almost exclusive contribution of pelagic algae to the diet of suspension feeders such as *Cerastoderma edule* and the soft-shell clam *Mya arenaria* (despite significant resuspension of diatoms at the study site). The epibenthic grazer *Peringia (= Hydrobia) ulvae* relies almost exclusively on microphytobenthos (Fig. 6.3, and see Chap. 8), while food selectivity in other species can be more flexible in space and time. For example, Rossi et al. (2004) showed ontogenetic variation in the diet of *Limecola balthica,* with small juveniles feeding entirely on microphytobenthos, and larger individuals gradually feeding more on phytoplankton.

Some species may alter their feeding mode according to the available food sources; the omnivorous polychaete *Hediste diversicolor* is capable of filter-feeding by pumping water and trapping suspended food particles in a mucous net secreted at the entrance of its burrow (Riisgard 1991), and also of deposit-feeding and direct consumption of infauna (i.e. predation). Aberson et al. (2016) showed that at sewage-polluted sites in three estuaries in SE England, *Hediste* sp. mainly consumed microphytobenthos, sediment organic matter and filamentous macroalgae, while at more pristine sites it relied more on suspension-feeding and consumption of the cordgrass *Spartina anglica*. *Hediste* sp. consumption of infauna can also be considerable. Hiddink et al. (2002b) calculated from stomach contents and field experiments that *Hediste* sp. consumption of settled juvenile *Limecola balthica* in the eastern Dutch Wadden Sea is greater than that of other epibenthic predators, such as shore crabs and brown shrimps. Sessile epifauna, on the other hand, are generally suspension-feeders. Active suspension-feeders such as *Mytilus edulis* pump water and food particles over their gills while other species, such as *Lanice conchilega*, are known to passively trap suspended food particles.

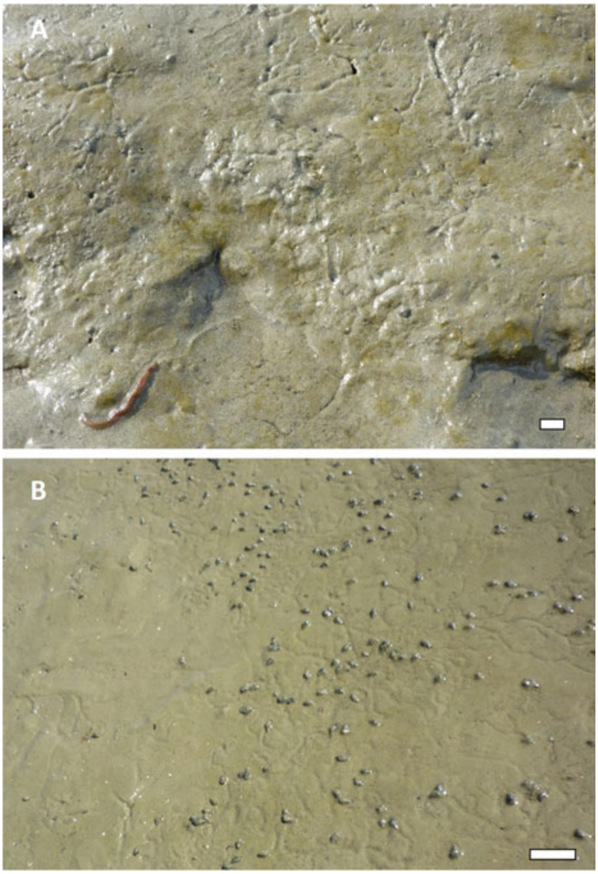

Fig. 6.3 Crawling tracks of *Hediste diversicolor* (**a**) and *Peringia ulvae* (**b**) grazing on microbial biofilm (brown patches). Scale bars are 1 cm. Photo credits: C. Van Colen (**a**) and P. Beninger (**b**).

Although most studies of macrofaunal trophic ecology concern adult animals, it should be kept firmly in mind that the young stages of macrofauna are often in the same size range as the co-occurring meiofauna. This puts them in an entirely different trophic network (see Chap. 5).

3.2 Bioturbation, Bio-Irrigation and Mucus Production

Macrofauna rework and relocate sediment particles through burrow construction and maintenance, ingestion and defecation. This ecosystem process, known as *bioturbation*, causes changes in the sediment matrix structure by altering sediment grain size distribution (Meysman et al. 2006 and references therein). In general, the way particles are displaced depend on the life style and feeding type of the species. Biodiffusors mix sediments homogeneously over short distances and include epifaunal species, gallery burrowers and surficial living infauna. Montserrat et al.

Fig. 6.4 Faecal casts of *Arenicola marina*, heaps of faecal pellets of *Heteromastus filiformis*, dead shell fragment (**a**). Shells serve as an attachment substratum for epifauna—and flora, e.g. anemones and *Ulva* spp. (**b**). Scale bars are 1 cm. Photo credits: C. Van Colen (**a**) and P. Beninger (**b**).

(2009) empirically demonstrated that bioturbation by *Cerastoderma edule* renders the sediment surface less muddy through resuspension of selectively mobilised fine particles. Upward conveyers like *Heteromastus filiformis* and *Arenicola marina* feed at depth in the sediment and deposit 'waste' at the surface (Fig. 6.4). The amount of deep sediment that is moved to the surface is impressive. For example, rates of sediment turnover by *Arenicola* and *Heteromastus* populations of respectively 4 l and 0.3 l per m^2 per day have been observed during periods of peak abundance, resulting in a complete mixing of the sediment down to a depth of about 40 and 4 cm annually (Cadee 1976, 1979). In contrast, downward conveyers like e.g. the spionid *Pygospio elegans* ingest particles at the surface and egest 'waste' deep(er) in the sediment. A last type of bioturbation is regenerator reworking, performed e.g. by fiddler crabs (*Uca* spp.) that dig and maintain burrows in the sediment by transferring particles from depth to the surface. Collapse of burrow walls or infilling of surface sediments replace the excavated sediment. This physical process contributes

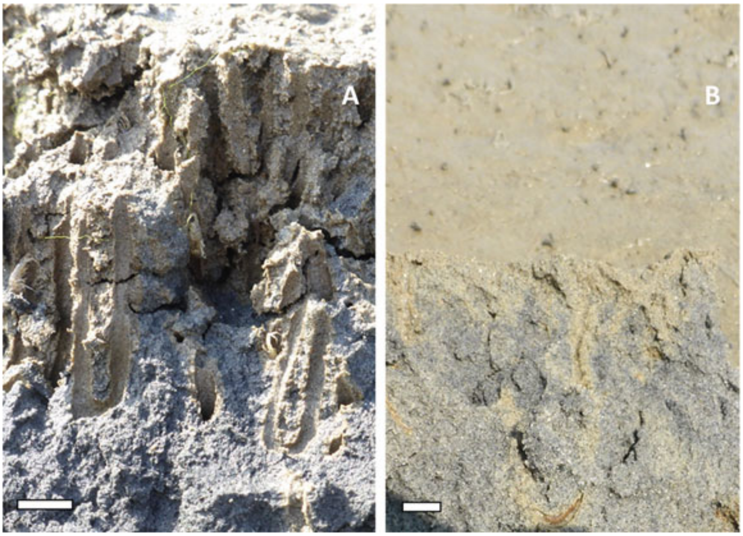

Fig. 6.5 U-shaped burrows of *Corophium volutator* (**a**) and burrows of *Hediste diversicolor* (**b**). Scale bars are 1 cm. Photo credits: C. Van Colen.

to about one fifth of the total sediment mixing rate mediated by *Corophium volutator* (De Backer et al. 2011).

Bioturbation influences the porosity of the water-saturated mudflat sediments, and therefore the exchange of pore water, between the sediment and the water column. Furthermore, macrofauna irrigate their burrows with overlying water during respiration and feeding, which further affects the biogeochemistry and exchange of solutes between the sediment and water column. Dominant irrigators of mudflat sediments are the gallery biodiffusors *Hediste diversicolor* and *Alitta virens* and the more shallow-living regenerator *Corophium volutator*.

Bio-irrigators often produce mucus that bind sediment grains and reinforce burrow structure, allowing sustained irrigation (Fig. 6.5). Mucus production is also used for feeding (e.g. *Hediste spp.*) and, in gastropods like the periwinkle *Littorina littorea* and *Peringia ulvae,* for locomotion (Fig. 6.3b). Interestingly, while pedal mucus production in gastropods is energetically expensive, studies show that snails following recently laid trails can save energy and that adherence of organic matter can probably facilitate microbial growth and thus macrofauna (including snail) food supply (Davies and Beckwith 1999; Davies and Blackwell 2007). Because the macrofauna-mediated displacement of particles and water in sediments is tightly coupled, and often performed simultaneously, Kristensen et al. (2012) recently proposed to define macrofauna bioturbation as all processes that directly and indirectly affect the sediment matrix, including both particle reworking and burrow ventilation, and to consider the effects of bioturbation on other species and associated process within the conceptual framework of ecosystem engineering (see Chap. 10).

4 Integrated Benthic Faunal Ecology

Benthic macrofauna form a central part of the mudflat ecosystem network, and interactions with the biotic and abiotic environment determine their spatio-temporal dynamics, as well as their impact on ecosystem functioning. Both a long history of experimental approaches, including caging, defaunation and density manipulations (Fig. 6.6), and the development of dedicated incubation chambers, flumes, and fine-scale measuring tools (e.g. microelectrodes and optodes) to quantify ecosystem processes, have shed light on the mechanisms underlying mudflat ecosystem functioning. In particular, this is true of macrofauna—meiofauna interactions, and

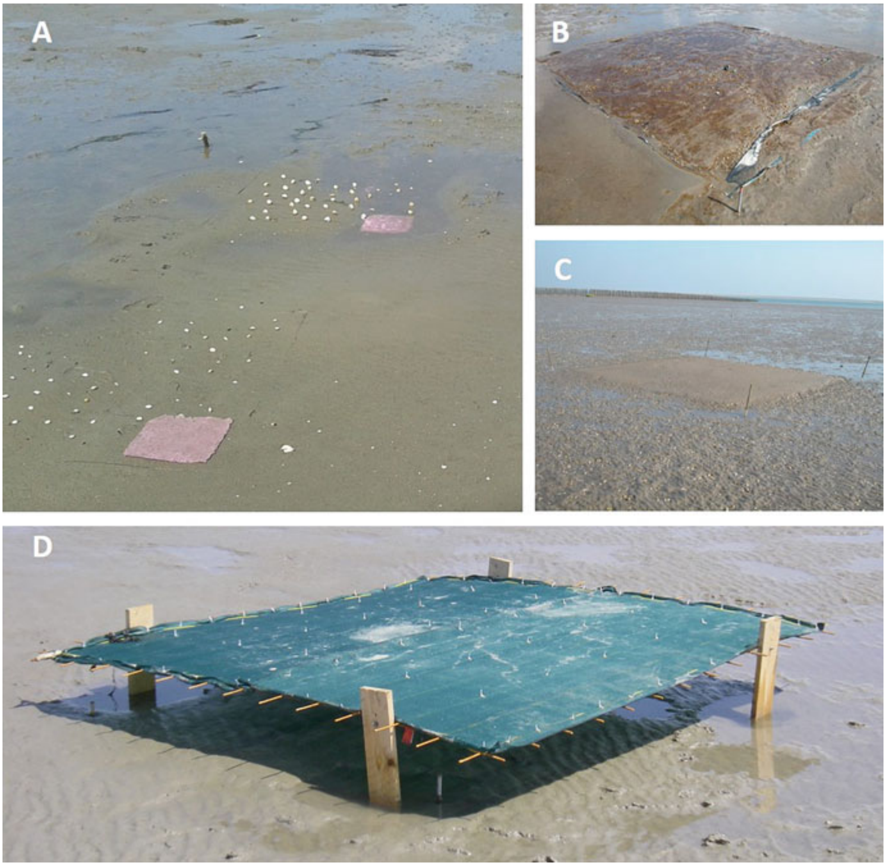

Fig. 6.6 Macrofauna experimental approaches on tidal mudflats: Application of inert colored particles (luminophores) to track macrofauna impact on surface sediment mixing in the Oosterschelde estuary, the Netherlands (**a**). (Dis)appearance of dense microbial biofilms after experimental macrofauna exclusion and subsequent colonization in the Westerschelde estuary (**b**, **c**). Manipulation of incident light regime in the Schelde estuary, the Netherlands (**d**). Photo credits: C. Van Colen.

macrofaunal biodiversity effects on ecosystem functions, such as biogeochemical cycling and sediment transport.

Apart from the carnivorous species, macrofauna are located in the middle region of the trophic pyramid, relying generally on freshly-produced carbon or detritus for their diet, while being preyed upon by wading birds (see Chap. 12), fish and larger crustaceans (see Chap. 8). Consequently, both top-down and bottom-up interactions determine the stability of benthic macrofaunal populations, in addition to interactions within their own community. For example, the development of dense microphytobenthic biofilms after experimental disturbance (Fig. 6.6b) has been shown to be instrumental in mediating settlement choice of juvenile macrofauna and in facilitating growth and persistence of the colonizing populations, inducing community divergence at the long-term (Van Colen et al. 2009, 2010b, c).

Both direct and indirect interactions determine the structuring effect that macrofauna has on meiofauna populations and communities (Chap. 5). A well-documented biotic interaction between both infaunal size classes is the predation on meiofauna by carnivorous macrofauna, either directly or as 'bycatch' during deposit feeding or suspension feeding (Coull 1999). Direct physical interference from bioturbation represents another interaction between both groups (e.g. Schratzberger and Warwick 1999). Probably the most common ways that macrofauna activities influence meiofauna are related to the above-mentioned engineering effects of bioturbation and bio-irrigation. Both activities not only extend the surface area of the sediment-water interface for solute exchange, but also stimulate biogeochemical processes along the macrofauna burrow walls (Fig. 6.7), which may alter the microbial community (Mermillod-Blondin et al. 2004; Kristensen and Kostka 2005), and hence diversify the menu for meiofauna. Furthermore, macrobenthic faecal casts (Fig. 6.4a) stimulate bacterial activity, due to a higher concentration of organically enriched fine particles (Reise 1985), in a similar way as gastropod pedal mucus does. The intermediate disturbance hypothesis (Connell 1978) has been frequently advanced to explain increased meiofauna abundances and diversity close to macrofaunal feeding or locomotion tracks.

Attempts to link mudflat benthic biodiversity to ecosystem functioning revealed that these relationships are very complex, context-dependent and may depend more on the density and presence of functional groups or species identities than on species richness or diversity (see e.g. Bolam et al. 2002). For example, *Corophium volutator* and *Hediste diversicolor* that construct and ventilate burrows increase solute transport, oxygen consumption and release of nutrients from the sediment more than shallower-living species such as *Peringia ulvae*, *Cerastoderma edule* and *Limecola balthica* that only effect particle reworking in the top few mm (e.g. Raffaelli et al. 2003; Mermillod-Blondin et al. 2004). Nevertheless, such surficial disturbance of the sediment bed is important in mediating biogeochemical cycling (Michaud et al. 2006), and inducing sediment erodibility and microalgal resuspension (Orvain et al. 2004) that all can have cascading effects on other mudflat biota (e.g. Reise 1983; Van Colen et al. 2013). Finally, the environmental context modulates the outcome of ecosystem interactions in which mudflat benthic invertebrates are involved. For example, enhanced concentrations of suspended solids were shown to increase the

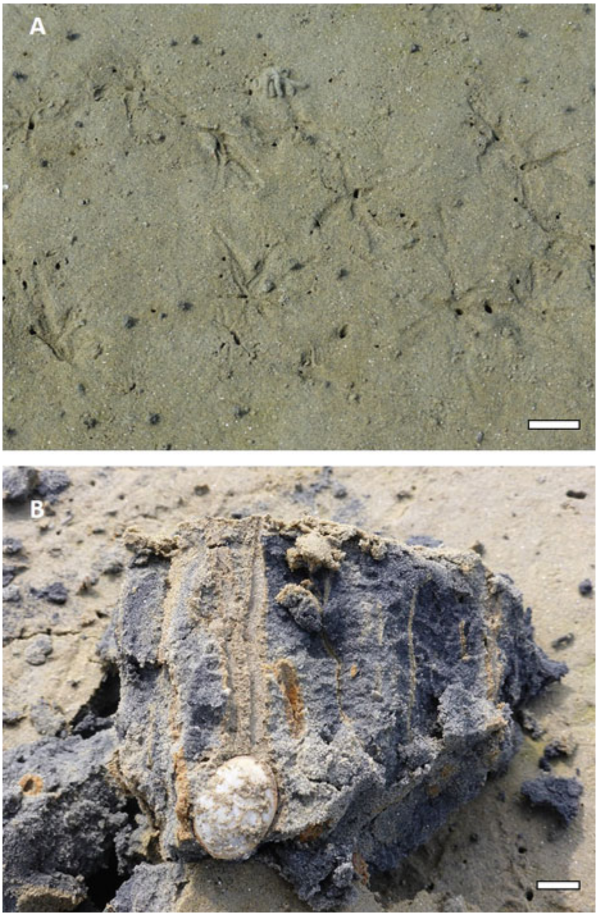

Fig. 6.7 Star-shaped surface traces (**a**) and subsurface oxidized microenvironments along siphon tracks (**b**) associated with deposit feeding of *Scrobicularia plana*. Scale bar is 5cm in (**a**) and 1 cm in (**b**). Photo credits: C. Van Colen.

bioturbation activity of *Cerastoderma edule* in laboratory incubations (Ciutat et al. 2007), and the strongest interference effects of this species on other macrofauna were found in periods with the highest suspended solids (Van Colen et al. 2013).

5 Conclusion

Invertebrate macrofauna play a pivotal role in mudflat ecosystem functioning, through trophic and non-trophic interactions associated with the functional traits of the often highly-abundant organisms. Decision-making in ecosystem-based management of these highly-valued habitats (Barbier et al. 2011) should therefore be supported by a solid understanding (and prediction) of macrofauna distribution patterns in space and time, complemented with mechanistic insights into the functional roles of macrofauna that contribute to ecosystem goods and service delivery. Such knowledge is particularly indispensable in tidal mudflats which are—due to their location between land and sea—at the frontline of the current rapid environmental change associated with multiple pressures.

References

Aberson MJR, Bolam SG, Hughes RG (2011) The dispersal and colonisation behaviour of the marine polychaete *Nereis diversicolor* (O. F. Muller) in south-east England. Hydrobiologia 672:3–14

Aberson MJR, Bolam SG, Hughes RG (2016) The effect of sewage pollution on the feeding behaviour and diet of Hediste (*Nereis diversicolor* (OF Muller, 1776)) in three estuaries in south-east England, with implications for saltmarsh erosion. Mar Pollut Bull 105:150–160

Alves RMS (2017) Spatial structure and temporal dynamics of an intertidal population of the marine ecosystem engineering worm *Lanice conchilega* (Pallas, 1766). PhD thesis, Ghent University, 168 p

Alves RMS, Vanaverbeke J, Bouma TJ, Guarini JM, Vincx M, Van Colen C (2017) Effects of temporal fluctuation in population processes of intertidal *Lanice conchilega* (Pallas, 1766) aggregations on its ecosystem engineering. Estuar Coast Shelf Sci 188:88–98

Anibal J, Rocha C, Sprung M (2007) Mudflat surface morphology as a structuring agent of algae and associated macroepifauna communities: a case study in the Ria Formosa. J Sea Res 57: 36–46

Armonies W, Hartke D (1995) Floating of mud snails *Hydrobia ulvae* in tidal waters of the Wadden Sea, and its implications in distribution patterns. Helgoländer Meeresun 49:529–538

Barbeau MA, Grecian LA, Arnold EE, Sheahan DC, Hamilton DJ (2009) Spatial and temporal variation in the population dynamics of the intertidal amphipod *Corophium volutator* in the upper Bay of Fundy, Canada. J Crustac Biol 29:491–506

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR (2011) The value of estuarine and coastal ecosystem services. Ecol Monogr 81:169–193

Beninger PG, Boldina I (2014) Fine-scale spatial distribution of the temperate infaunal bivalve *Tapes* (*=Ruditapes*) *philippinarum* (Adams and Reeve) on fished and unfished intertidal mudflats. J Exp Mar Biol Ecol 457:128–134

Beukema JJ, Dekker R (2014) Variability in predator abundance links winter temperatures and bivalve recruitment: correlative evidence from long-term data in a tidal flat. Mar Ecol Prog Ser 513:1–15

Beukema JJ, Flach EC (1995) Factors controlling the upper and lower limits of the intertidal distribution of 2 *Corophium* species in the Wadden Sea. Mar Ecol Prog Ser 125:117–126

Beukema JJ, Essink K, Michaelis H, Zwarts L (1993) Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds? Neth J Sea Res 31(4):319–330

Bocher P, Piersma T, Dekinga A, Kraan C, Yates MG, Guyot T, Folmer EO, Radenac G (2007) Site- and species-specific distribution patterns of molluscs at five intertidal soft-sediment areas in northwest Europe during a single winter. Mar Biol 151:577–594

Bolam SG, Fernandes TF, Huxham M (2002) Diversity, biomass, and ecosystem processes in the marine benthos. Ecol Monogr 72:599–615

Boldina I, Beninger PG (2013) Fine-scale spatial structure of the exploited infaunal bivalve *Cerastoderma edule* on the French Atlantic coast. J Sea Res 76:193–200

Boldina I, Beninger PG (2014) Fine-scale spatial distribution of the common lugworm Arenicola marina, and effects of intertidal clam fishing. Estuar Coast Shelf Sci 143:32–40

Bouma TJ, Ortells V, Ysebaert T (2009) Comparing biodiversity effects among ecosystem engineers of contrasting strength: macrofauna diversity in *Zostera noltii* and *Spartina anglica* vegetations. Helgol Mar Res 63:3–18

Cadee GC (1976) Sediment reworking by Arenincola marina on tidal flats in Dutch Wadden Sea. J Sea Res 10(4):440–460

Cadee GC (1979) Sediment reworking by the polychaete *Heteromastus filiformis* on a tidal Flat in the Dutch Wadden Sea. Neth J Sea Res 13:441–456

Chapman MG, Tolhurst TJ, Murphy RJ, Underwood AJ (2010) Complex and inconsistent patterns of variation in benthos, micro-algae and sediment over multiple spatial scales. Mar Ecol Prog Ser 398:33–47

Ciutat A, Widdows J, Pope ND (2007) Effect of *Cerastoderma edule* density on near-bed hydrodynamics and stability of cohesive muddy sediments. J Exp Mar Biol Ecol 346:114–126

Connell JH (1978) Diversity in tropical rain forests and coral reefs – high diversity of trees and corals is maintained only in a non-equilibrium state. Science 199:1302–1310

Coull BC (1999) Role of meiofauna in estuarine soft-bottom habitats. Aust J Ecol 24:327–343

Davies MS, Beckwith P (1999) Role of mucus trails and trail-following in the behaviour and nutrition of the periwinkle *Littorina littorea*. Mar Ecol Prog Ser 179:247–257

Davies MS, Blackwell J (2007) Energy saving through trail following in a marine snail. Proc R Soc Biol Sci 274:1233–1236

De Backer A, Van Ael E, Vincx M, Degraer S (2010) Behaviour and time allocation of the mud shrimp, *Corophium volutator*, during the tidal cycle: a laboratory study. Helgol Mar Res 64:63–67

De Backer A, Van Coillie F, Montserrat F, Provoost P, Van Colen C, Vincx M, Degraer S (2011) Bioturbation effects of *Corophium volutator*: importance of density and behavioural activity. Estuar Coast Shelf Sci 91:306–313

De Smet B, D'Hondt AS, Verhelst P, Fournier J, Godet L, Desroy N, Rabaut M, Vincx M, Vanaverbeke J (2015) Biogenic reefs affect multiple components of intertidal soft-bottom benthic assemblages: the *Lanice conchilega* case study. Estuar Coast Shelf Sci 152:44–55

Drolet D, Barbeau MA (2009a) Diel and semi-lunar cycles in the swimming activity of the intertidal, benthic amphipod *Corophium volutator* in the upper Bay of Fundy, Canada. J Crustac Biol 29:51–56

Drolet D, Barbeau MA (2009b) Differential emigration causes aggregation of the amphipod *Corophium volutator* (Pallas) in tide pools on mudflats of the upper Bay of Fundy, Canada. J Exp Mar Biol Ecol 370:41–47

Esselink P, Zwarts L (1989) Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis diversicolor*. Mar Ecol Prog Ser 56:243–254

Essink K (2003) Response of an estuarine ecosystem to reduced organic waste discharge. Aquat Ecol 37:65–76

Flach EC (1992) The Influence of 4 macrozoobenthic species on the abundance of the amphipod *Corophium volutator* on tidal flats of the Wadden Sea. Neth J Sea Res 29:379–394

Flynn AM, Smee DL (2010) Behavioral plasticity of the soft-shell clam, *Mya arenaria* (L.), in the presence of predators increases survival in the field. J Exp Mar Biol Ecol 383:32–38

Giere O (2006) Ecology and biology of marine oligochaeta – an inventory rather than another review. Hydrobiologia 564:103–116

Green L, Fong P (2016) The good, the bad and the *Ulva*: the density dependent role of macroalgal subsidies in influencing diversity and trophic structure of an estuarine community. Oikos 125: 988–1000

Grilo TF, Cardoso PG, Dolbeth M, Bordalo MD, Pardal MA (2011) Effects of extreme climate events on the macrobenthic communities' structure and functioning of a temperate estuary. Mar Pollut Bull 62:303–311

Guarini JM, Blanchard GF, Bacher C, Gros P, Riera P, Richard P, Gouleau D, Galois R, Prou J, Sauriau PG (1998) Dynamics of spatial patterns of microphytobenthic biomass: inferences from a geostatistical analysis of two comprehensive surveys in Marennes-Oléron Bay (France). Mar Ecol Prog Ser 166:131–141

Hampel H, Cattrijsse A, Mees J (2004) Changes in marsh nekton communities along the salinity gradient of the Schelde river, Belgium and The Netherlands. Hydrobiologia 515: 137–146

Herman PMJ, Middelburg JJ, Widdows J, Lucas CH, Heip CHR (2000) Stable isotopes' as trophic tracers: combining field sampling and manipulative labelling of food resources for macrobenthos. Mar Ecol Prog Ser 204:79–92

Herman PMJ, Middelburg JJ, Heip CHR (2001) Benthic community structure and sediment processes on an intertidal flat: results from the ECOFLAT project. Cont Shelf Res 21:2055–2071

Hiddink JG, Kock RP, Wolff WJ (2002a) Active pelagic migrations of the bivalve *Macoma balthica* are dangerous. Mar Biol 140:1149–1156

Hiddink JG, Marijnissen SAE, Troost K, Wolff WJ (2002b) Predation on O-group and older year classes of the bivalve *Macoma balthica*: interaction of size selection and intertidal distribution of epibenthic predators. J Exp Mar Biol Ecol 269:223–248

Hiddink JG, ter Hofstede R, Wolff WJ (2002c) Predation of intertidal infauna on juveniles of the bivalve *Macoma balthica*. J Sea Res 47:141–159

Hunt HL (2004) Transport of juvenile clams: effects of species and sediment grain size. J Exp Mar Biol Ecol 312:271–284

Huxham M, Richards M (2003) Can postlarval bivalves select sediment type during settlement? A field test with *Macoma balthica* (L.) and *Cerastoderma edule* (L.). J Exp Mar Biol Ecol 288:279–293

Kaiser MJ, Broad G, Hall SJ (2001) Disturbance of intertidal soft-sediment benthic communities by cockle hand raking. J Sea Res 45:119–130

Kraan C, van der Meer J, Dekinga A, Piersma T (2009) Patchiness of macrobenthic invertebrates in homogenized intertidal habitats: hidden spatial structure at a landscape scale. Mar Ecol Prog Ser 383:211–224

Kristensen E, Kostka JE (2005) Macrofaunal burrows and irrigation in marine sediment: microbiological and biogeochemical interactions. In: Kristensen E, Haese RR, Kostka JE (eds) Interactions between macro- and microorganisms in marine sediments. American Geophysical Union, New York, pp 125–157

Kristensen E, Penha-Lopes G, Delefosse M, Valdemarsen T, Quintana CO, Banta GT (2012) What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar Ecol Prog Ser 446:285–302

Le Pennec M, Beninger PG, Herry A (1995) Feeding and digestive adaptations of bivalve molluscs to sulphide-rich habitats. Comp Biochem Physiol A Physiol 111(2):183–189

Mermillod-Blondin F, Rosenberg R, Francois-Carcaillet F, Norling K, Mauclaire L (2004) Influence of bioturbation by three benthic infaunal species on microbial communities and biogeochemical processes in marine sediment. Aquat Microb Ecol 36:271–284

Meysman FJR, Middelburg JJ, Heip CHR (2006) Bioturbation: a fresh look at Darwin's last idea. Trends Ecol Evol 21:688–695

Michaud E, Desrosiers G, Mermillod-Blondin F, Sundby B, Stora G (2006) The functional group approach to bioturbation: II. The effects of the *Macoma balthica* community on fluxes of nutrients and dissolved organic carbon across the sediment-water interface. J Exp Mar Biol Ecol 337:178–189

Montserrat F, Van Colen C, Provoost P, Milla M, Ponti M, Van den Meersche K, Ysebaert T, Herman PMJ (2009) Sediment segregation by biodiffusing bivalves. Estuar Coast Shelf Sci 83:379–391

Murphy RJ, Tolhurst TJ, Chapman MG, Underwood AJ (2008) Spatial variation of chlorophyll on estuarine mudflats determined by field-based remote sensing. Mar Ecol Prog Ser 365:45–55

Nieuwhof S, Herman PMJ, Dankers N, Troost K, van der Wal D (2015) Remote sensing of epibenthic shellfish using synthetic aperture radar satellite imagery. Remote Sens 7:3710–3734

Orvain F, Sauriau PG, Sygut A, Joassard L, Le Hir P (2004) Interacting effects of *Hydrobia ulvae* bioturbation and microphytobenthos on the erodibility of mudflat sediments. Mar Ecol Prog Ser 278:205–223

Peterson CH, Summerson HC, Fegley SR (1983) Relative efficiency of 2 clam rakes and their contrasting impacts on seagrass meadows. Fish Bull 81:429–434

Raffaelli D, Emmerson M, Solan M, Biles C, Paterson D (2003) Biodiversity and ecosystem processes in shallow coastal waters: an experimental approach. J Sea Res 49:133–141

Reise K (1983) Biotic enrichment of intertidal sediments by experimental aggregates of the deposit feeding bivalve *Macoma balthica*. Mar Ecol Prog Ser 12:229–236

Reise K (1985) Macrofauna promotes meiofauna. Tidal flat ecology. An experimental approach to species interactions. Springer, Berlin

Reise K, Simon M, Herre E (2001) Density-dependent recruitment after winter disturbance on tidal flats by the lugworm *Arenicola marina*. Helgol Mar Res 55:161–165

Riisgard HU (1991) Suspension feeding in the polychaete *Nereis diversicolor*. Mar Ecol Prog Ser 70:29–37

Rossi F, Como S, Corti S, Lardicci C (2001) Seasonal variation of a deposit feeder assemblage and sedimentary organic matter in a brackish basin mudflat (Western Mediterranean, Italy). Estuar Coast Shelf Sci 53:181–191

Rossi F, Herman PMJ, Middelburg JJ (2004) Interspecific and intraspecific variation of delta C-13 and delta N-15 in deposit- and suspension-feeding bivalves (*Macoma balthica* and *Cerastoderma edule*): evidence of ontogenetic changes in feeding mode of *Macoma balthica*. Limnol Oceanogr 49:408–414

Rossi F, Forster RM, Montserrat F, Terlizzi A, Ysebaert T, Middelburg JJ (2007) Human trampling as short-term disturbance on intertidal mudflats: effects on macrofauna biodiversity and population dynamics of bivalves. Mar Biol 151:2077–2090

Schratzberger M, Warwick RM (1999) Impact of predation and sediment disturbance by *Carcinus maenas* (L.) on free-living nematode community structure. J Exp Mar Biol Ecol 235:255–271

Seuront L, Spilmont N (2002) Self-organized criticality in intertidal microphytobenthos patch patterns. Phys A Stat Mech Appl 313:513–539

Thrush SF, Pridmore RD, Hewitt JE, Cummings VJ (1991) Impact of ray feeding disturbances on sandflat macrobenthos – do communities dominated by polychaetes or shellfish respond differently. Mar Ecol Prog Ser 69:245–252

Van Colen C, Lenoir J, De Backer A, Vanelslander B, Vincx M, Degraer S, Ysebaert T (2009) Settlement of *Macoma balthica* larvae in response to benthic diatom films. Mar Biol 156: 2161–2171

Van Colen C, De Backer A, Meulepas G, van der Wal D, Vincx M, Degraer S, Ysebaert T (2010a) Diversity, trait displacements and shifts in assemblage structure of tidal flat deposit feeders along a gradient of hydrodynamic stress. Mar Ecol Prog Ser 406:79–89

Van Colen C, Montserrat F, Vincx M, Herman PMJ, Ysebaert T, Degraer S (2010b) Macrobenthos recruitment success in a tidal flat: feeding trait dependent effects of disturbance history. J Exp Mar Biol Ecol 385:79–84

Van Colen C, Montserrat F, Vincx M, Herman PMJ, Ysebaert T, Degraer S (2010c) Long-term divergent tidal flat benthic community recovery following hypoxia-induced mortality. Mar Pollut Bull 60:178–186

Van Colen C, Thrush SF, Vincx M, Ysebaert T (2013) Conditional responses of benthic communities to interference from an intertidal bivalve. PLoS One 8:e65861

Van de Koppel J, Herman PMJ, Thoolen P, Heip CHR (2001) Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. Ecology 82:1449–3461

van der Wal D, Herman PMJ, Forster RM, TYsebaert T, Rossi F, Knaeps E, Plancke YMG, Ides SJ (2008) Distribution and dynamics of intertidal macrobenthos predicted from remote sensing: response to microphytobenthos and environment. Mar Ecol Prog Ser 367:57–72

van Oevelen D, Soetaert K, Middelburg JJ, Herman PMJ, Moodley L, Hamels I, Moens T, Heip CHR (2006) Carbon flows through a benthic food web: integrating biomass, isotope and tracer data. J Mar Res 64:453–482

Yap WG (1977) Population biology of the Japanese Little-neck clam, *Tapes philippinarum*, in Kaneohe Bay, Oahu, Hawaiian Islands. Pac Sci 31:223–244

Ysebaert T (2000) Macrozoobenthos and waterbirds in the estuarine environment: spatio-temporal patterns at different scales. PhD thesis, University of Antwerp, 180 p

Ysebaert T, De Neve L, Meire P (2000) The subtidal macrobenthos in the mesohaline part of the Schelde estuary (Belgium): influenced by man? J Mar Biol Assoc UK 80:587–597

Ysebaert T, Herman PMJ, Meire P, Craeymeersch J, Verbeek H, Heip CHR (2003) Large-scale spatial patterns in estuaries: estuarine macrobenthic communities in the Schelde estuary, NW Europe. Estuar Coast Shelf Sci 57:335–355

Zajac RN (2004) Macrofaunal responses to pit-mound patch dynamics in an intertidal mudflat: local versus patch-type effects. J Exp Mar Biol Ecol 313:297–315

Zwarts L, Wanink JH (1993) How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. Neth J Sea Res 31(4):441–476

Chapter 7
Bivalve Chemosymbioses on Mudflats

Suzanne C. Dufour

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Abstract Mudflat sediments are typically enriched in reduced sulfur compounds, which can fuel bacterial chemoautotrophic production. Symbiotic associations between marine bivalves and chemolithoautotrophic, sulfur-oxidizing bacteria are common in sulfur-rich marine habitats, and the presence of infaunal chemosymbiotic bivalves in mudflats is reviewed herein. Chemosymbiotic bivalves from the families Lucinidae, Solemyidae and Thyasiridae have been reported to inhabit intertidal sediments, especially within, or near seagrass beds or mangroves; of the three families, the Lucinidae can be particularly abundant. Chemosymbiotic bivalves can alter chemical conditions in sediments, influence carbon and sulfur cycles, and provide a food source to invertebrates, birds and humans. In general, chemosymbiotic bivalves are uncommon in mudflats, despite the abundance of reduced sulfur, and reasons for their relative paucity in intertidal sediments are discussed.

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1 Sulfide Production and Chemosynthesis

Mudflats may occupy extensive portions of the world's coastlines, where they often border vegetated intertidal environments (salt marshes and mangroves), as well as subtidal seagrass beds. Due to their location, mudflats often receive organic matter from a range of sources, with exports from adjacent vegetated, terrestrial and marine environments supplementing autochthonous production from microphytobenthos, macroalgae and bacteria (Cammen 1991; Sundbäck et al. 2000; Cook et al. 2004). Organic matter is often abundant in mudflats, fueling microbial respiration and generating the chemical conditions that characterize mudflat sediments.

Compared to intertidal sediments with coarser substrates, mudflats have low permeability, limiting the depth to which oxygen can diffuse into the sediment matrix. Oxygen is the most favorable electron acceptor for microbial respiration and is rapidly consumed during organic matter degradation; in muddy substrates with low permeability, the oxic surface layer of sediments may be on the order of millimeters (Kristensen 2000). Beneath the oxic surface, sediments are anoxic, and organic matter breakdown proceeds anaerobically. Sulfate is the major electron acceptor for respiration in anoxic sediments, a process which leads to the accumulation of reduced sulfur compounds such as dissolved sulfides, thiosulfate, elemental sulfur and iron sulfides (Howarth 1984; see also Chaps. 2, 3, 8) Sulfides are toxic for many animals, but are energy-rich substrates for chemolithoautophic bacteria near the oxic-anoxic interface (Kristensen 2000). Chemolithoautotrophic production may constitute a major pathway for energy production in coastal marine sediments (Howarth 1984).

Many invertebrates have evolved highly specialized symbioses with chemolithoautotrophic, sulfur-oxidizing bacteria, where hosts derive nutrients from bacterial symbionts living within or at the surface of their tissues or bodies (Dubilier et al. 2008). Chemosymbioses were first discovered in 1977 at deep-sea hydrothermal vents, and most of the research on chemosymbiotic animals has centered around inhabitants from vents and cold seeps. However, many other marine habitats contain sulfide-oxygen interfaces and can support chemosynthesis, and it has been noted that the most widespread sulfidic habitat is the anoxic zone of shallow marine sediments (Fenchel and Reidl 1970; Stewart et al. 2005). Infaunal chemosymbiotic bivalves from three families have been reported to inhabit mudflats, and their biology, ecological, and economical importance are reviewed herein. Rather than being a comprehensive survey of all known chemosymbiotic bivalves, representative examples have been chosen from each family. Most chemosymbiotic bivalves inhabiting mudflats are seagrass bed or mangrove inhabitants that can also colonize marginal, non-vegetated sediments, rather than being restricted to mudflat environments.

2 Survey of Chemosymbiotic Bivalves in Mudflats

2.1 Lucinids

The family Lucinidae is the most diverse family of chemosymbiotic bivalves, comprising approximately 500 living species (Taylor and Glover 2006). All species examined within the family establish symbioses with sulfur-oxidizing bacteria, and many authors consider that all living species are chemosymbiotic (Taylor and Glover 2006). The family has a wide geographic and habitat distribution: some lucinid species are deep-water inhabitants, colonizing shelf and slope sediments (Taylor et al. 2014) or cold seeps (Salas and Woodside 2002), while many others inhabit substrates at shallower depths, predominantly in the tropics (Taylor and Glover 2000; van der Heide et al. 2012). In the past few decades, a considerable effort has been directed at describing lucinids from tropical regions, notably the Indo-Pacific, and numerous new species and some new genera have been described (e.g. Glover and Taylor 2001, 2007; von Cosel 2006; Glover et al. 2008).

In shallow water and the intertidal zone, lucinids are often found at high densities among the roots and rhizomes of seagrasses (Allen 1958; Jackson 1973; Barnes and Hickman 1999; van der Heide et al. 2012; van der Geest et al. 2014) or mangroves (Oliver 1986; Frenkiel et al. 1995; Lebata 2001; Glover et al. 2008; Meyer et al. 2008; Zabbey et al. 2010), with only a few species found in non-vegetated sediments (Glover et al. 2008). The latter species occur, often in high abundance, in organic-rich outer fringes of mangroves (e.g. *Anodontia philippiana* and *Austriella corrugata*, Taylor and Glover 2000; *Indoaustriella plicifera*, *I. lamprelli*, *I. dall* and *I. scarlatoi*, Glover et al. 2008) or in the vicinity of seagrass beds (*Lucinella divaricata*, Herry and Le Pennec 1987, *Loripes lucinalis*, Petersen et al. 2016). Some lucinids were described as inhabiting (presumably non- or sparsely-vegetated) intertidal mud, fine sand or muddy sand (e.g. *Pillucina* spp., Glover and Taylor 2001; *Lucinoma borealis*, Allen 1958; Dando et al. 1986; Southward 1986; Herry et al. 1989; *Lucina floridana*, Distel and Felbeck 1987; *Linga pensylvanica*, Gros et al. 1996); some such locations may consist of mudflats. The species *P. pacifica* was specifically reported to occupy mudflats (Glover and Taylor 2001).

Lucinids form symbiotic associations with sulfur-oxidizing gammaproteobacteria, maintained intracellularly within specialized cells in the abfrontally-expanded 'bacteriocyte zone' of gill filaments (Fisher 1990; Duperron et al. 2013). Lucinid symbionts are acquired from free-living populations in their sedimentary environment (Gros et al. 2003). Symbiont acquisition is initiated at the juvenile stage, following metamorphosis (Gros et al. 1996), and can also take place in adults (Gros et al. 2012). Lucinid species associate with one or, in some species, a few symbiont phylotypes (Ball et al. 2009). Three closely related species of symbionts, each comprised of multiple haplotypes, have been described from lucinids sampled worldwide; host-symbiont associations reflect habitat type rather than co-evolution (Brissac et al. 2011). Two lucinid symbiont species may be specialists of mangrove swamps (Brissac et al. 2011).

Lucinids are dependent upon their symbionts as a source of fixed carbon (Spiro et al. 1986) but retain the ability to suspension-feed; they have both hypertrophied gills with a large number of bacteriocytes and a fully functional digestive tract (Le Pennec et al. 1995a). Seston is considered to be nutritionally important to many chemosymbiotic bivalves, with seasonal peaks in phytoplankton regulating host growth and reproductive cycles (Le Pennec et al. 1995b; Le Pennec and Beninger 2000), even in tropical lucinids from seagrass covered intertidal flats, where seasonal changes are less pronounced than at higher latitudes (*Loripes lucinalis*, van der Geest et al. 2014). Lucinids may also obtain fixed nitrogen from their symbionts, as demonstrated in *Loripes lucinalis* sampled from mudflats adjacent to seagrass beds (Petersen et al. 2016).

2.2 Solemyids

Solemyids (order Solemyida) contain approximately 25 species (Roeselers and Newton 2012) and belong to what is generally considered to be the most ancient group of living bivalves, the Protobranchia (Healy et al. 2017). Solemyids are entirely infaunal, found in sediments with a high silt/clay fraction, including in the intertidal zone (Zardus 2002); they can be particularly abundant in seagrass beds (Stanley 1970; Rainer and Wadley 1991). *Solemya velum*, the best studied among the solemyids, lives within or near intertidal or subtidal beds of *Zostera marina*, from Nova Scotia to Florida (Roeselers and Newton 2012), and is one of the few protobranchs living intertidally (Zardus 2002), including in mudflats.

All solemyids examined have a gut that is either reduced (e.g. *Solemya velum*; Reid and Bernard 1980, *S. parkinsoni*; Owen 1961) or absent (e.g. *S. reidii*; Reid 1980), and hypertrophied gills that maintain large populations of intracellular, sulfur-oxiziding chemoautotrophic symbionts (Cavanaugh 1985; Zardus 2002; Scott 2005; Stewart and Cavanaugh 2006); some derive additional nutrients by suspension-feeding (Krueger et al. 1992). Different symbiont species associate with a single, distinct species of gammaproteobacteria (Stewart and Cavanaugh 2006), which may form heterogeneous populations within a host (Russell and Cavanaugh 2017).

Solemyids are notable in their extensive reliance upon symbiont-derived nutrients; the latter were estimated to meet up to 98% of host carbon requirements in *Solemya velum* sampled from subtidal sediments (Conway et al. 1989). In the same species, symbionts are transmitted vertically, via oocytes (Krueger et al. 1996) and through frequent horizontal transmission events (Russell et al. 2017). Unlike other solemyids, which produce free-swimming pericalymma larvae (Zardus 2002), there is no planktonic stage in *S. velum*: embryos develop in negatively buoyant, benthic gelatinous capsules, and juveniles burrow directly in sediments after hatching (Gustafson and Lutz 1992). However, postmetamorphic solemyids are able to swim (Drew 1900; Yonge 1939) and *S. velum* has been observed to be periodically common in meroplankton samples (Williams and Porter 1971). Nevertheless, dispersal in *S. velum* is likely limited given the observed geographic subdivision of host and symbiont populations (Russell et al. 2017).

2.3 Thyasirids

The family Thyasiridae (Super-Family Thyasiroidae) contains approximately 100 described species, most of which measure less than 10 mm in shell length (Taylor et al. 2007). The family has a global distribution but is mainly restricted to colder waters: although they may be found intertidally at high latitudes, thyasirids are most common in the deep-sea (Payne and Allen 1991). Some species in the family establish symbioses with chemoautotrophic, sulfur-oxidizing bacteria while others are asymbiotic (Dando and Southward 1986; Southward 1986; Dufour 2005). Symbiotic thyasirids are mixotrophs and vary in their degree of dependence upon their symbionts as a source of nutrients (Dando and Spiro 1993). Thyasirid symbionts are extracellular, maintained among microvilli at the apical end of gill epithelial cells, with the degree of abfrontal expansion of gill filaments varying among species (Southward 1986; Dufour 2005). The symbionts of thyasirids are acquired from surrounding sediments (Dufour et al. 2014) and host individuals may host mixed symbiont populations, consisting of more than one bacterial phylotype (McCuaig et al. 2017).

Chemosymbiotic thyasirids can colonize a range of sediment types and are often found in organic-rich substrates (Taylor et al. 2007). Very few thyasirid species were reported from mudflats: *Thyasira flexuosa* was sampled from the level of the extreme low water spring tide in the Salcombe estuary, UK (Dando and Southward 1986), and *T. gouldi* was occasionally found intertidally at various locations along the eastern coast of Greenland (Ockelmann 1958).

3 Ecological Importance

All chemosymbiotic bivalves that colonize mudflats are infaunal and share physiological and behavioural traits that can impact their sedimentary habitats. The ecological consequences of chemosymbiotic bivalve burrowing and bioirrigation in mudflats are briefly discussed below, along with some examples of how these bivalves can subsidize higher trophic levels. Finally, an overview of the human harvesting of tropical chemosymbiotic bivalves is presented.

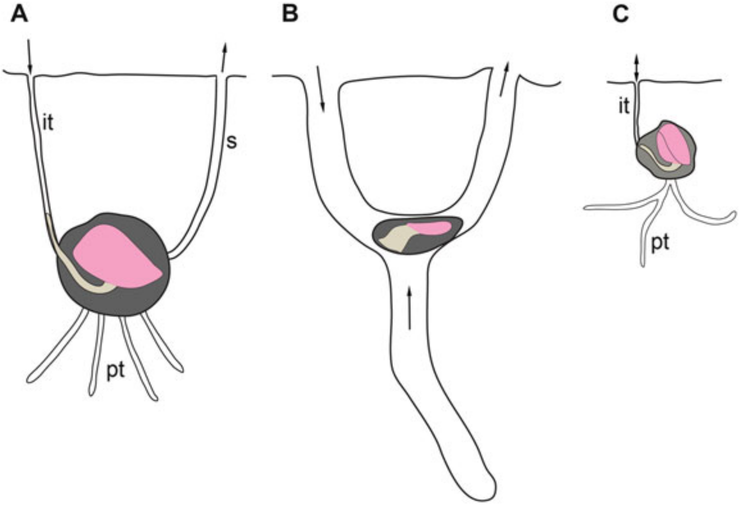

Fig. 7.1 Biogenic structures of infaunal chemosymbiotic bivalves, with arrows showing the direction of water flow. (**a**) Lucinids construct a mucus-lined inhalant tube (it) and pedal tracts (pt). Exhalant current is through a siphon (s) in many species. (**b**) Solemyids construct U or Y shaped burrows. (**c**) Thyasirids have a single inhalant tube (it) through which water flows in both directions, as well as branched pedal tracts (pt). Bacteria-housing gills are in pink, and the foot is in beige. Modified from Stanley (2014), Stewart and Cavanaugh (2006), Zanzerl and Dufour (2017). Not to scale.

3.1 Bioturbation and Bioirrigation

Lucinids, solemyids and thyasirids are relatively slow, deep burrowers that lack an inhalant siphon and maintain contact with overlying water through mucus-lined inhalant tubes (Fig. 7.1); solemyids and some lucinids lacking an exhalant siphon also form exhalant tubes (Allen 1953; Frey 1968; Stanley 1970; Dando and Southward 1986). Examined specimens from the three taxa also produce biogenic structures that radiate from the ventral edge of the shell and presumably act as sulfide wells (Stanley 1970; Dando et al. 1985; Dufour and Felbeck 2003). Altogether, the sedimentary structures formed by lucinids, solemyids and thyasirids are permanent or semi-permanent, and the amount of sediment mixing induced during burrow formation and maintenance is likely to be minimal, consisting mainly of the downward-conveying of particles through inhalant tubes along with some surficial reworking (Queirós et al. 2013). The biogeochemical consequences of irrigating the structures constructed by those bivalves are probably of greater ecological importance than sediment reworking (bioturbation) in itself, although this has not been directly studied.

Stanley (1970) performed detailed observations of burrowing behaviours in a wide range of bivalves from the Western Atlantic, including the lucinids *Codakia orbicularis* and *Anodontia alba* from intertidal seagrass beds, *Phacoides pectinatus* from intertidal muds and a protected pond near mangroves, and *Divaricella quadrisulcata* from moderately exposed, sparsely vegetated intertidal flats. Lucinids either remained close to the sediment surface (2–5 cm depth for *C. orbicularis* of <9 cm in shell length), or burrowed to depths between 5 and 20 cm; notably, larger *P. pectinatus* (5–7 cm in length) were found 50 cm below the sediment surface in muddy peat near mangroves (Stanley 1970). Once buried, lucinids constructed nearly vertical, mucus-lined inhalant tubes, as well as a posterior exhalant tube, using their vermiform foot. Additionally, pedal probing marks were noted beneath the ventral shell margin for *C. orbicularis, P. pectinatus* (Fig. 7.1a; Stanley 1970), and for *Lucinoma borealis* (Dando et al. 1986). In the latter species, sediment surrounding the inhalant tubes becomes visibly oxidized as oxygen from the inhalant stream diffuses into surrounding porewater (resulting in a cone of paler sediment), and the animal frequently forms a new inhalant tube to access additional reduced sulfur (Dando et al. 1986).

Solemyids can also be deep burrowers: burrowing depths of 50 cm or more were recorded for *S. parkinsoni* sampled from sandy mud near low water spring tide (Owen 1961). *S. velum* observed in tidal flats commonly burrow to a depth of 7–8 cm (Frey 1968); in the lab, they attained depths of 15–23 cm (Morse 1913). Intertidal species have been observed to construct Y-shaped burrows (Frey 1968; Stanley 1970), or U-shaped burrows (*S. velesiana*; Reid and Brand 1987), with the bivalve ordinarily resting at the bottom of the U-shaped part of the burrow (Fig. 7.1b; Stanley 1970). Burrow openings to the sediment surface are not always evident (Yonge 1939; Owen 1961). The upper portions of solemyid burrows act as inhalant and exhalant tubes, and solemyids are thought to pump oxygenated water from their resting position down to their mantle cavity, and access reduced sulfur via diffusion from lower portions of the burrow (Stewart and Cavanaugh 2006).

Chemosymbiotic thyasirids sampled from subtidal regions vary in burial depth, having been reported both within the upper few cm of cores (*Thyasira flexuosa*; Dando and Southward 1986; Dauwe et al. 1998), within the first 8 cm (*T. sarsi*; Dando and Southward 1986) as well as at greater than 10 cm depth (*T. equalis*; Rosenberg et al. 2007). Thyasirids also use their foot to establish a mucus-lined inhalant tube (Allen 1958; Dando and Southward 1986), but construct no exhalant tube. Chemosymbiotic thyasirids, as well as some asymbiotic thyasirids (Zanzerl and Dufour 2017), establish elongate, ramifying burrows, or pedal tracts, that radiate within sediments (Fig. 7.1c; Dando and Southward 1986; Dufour and Felbeck 2003). Thyasirid pedal tracts allow the bivalves to access reduced sulfur in sediments (Dufour and Felbeck 2003), and their length and number are related to dissolved sulfide availability (Dufour and Felbeck 2003).

3.2 Biogeochemistry and Nutrient Fluxes

The bioirrigation induced by lucinids and thyasirids clearly impacts sediment chemistry, and has led some authors to qualify them as ecosystem engineers (Dando et al. 2004;

Chap. 10). Lucinids and thyasirids (and probably also solemyids—see Stewart and Cavanaugh 2006) mainly affect sediment biogeochemistry through three pathways: the oxygenation of sediments around permeable biogenic structures (inhalant tube and pedal tracts), the enhancement of sulfur oxidation, and the symbiont's carbon fixation. Where abundant, chemosymbiotic bivalves can deplete sedimentary sulfides and facilitate subsequent colonization of sediments by less sulfur-tolerant species (Dando and Spiro 1993; Reynolds et al. 2007). In shallow waters, lucinid-enhanced sulfide depletion was shown to enhance seagrass production (van der Heide et al. 2012). In a seagrass bed with abundant *Loripes lacteus*, the latter played significant roles in carbon cycling, as chemoautotrophic production was calculated to represent 16% of the total primary production in that ecosystem (Johnson et al. 2002).

Where lucinids inhabit sulfidic sediments (as in many seagrass beds), they may lead to significant decreases in porewater sulfide concentration (Reynolds et al. 2007). Elsewhere, such as in the Salcombe Estuary, UK, lucinids occur in sediments with little to no measurable sulfide or thiosulfate, as reduced sulfur is bound to metals such as iron or manganese (Dando et al. 1986). At this site, the lucinid *Lucinoma borealis* lives intertidally near seagrass beds and obtains reduced sulfur species by mining iron-bound sulfides from surficial sediments: as oxygenated water is pumped into the mantle cavity through the inhalant tube, iron-bound sulfides are chemically oxidized into forms that can be used by the symbionts (Dando et al. 1994). The thyasirid *Thyasira sarsi* can also mine unsoluble sulfides from sediments surrounding its permeable inhalant tube (Dando et al. 2004).

In thyasirids, the oxidation of near-burrow sediments is not restricted to the inhalant tube. Observations of pH distributions around the biogenic structures of *Thyasira sarsi* using optodes have revealed the presence of steep pH gradients (indicative of zones of active redox cycling) around both the inhalant tube and pedal tracts (Hakonen et al. 2010). Therefore, sediment oxidation and associated sulfur cycling may occur in a greater volume of sediment than solely around the animal's inhalant tube.

Bioirrigation of the inhalant tube and pedal tracts of infaunal chemosymbiotic bivalves, combined with the secretion of a mucus lining, may enhance the productivity of microbes (particularly sulfur-oxidizers) around the burrow lining, as observed for other burrowing invertebrates (Papaspyrou et al. 2006; Vasquez-Cardenas et al. 2016). This microbiota may serve as a supplementary source of food to those bivalves (Zanzerl and Dufour 2017), and enhance the food supply for other meiofauna and macrofauna.

Some chemosymbiotic bivalves may also play important roles in nitrogen cycling. Recently, the symbiont of *Loripes lucinalis* was shown to be capable of nitrogen fixation, and it was suggested that these chemosymbionts may contribute new nitrogen to their ecosystems (Petersen et al. 2016). The increased seagrass production associated with lucinid presence (van der Heide et al. 2012) may therefore be related not only to sulfur removal, but also to nitrogen provisioning via symbiont metabolism (Petersen et al. 2016). Mudflat ecosystems might also benefit from those ecosystem functions related to chemosymbiotic bivalves, especially where they occur at high densities.

3.3 Food Source

Intertidal-dwelling chemosymbiotic bivalves may serve as an important food source for specialist predators, including species of commercial importance. In seagrass beds off Australia, solemyids constituted up to 22% of nutrients required by juvenile rock lobsters, *Panulirus cygnus* (Rainer and Wadley 1991), and similarly, the lucinid *Codakia orbicularis* from seagrass meadows contributed approximately 20% of the nutrient needs of the Caribbean spiny lobster *Panulirus argus* (Higgs et al. 2016). *C. orbicularis* are also commonly preyed upon by *Sinum spp.* moon snails (Higgs et al. 2016), and lucinid shells showing obvious signs of gastropod predation have been noted elsewhere (Johnson et al. 2002; Rattanachot and Prathep 2015). In mangrove swamps of the Niger Delta, the lucinid *Keletistes rhizoecus* is preyed upon by the African mud crab *Panopeus africanus* (Zabbey et al. 2010). Molluscivorous birds were also shown to consume chemosymbiotic lucinids. *Loripes lucinalis*, an abundant inhabitant of seagrass beds, is a food source for large flocks of Red Knots in the Banc d'Arguin, Mauritania (van Gils et al. 2012), despite the fact that the lucinid is mildly toxic to the bird due to its sulfide content (van Gils et al. 2013). Some shallow-water chemosymbiotic bivalves can therefore be important prey items, especially where they occur in high abundance. However, it is important to note that the aforementioned bivalves show a clear preference for seagrass habitats, and it remains unclear whether the more sparse chemosymbiotic fauna of unvegetated mudflats make a considerable contribution to the diet of any predators.

Some chemosymbiotic bivalves are also an important source of food and income for humans. *Anodontia edentulata* (*A. philippiana*, see Taylor and Glover 2005) has a wide distribution in mangroves and adjacent mudflats in the Indo-West Pacific, and is harvested in central and southern regions of the Philippines, where it is a valuable and highly prized delicacy (Lebata 2000, 2001), with alleged aphrodisiac qualities (Primavera et al. 2002). The species burrows up to a meter deep in sulfidic muds around mangroves, and harvesting is performed using a blade or bare hands following the localization of the inhalant tube aperture, or, more destructively, by digging trenches in mangrove stands (Fig. 7.2; Primavera et al. 2002). The large lucinid *Austriella corrugata*, an inhabitant of mangrove muds and bordering sediments, is also commercially harvested in the Philippines (Glover et al. 2008). On the coast of Bahia (Brazil), the lucinid *Lucina pectinata* (= *Phacoides pectinatus*) inhabits mangrove channels and stands, and forms an important source of income to local shellfish harvesters (Rondinelli and Barros 2010). *Codakia orbicularis* is also consumed in the Caribbean and South America (Berg and Alatalo 1984). Lucinids have been reared from larvae (Gros et al. 1997, 1999) and show potential for aquaculture: larger, valuable species could be cultivated in tidal channels or mangroves, with economic benefit to coastal communities (Berg and Alatalo 1984; Christo et al. 2016).

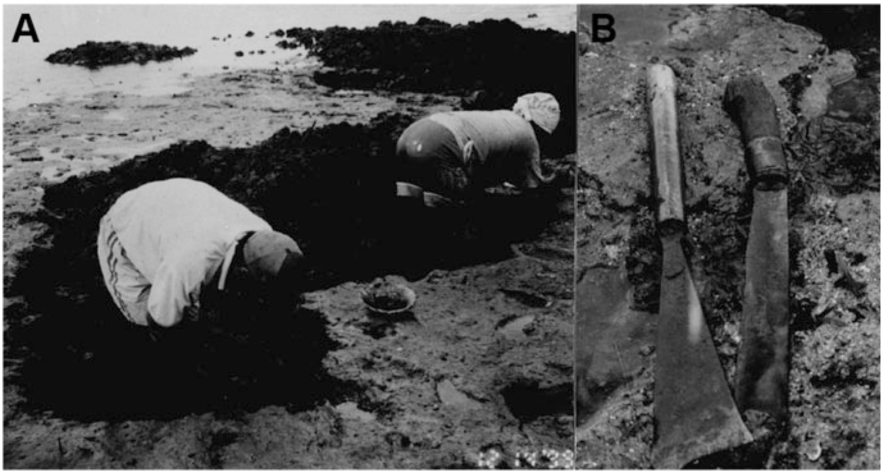

Fig. 7.2 (**a**) Harvesting of the mangrove lucinid *Anodontia philippiana* in Guimaras, Philippines. (**b**) Blades used for digging in mangrove mudflat. Reprinted by permission from Springer Nature, Wetlands Ecology and Management, Collection of the clam *Anodontia edentula* in mangrove habitats in Panay and Guimaras, central Philippines. J.H. Primavera, M.J.H.L. Lebata, L.F. Gustilo, J.P. Altamirano (2002).

4 The Paradox of Chemosymbiotic Bivalve Rarity in Mudflats

Considering the extensive degree of sulfate oxidation in mudflat sediments (Stewart et al. 2005), as well as the ubiquity of chemosymbioses among meiofaunal mudflat inhabitants (Chap. 5), a greater diversity and abundance of chemosymbiotic bivalves might be expected to inhabit non-vegetated mudflats, particularly outside the tropics. However, most chemosymbiotic bivalves reported from non-vegetated habitats appear to prefer sandy mud to the finer particles that characterize mudflats. Most intertidal-dwelling chemosymbiotic bivalves are associated with the roots and rhizomes of marine angiosperms, which provide them with key benefits: protection from predation, sediment stabilization and the modulation of sedimentary chemical conditions (Stanley 2014).

Dense root and rhizome mats may inhibit lucinid predation (Stanley 1970), although Caribbean spiny lobsters living closer to dense seagrass beds assimilated more lucinid-derived carbon than those living near sparse seagrass beds (Higgs et al. 2016). Periodic emergence during low tide may deter some predators (e.g. gastropods and crustaceans) that prefer subtidal areas: in the Caribbean, the percentage of lucinid shells drilled by naticids increased with distance to shore (Jackson 1972). In contrast, molluscivorous Red Knots successfully forage on *Loripes lucinalis* living in intertidal seagrass beds (van Gils et al. 2012).

Perhaps more important than a possible refuge from predation is the physical and chemical stabilization created by seagrass and mangrove roots and rhizomes. Sediments in seagrass and mangrove habitats are fine and cohesive, facilitating the establishment of the chemosymbiotic bivalve burrows. In contrast, some mudflat sediments are thixotrophic and not conducive to infauna that form permanent or semi-permanent burrows (Dashtgard et al. 2008). Seagrass and mangrove habitats also show lower degrees of bioturbation than do mudflats populated by burrowing crabs or other fauna that can disrupt burrows (Stanley 2014). Marine angiosperms also offer some protection against disturbance events such as storms, which could resuspend some of the less deeply buried chemosymbiotic bivalves.

Sediments around the roots and rhizomes of marine angiosperms are reduced and sulfide-rich due to their high organic matter content and low permeability, but may show a higher redox potential than surrounding bare sediments due to the release of oxygen by seagrass roots (Marbà et al. 2010). Seagrasses, lucinids and their symbionts were described as forming a three-stage symbiosis, where seagrasses benefit lucinids by stimulating sulfide production in sediments as well as by releasing oxygen through the roots, and lucinids enhance seagrass productivity by decreasing sedimentary sulfides (van der Heide et al. 2012); mangroves and lucinids likely show a similar relationship (Stanley 2014). In contrast, sediments in non-vegetated mudflats lack a similar capacity to modulate sedimentary sulfides and can experience fluctuating conditions that are more difficult to tolerate, even for chemosymbiotic bivalves. This was observed when a period of drought that led to seagrass mortality disrupted the lucinid-seagrass mutualistic feedback loop, to the detriment of lucinids (de Fouw et al. 2016).

Mutualistic relationships between marine angiosperms and chemosymbiotic thyasirids or solemyids have yet to be demonstrated, and additional factors may explain their rarity in mudflats. Most chemosymbiotic thyasirids are smaller than lucinids and solemyids, and burrow less deeply (generally to a depth of 8–9 times their shell length; Kauffmann 1967). For this reason, they may be relatively sensitive to sediment disturbance events (for example, due to high winds coinciding with spring tides; Dando and Southward 1986) and an associated deepening of the anoxic layer within the sediment column. Additionally, thyasirids are sensitive to elevated sulfide levels: population collapses have been attributed to rising concentrations in porewater sulfide (Dando and Southward 1986). The more dynamic physical and chemical conditions present in mudflats are therefore challenging to thyasirids, and this may explain their relative paucity in such habitats. Solemyids are capable of swimming and may be able to relocate when conditions are unfavorable (Stewart and Cavanaugh 2006).

Away from the physical and chemical protection afforded by seagrasses and mangroves, mudflat conditions are probably too dynamic for most chemosymbiotic bivalves. The most successful chemosymbiotic bivalve inhabitants of mudflats appear to be the large, deeply burrowed lucinids found in organic-rich sediments around mangroves (e.g. *Phacoides pectinatus*), where seasonal changes are less pronounced than at higher latitudes.

References

Allen JA (1953) Function of the foot in the Lucinacea (Eulamelibranchia). Nature 171:1117–1118

Allen JA (1958) On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). Philos Trans R Soc Lond B 241:421–484

Ball AD, Purdy KJ, Glover EA, Taylor JD (2009) Ctenidial structure and three bacterial symbiont morphotypes in *Anodontia* (Euanodontia) *ovum* (Reeve, 1850) from the Great Barrier Reef, Australia (Bivalvia: Lucinidae). J Mollusc Stud 75:175–185

Barnes PAG, Hickman CS (1999) Lucinid bivalves and marine angiosperms: a search for causal relationships. In: Walker DI, Wells FE (eds) The seagrass flora and fauna of Rottnest Island. Western Australian Museum, Perth, Western Australia, pp 215–238

Berg CJ Jr, Alatalo P (1984) Potential of chemosynthesis in molluscan mariculture. Aquaculture 39:165–179

Brissac T, Merçot H, Gros O (2011) Lucinidae/sulfur-oxidizing bacteria: ancestral heritage or opportunistic association? Further insights from the Bohol Sea (the Philippines). FEMS Microbiol Ecol 75:63–76

Cammen LM (1991) Annual bacterial production in relation to benthic microalgal production and sediment oxygen uptake in an intertidal sandflat and an intertidal mudflat. Mar Ecol Prog Ser 71:13–25

Cavanaugh CM (1985) Symbioses of chemoautotrophic bacteria and marine invertebrates from hydrothermal vents and reducing sediments. Biol Soc Wash Bull 6:373–388

Christo SW, Ivachuk CS, Ferreira-Júnior AL, Absher TM (2016) Reproductive periods of *Lucina pectinata* (Bivalve; Lucinidae) in the Paranaguá Estuarine Complex, Paraná – Brazil. Braz J Biol 76:300–306

Conway N, McDowell Capuzzo J, Fry B (1989) The role of endosymbiotic bacteria in the nutrition of *Solemya velum*: evidence from a stable isotope analysis of endosymbionts and host. Limnol Oceanogr 34:249–255

Cook PLM, Revill AT, Clementson LA, Volkman JK (2004) Carbon and nitrogen cycling on intertidal mudflats of a temperate Australian estuary. III. Sources of organic matter. Mar Ecol Prog Ser 280:55–72

Dando PR, Southward AJ (1986) Chemoautotrophy in bivalve molluscs of the genus *Thyasira*. J Mar Biol Assoc UK 66:915–929

Dando PR, Spiro B (1993) Varying nutritional dependence of the thyasirid bivalves *Thyasira sarsia* and *T. equalis* on chemoautotrophic symbiotic bacteria, demonstrated by isotope ratios of tissue carbon and shell carbonate. Mar Ecol Prog Ser 92:151–158

Dando PR, Southward AJ, Southward EC, Terwilliger NB, Terwilliger RC (1985) Sulphur-oxidizing bacteria and haemoglobin in gills of the bivalve mollusc *Myrtea spinifera*. Mar Ecol Prog Ser 23:85–98

Dando PR, Southward AJ, Southward EC (1986) Chemoautotrophic symbionts in the gills of the bivalve mollusc *Lucinoma borealis* and the sediment chemistry of its habitat. Proc R Soc Lond Ser B 227:227–247

Dando PR, Ridgway SA, Spiro B (1994) Sulphide 'mining' by lucinid bivalve molluscs: demonstrated by stable sulphur isotope measurements and experimental models. Mar Ecol Prog Ser 107:169–175

Dando PR, Southward AJ, Southward EC (2004) Rates of sediment sulphide oxidation by the bivalve mollusc *Thyasira sarsi*. Mar Ecol Prog Ser 280:181–187

Dashtgard SE, Gingras MK, Pemberton SG (2008) Grain-size controls on the occurrence of bioturbation. Palaeogeogr Palaeoclimatol Palaeoecol 257:224–243

Dauwe B, Herman PMJ, Heip CHR (1998) Community structure and bioturbation potential of macrofauna at found North Sea stations with contrasting food supply. Mar Ecol Prog Ser 173:67–83 de Fouw J, Govers LL, van de Koppel J, van Belzen J, Dorigo W, Cheikh MAS, Christianen MJA, van der Reijden KJ, van der Geest M, Piersma T, Smolders AJP, Olff H, Lamers LPM, van Gils JA, van der Heide T (2016) Drought, mutualism breakdown, and landscape-scale degradation of seagrass beds. Curr Biol 26:1051–1056

Distel DL, Felbeck H (1987) Endosymbiosis in the lucinid clams *Lucinoma aequizonata*, *Lucinoma annulata* and *Lucina floridana*: a reexamination of the functional morphology of the gills as bacteria-bearing organs. Mar Biol 96:79–86

Drew GA (1900) Locomotion in *Solenomya* and its relatives. Anat Anz 17:257–266

Dubilier N, Bergin C, Lott C (2008) Symbiotic diversity in marine animals: the art of harnessing chemosynthesis. Nat Rev Microbiol 6:725–740

Dufour SC (2005) Gill anatomy and the evolution of symbiosis in the bivalve family Thyasiridae. Biol Bull 208:200–212

Dufour SC, Felbeck H (2003) Sulphide mining by the superextensile foot of symbiotic thyasirid bivalves. Nature 426:65–67

Dufour SC, Laurich JR, Batstone RT, McCuaig B, Elliott A, Poduska KM (2014) Magnetosome-containing bacteria living as symbionts of bivalves. ISME J 8:2453–2462

Duperron S, Gaudron SM, Rodrigues CF, Cunha MR, Decker C, Olu K (2013) An overview of chemosynthetic symbioses in bivalves from the North Atlantic and Mediterranean Sea. Biogeosciences 10:3241–3267

Fenchel T, Reidl RJ (1970) The sulfide system: a new biotic community underneath the oxidized layer of marine sand bottoms. Mar Biol 7:59–68

Fisher CR (1990) Chemoautotrophic and methanotrophic symbioses in marine invertebrates. Rev Aquat Sci 2:399–613

Frenkiel L, Gros O, Mouëza M (1995) Gill structure in *Lucina pectinata* (Bivalvia: Lucinidae) with reference to hemoglobin in bivalves with symbiotic sulphur-oxidizing bacteria. Mar Biol 125:511–524

Frey RW (1968) The lebensspuren of some common marine invertebrates near Beaufort, North Carolina. I. Pelecypod burrows. J Paleontol 42:570–574

Glover EA, Taylor JD (2001) Systematic revision of Australian and Indo-Pacific Lucinidae (Mollusca: Bivalvia): *Pillucina*, *Wallucina* and descriptions of two new genera and four new species. Rec Aust Mus 53:263–292

Glover EA, Taylor JD (2007) Diversity of chemosymbiotic bivalves on coral reefs: Lucinidae of New Caledonia and Lifou (Mollusca, Bivalvia). Zoosystema 29:109–181

Glover EA, Taylor JD, Williams ST (2008) Mangrove-associated lucinid bivalves of the central Indo-West Pacific: review of the "*Austriella*" group with a new genus and species (Mollusca: Bivalvia: Lucinidae). Raffles Bull Zool Suppl 18:25–40

Gros O, Frenkiel L, Mouëza M (1996) Gill ultrastructure and symbiotic bacteria in the tropical lucinid, *Linga pensylvanica* (Linné). Symbiosis 20:259–280

Gros O, Frenkiel L, Mouëza M (1997) Embryonic, larval, and post-larval development in the symbiotic clam, *Codakia orbicularis* (Bivalvia: Lucinidae). Invertebr Biol 116:86–101

Gros O, Duplessis MR, Felbeck H (1999) Embryonic development and endosymbiont transmission mode in the symbiotic clam *Lucinoma aequizonata* (Bivalvia: Lucinidae). Invertebr Reprod Dev 36:93–103

Gros O, Liberge M, Heddi A, Khatchadourian C, Felbeck H (2003) Detection of the free-living forms of sulfide-oxidizing gill endosymbionts in the lucinid habitat (*Thalassia testudinum* environment). Appl Environ Microbiol 69:6264–6267

Gros O, Elisabeth NH, Gustave SDD, Caro A, Dubilier N (2012) Plasticity of symbiont acquisition throughout the life cycle of the shallow-water tropical lucinid *Codakia orbiculata* (Mollusca: Bivalvia). Environ Microbiol 14:1584–1595

Gustafson RG, Lutz RA (1992) Larval and early post-larval development of the protobranch bivalve *Solemya velum* (Mollusca: Bivalvia). J Mar Biol Assoc U K 72:383–402

Hakonen A, Hulth S, Dufour S (2010) Analytical performance during ratiometric long-term imaging of pH in bioturbated sediments. Talanta 81:1393–1401

Healy JM, Mikkelsen PM, Giribet G, Bieler R (2017) Sperm ultrastructure of the Protobranchia: comparison with other bivalve mollusks and potential taxonomic and phylogenetic significance. Fieldiana Life Earth Sci 11:1–28

Herry A, Le Pennec M (1987) Endosymbiotic bacteria in the gills of the littoral bivalve molluscs *Thyasira flexuosa* (Thyasiridae) and *Lucinella divaricata* (Lucinidae). Symbiosis 4:25–36

Herry A, Diouris M, Le Pennec M (1989) Chemoautotrophic symbionts and translocation of fixed carbon from bacteria to host tissues in the littoral bivalve *Loripes lucinalis* (Lucinidae). Mar Biol 101:305–312

Higgs ND, Newton H, Attrill MJ (2016) Caribbean spiny lobster fishery is underpinned by trophic subsidies from chemosynthetic primary production. Curr Biol 26:3393–3398

Howarth RW (1984) The ecological significance of sulfur in the energy dynamics of salt marsh and coastal marine sediments. Biogeochemistry 1:5–27

Jackson JBC (1972) The ecology of molluscs of *Thalassia* communities, Jamaica, West Indies. II. Molluscan population variability along an environmental stress gradient. Mar Biol 14:304–337

Jackson JBC (1973) The ecology of molluscs of *Thalassia* communities, Jamaica, West Indies. I. Distribution, environmental physiology, and ecology of common shallow-water species. Bull Mar Sci 23:313–350

Johnson MA, Fernandez C, Pergent G (2002) The ecological importance of an invertebrate chemoautotrophic symbiosis to phanerogam seagrass beds. Bull Mar Sci 71:1343–1351

Kauffmann EG (1967) Cretaceous *Thyasira* from the Western Interior of North America. Smithson Misc Collect 152:1–159

Kristensen E (2000) Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. Hydrobiologia 426:1–24

Krueger DM, Gallagher SM, Cavanaugh CM (1992) Suspension feeding on phytoplankton by *Solemya velum*, a symbiont-containing clam. Mar Ecol Prog Ser 86:145–151

Krueger DM, Gustafson RG, Cavanaugh CM (1996) Vertical transmission of chemoautotrophic symbionts in the bivalve *Solemya velum* (Bivalvia: Protobranchia). Biol Bull 190:195–202

Le Pennec M, Beninger PG (2000) Reproductive characteristics and strategies of reducing-system bivalves. Comp Biochem Physiol A 126:1–16

Le Pennec M, Beninger PG, Herry A (1995a) Feeding and digestive adaptations of bivalve molluscs to sulphide-rich habitats. Comp Biochem Physiol 111A:183–189

Le Pennec M, Herry A, Johnson M, Beninger PG (1995b) Nutrition-gametogenesis relationship in the endosymbiont host bivalve *Loripes lucinalis* (Lucinidae) from reducing coastal habitats. In: Eleftheriou A, Ansell AD, Smith CJ (eds) Biology and ecology of shallow coastal waters. Olsen and Olsen, Fredensborg, pp 139–142

Lebata MJHL (2000) Elemental sulfur in the gills of the mangrove mud clam *Anodontia edentula* (Family Lucinidae). J Shellfish Res 19:241–245

Lebata MJHL (2001) Oxygen, sulphide and nutrient uptake of the mangrove mud clam *Anodontia edentulata* (Family: Lucinidae). Mar Pollut Bull 42:1133–1138

Marbà N, Duarte CM, Terrados J, Halun Z, Gacia E, Fortes MD (2010) Effects of seagrass rhizospheres on sediment redox conditions in SE Asian coastal ecosystems. Mar Ecol Prog Ser 33:107–117

McCuaig B, Liboiron F, Dufour SC (2017) The bivalve *Thyasira* cf. *gouldi* hosts chemoautotrophic symbiont populations with strain level diversity. PeerJ 5:e3597

Meyer E, Nilkerd B, Glover EA, Taylor JD (2008) Ecological importance of chemoautotrophic lucinid bivalves in a peri-mangrove community in eastern Thailand. Raffles Bull Zool 18:41–55

Morse ES (1913) Observations on living *Solenomya*. Biol Bull 25:261–281

Ockelmann WK (1958) The zoology of East Greenland: marine lamellibranchiata. Medd Grønland 122:1–256

Oliver PG (1986) A new lucinid bivalve from the Niger Delta and an appraisal of the *Loripes* group (Bivalvia, Lucinacea). Basteria 50:47–64

Owen G (1961) A note on the habits and nutrition of *Solemya parkinsoni* (Protobranchia: Bivalvia). Q J Microsc Sci 102:15–21

Papaspyrou S, Gregersen T, Kristensen E, Christensen B, Cox RP (2006) Microbial reaction rates and bacterial communities in sediment surrounding burrows of two nereidid polychaetes (*Nereis diversicolor* and *N. virens*). Mar Biol 148:541–550

Payne CM, Allen JA (1991) The morphology of deep-sea Thyasiridae (Mollusca: Bivalvia) from the Atlantic Ocean. Philos Trans R Soc Lond B 334:481–562

Petersen JM, Kemper A, Gruber-Vodicka H, Cardini U, van der Geest M, Kleiner M, Bulgheresi S, Mussmann M, Herbold C, Seah BKB, Antony CP, Liu D, Belitz A, Weber M (2016) Chemosynthetic symbionts of marine invertebrate animals are capable of nitrogen fixation. Nat Microbiol 2:16195

Primavera JH, Lebata MJHL, Gustilo LF, Altamirano JP (2002) Collection of the clam *Anodontia edentula* in mangrove habitats in Panay and Guimaras, central Philippines. Wetl Ecol Manag 10:363–370

Queirós AM, Birchenough SNR, Bremner J, Godbold JA, Parker RE, Romero-Ramirez A, Reiss H, Solan M, Somerfield PJ, Van Colen C, Van Hoey G, Widdicombe S (2013) A bioturbation classification of European marine infaunal invertebrates. Ecol Evol 3:3958–3985

Rainer SF, Wadley VA (1991) Abundance, growth and production of the bivalve *Solemya* sp, a food source for juvenile rock lobsters in a seagrass community in western Australia. J Exp Mar Biol Ecol 152:201–223

Rattanachot E, Prathep A (2015) Species-specific effects of seagrass on belowground biomass, redox potential and *Pillucina vietnamica* (Lucinidae). J Mar Biol Assoc U K 95:1693–1704

Reid RGB (1980) Aspects of the biology of a gutless species of *Solemya* (Bivalvia: Protobranchia). Can J Zool 58:386–393

Reid RGB, Bernard FR (1980) Gutless bivalves. Science 208:609–610

Reid RGB, Brand DG (1987) Observations of Australian Solemyidae. J Malacol Soc Aust 8:41–50

Reynolds LK, Berg P, Zieman JC (2007) Lucinid clam influence on the biogeochemistry of the seagrass *Thalassia testudinum* sediments. Estuar Coasts 30:482–490

Roeselers G, Newton ILG (2012) On the evolutionary ecology of symbioses between chemosynthetic bacteria and bivalves. Appl Microbiol Biotechnol 94:1–10

Rondinelli SF, Barros F (2010) Evaluating shellfish gathering (*Lucina pectinata*) in a tropical mangrove system. J Sea Res 64:401–407

Rosenberg R, Davey E, Gunnarsson J, Norling K, Frank M (2007) Application of computer-aided tomography to visualize and quantify biogenic structures in marine sediments. Mar Ecol Prog Ser 331:23–34

Russell SL, Cavanaugh CM (2017) Intra-host genetic diversity of bacterial symbionts exhibits evidence of mixed infections and recombinant haplotypes. Mol Biol Evol msx188

Russell SL, Corbett-Detig RB, Cavanaugh CM (2017) Mixed transmission modes and dynamic genome evolution in an obligate animal-bacterial symbiosis. ISME J 11:1359–1371

Salas C, Woodside J (2002) *Lucinoma kazani* n. sp. (Mollusca: Bivalvia): Evidence of a living benthic community associated with a cold seep in the eastern Mediterranean Sea. Deep-Sea Res I Oceanogr Res Pap 49:991–1005

Scott KM (2005) Allometry of gill weights, gill surface areas, and foot biomass ∂^{13}C values of the chemoautotroph-bivalve symbiosis *Solemya velum*. Mar Biol 147:935–941

Southward EC (1986) Gill symbionts in thyasirids and other bivalve molluscs. J Mar Biol Assoc U K 66:889–914

Spiro B, Greenwood PB, Southward AJ, Dando PR (1986) ^{13}C/^{12}C ratios in marine invertebrates from reducing sediments: confirmation of nutritional importance of chemoautotrophic endosymbiotic bacteria. Mar Ecol Prog Ser 28:233–240

Stanley SM (1970) Relation of shell form to life habits of the Bivalvia (Mollusca). Geol Soc Am Mem 125:296 pp

Stanley SM (2014) Evolutionary radiation of shallow-water Lucinidae (Bivalvia with endosymbionts) as a result of the rise of seagrasses and mangroves. Geology 42:803–806

Stewart FJ, Cavanaugh CM (2006) Bacterial endosymbiosis in *Solemya* (Mollusca: Bivalvia) – model systems for studies of symbiont-host adaptation. Antonie Van Leeuwenhoek 90:343–360

Stewart FJ, Newton ILG, Cavanaugh CM (2005) Chemosymbiotic endosymbioses: adaptations to oxic-anoxic interfaces. Trends Microbiol 13:439–448

Sundbäck K, Miles A, Göransson E (2000) Nitrogen fluxes, denitrification and the role of microphytobenthos in microtidal shallow-water sediments: an annual study. Mar Ecol Prog Ser 200:59–76

Taylor JD, Glover EA (2000) Functional anatomy, chemosymbiosis and evolution of the Lucinidae. In: Harper EM, Taylor JD, Crame JA (eds) The evolutionary biology of the bivalvia. Geological Society, London, Special Publications 177, pp 207–225

Taylor JD, Glover EA (2005) Cryptic diversity of chemosymbiotic bivalves: a systematic revision of worldwide *Anodontia* (Mollusca: Bivalvia: Lucinidae). Syst Biodivers 3:281–338

Taylor JD, Glover EA (2006) Lucinidae (Bivalvia) – the most diverse group of chemosymbiotic molluscs. Zool J Linnean Soc 148:421–438

Taylor JD, Williams ST, Glover EA (2007) Evolutionary relationships of the bivalve family Thyasiridae (Mollusca: Bivalvia), monophyly and superfamily status. J Mar Biol Assoc UK 87:565–574

Taylor JD, Glover EA, Smith L, Williams ST (2014) Diversification of chemosymbiotic bivalves: origins and relationships of deeper water Lucinidae. Biol J Linn Soc 111:401–420

van der Geest M, Sall AA, Ely SO, Nauta RW, van Gils JA, Piersma T (2014) Nutritional and reproductive strategies in a chemosymbiotic bivalve living in a tropical intertidal seagrass bed. Mar Ecol Prog Ser 501:113–126

van der Heide T, Govers LL, de Fouw J, Olff H, van der Geest M, van Katwijk MM, Piersma T, van de Koppel J, Silliman BR, Smolders AJP, van Gils JA (2012) A three-stage symbiosis forms the foundation of seagrass ecosystems. Science 336:1432–1434

van Gils JA, van der Geest M, Jansen EJ, Govers LL, de Fouw J, Piersma T (2012) Trophic cascade induced by molluscivore predator alters pore-water biogeochemistry via competitive release of prey. Ecology 93:1143–1152

van Gils JA, van der Geest M, Leyrer J, Oudman T, Lok T, Onrust J, de Fouw J, van der Heide T, van den Hout PJ, Spaans B, Dekinga A, Brugge M, Piersma T (2013) Toxin constraint explains diet choice, survival and population dynamics in a molluscivore shorebird. Proc R Soc B 280:20130861

Vasquez-Cardenas D, Quintana CO, Meysman FJR, Kristensen E, Boschker HTS (2016) Species-specific effects of two bioturbating polychaetes on sediment chemoautotrophic bacteria. Mar Ecol Prog Ser 549:55–68

von Cosel R (2006) Taxonomy of West African bivalves VIII. Remarks on Lucinidae, with descriptions of five new genera and nine new species. Zoosystema 28:805–851

Williams AB, Porter HJ (1971) A ten-year study of meroplankton in North Carolina estuaries: occurrence of postmetamorphal bivalves. Chesap Sci 12:26–32

Yonge CM (1939) The protobranchiate Mollusca; a functional interpretation of their structure and evolution. Philos Trans R Soc Lond Ser B Biol Sci 230:79–148

Zabbey N, Hart AI, Wolff WJ (2010) Population structure, biomass and production of the West African lucinid *Keletistes rhizoecus* (Bivalvia, Mollusca) in Sivibilagbara swamp at Bodo Creek, Niger Delta, Nigeria. Hydrobiologia 654:193–203

Zanzerl H, Dufour SC (2017) The burrowing behaviour of symbiotic and asymbiotic thyasirid bivalves. J Conchol 42:299–308

Zardus JD (2002) Protobranch bivalves. In: Southward AJ, Tyler PA, Young CM, Fuiman LA (eds) Advances in marine biology, vol 42. Academic, London, pp 1–65

Chapter 8
Sedimentary and Biological Patterns on Mudflats

Peter G. Beninger, Diana Cuadrado, and Johan van de Koppel

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Abstract Apparently featureless 'flat' mudflats actually present striking biological patterning beneath the sediment surface, and even slight physical patterning by sediment ripple marks also leads to biological patterning of the surficial biofilm. The more topographically-complex hummock-forming mudflats are characterized by even more striking physical and biological patterning. In this chapter we first consider how the sediment-microbe association resists wave- and current-induced erosion, creating within-sediment structure (microbially-induced sedimentary structures, MISS). These structures may eventually succumb to high-energy erosion, creating superficial irregularity. We then describe how microbial and physical processes conjugate to form the spatially-complex, transitory hummock patterns.

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Finally, we summarize the biological patterning which emerges from the sedimentary structure and pattern on both flat and hummock mudflats.

1 Introduction

Although many mudflats are indeed ‘flat’, others are characterized by a low-grade topography; and while many mudflats are ‘all-mud’, others have mixed-sediment beds. In this chapter, we will see how the opposing forces of cohesion and erosion may create sedimentary structure and patterning, and how physical forces and sedimentary parameters may influence biological patterning on mudflats.

Casual examination of ‘flat’ mudflats gives an impression of relatively featureless mud, punctuated by seemingly random lugworm fecal casts (Fig. 8.1); however, even here, organism spatial patterns are, in fact, strikingly pronounced, over a wide range of spatial scales and organism sizes (Chapman 2000; Wahl et al. 2005; Rodrigues et al. 2006; Boldina and Beninger 2013, 2014; Boldina et al. 2014; Beninger and Boldina 2014). These patterns may initially organize as a passive consequence of external abiotic conditions (current velocity, sediment particle size), and also contribute to their own establishment (secretion of extracellular polymeric substances EPS, self-organization, behaviour) as well as influence the patterns of other organisms (e.g. through grazing or sediment stabilization—Rietkerk and van de Koppel 2008). A mudflat can thus be viewed as a dynamic, evolving landscape of juxtaposed sedimentary and living patterns. This chapter will focus on the genesis, maintenance, and interactions of both physical and biological patterns in this landscape.

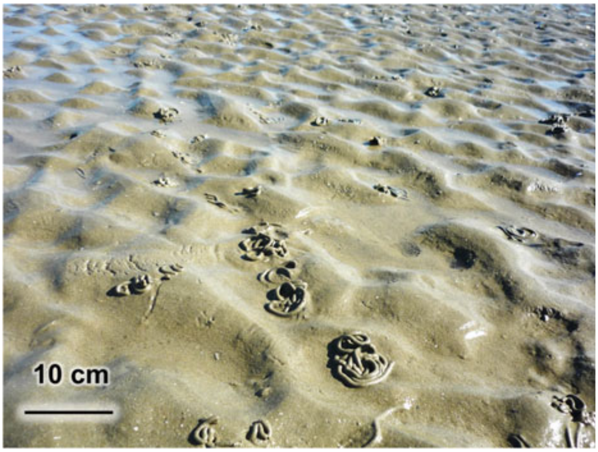


Fig. 8.1 General view of a fine-sediment mudflat, showing ripple marks and numerous lugworm (*Arenicola marina)* fecal casts. Scale indicates foreground. Le Gois, France. Photo P. G. Beninger.

2 The Players and Their Roles: Biofilms, Microbial Mats, Sediment and Hydrodynamics

When considering the forces and protagonists at play in the formation of sedimentary structures on mudflats, it helps to have a clear understanding of what they are. The following terms have been defined in Chap. 1*: biofilm, microphytobenthos, epi- and endobenthic microbial mats, epipelic, endopsammic*.

2.1 Biofilm Composition and EPS Secretion

From the previous chapters in which biofilms and microbial mats were discussed in varying detail (Chaps. 1, 3 and 4), it is clear that much mudflat ecology cannot be understood without a grounding in this subject. Microorganisms have been forming biofilms for nearly 3.5 billion years, plying an ancient skill for colonization and organization on moist surfaces (Hall-Stoodley et al. 2004; Noffke et al. 2013a, b). From a physical perspective, biofilms are considered hydrogels (extremely hydrated polymer gels), characterized by a high viscoelasticity, allowing them to be stretched in the direction of flow (Stoodley 2016). From a biological perspective, a biofilm is a complex composite, comprising microbial cells embedded in a matrix of EPS, itself a complex mixture of proteins, polysaccharides, and nucleic acids, along with sediment particles and precipitates (Stal 2010). A high degree of cooperation is evident in the community, changing behaviors and metabolic activities as a function of the requirements of the entire biofilm (Noffke et al. 2013b; Hall-Stoodley and Stoodley 2002). Biofilms integrate the metabolic processes of prokaryote (cyanobacteria, heterotrophic bacteria, archaea) and microbial eukaryote (diatoms, dinoflagellates, protozoa, fungi) genomes to create a hologenome; the community itself is a holobiont (Zilber-Rosenberg and Rosenberg 2008).

Biofilms generate two broad types of EPS: colloidal EPS, which is used as a trophic resource by different micro-organisms (e.g. heterotrophic bacteria), and bound EPS, secreted as the mucilaginous slime coating the cells (Underwood and Paterson 2003; Fernández et al. 2016). Colloidal EPS concentrations in sediments are directly related to epipelic diatom biomass (Madsen et al. 1993), but this predictable relationship is not apparent in mixed assemblages such as mats of cyanobacteria and diatoms of the supratidal zone (Underwood 1997; Underwood and Smith 1998). Nevertheless, measurement of the colloidal carbohydrate fraction is a useful operational proxy for microbial EPS (Underwood et al. 1995). EPS exudation in benthic diatoms occurs mostly during daytime and emersion (Stal and de Brouwer 2005), as the production of EPS serves a protective function against external environmental stressors such as desiccation and UV-light exposure (Fig. 8.2), and is either a result of their migration (influenced by inundation), an imbalance between photosynthesis and growth potential, or both (Stal and de Brouwer 2003; Stal 2010). EPS plays important roles in diatom and cyanobacteria motility/vertical migration, cell/substratum adhesion, sediment stabilization, and in

Fig. 8.2 A multilayered epibenthic microbial mat consisting of cyanobacteria (thin dark green layer) atop the oxic (brown) and anoxic (black) sediment layers. The microbial mat is covered by a thick gelatinous EPS layer secreted by light-coloured diatoms on the top of the sediments (often simply termed 'biofilm' by ecologists). Note the entrapped gas bubbles in the EPS matrix, a product of photosynthesis and microorganism respiration (Cuadrado et al. submitted).

buffering dehydration, salinity extremes, and metal toxicity (Decho 2000; Steele et al. 2014). Tidal cycle and light are the main factors regulating EPS secretion, which increases during epipelic diatom vertical migration (Ubertini et al. 2015); EPS secretion is also influenced by other environmental conditions (Underwood et al. 2004; Pierre et al. 2014).

2.2 Formation and Development of Biofilms and Microbial Mats

Strictly speaking, any solid surface in a humid environment will be colonized by microbes; these organisms and their secretions constitute a biofilm. On mudflats, such biofilms develop first on the surfaces of sediment grains, eventually forming endobenthic or epibenthic microbial mats; on the sediment surface, transient epibenthic biofilms may develop within hours of emersion (Chap. 1). As will be discussed below, it is the microbial mats which are most important in stabilizing mudflat sediment, leading to within-sediment patterning, as well as to superficial features when the stabilized sediment is nonetheless eroded by sudden strong shear forces.

2.2.1 Biofilms

The main metabolic process in mudflat biofilms and microbial mats is oxygenic photosynthesis (van Gemerden 1993; Stolz 2000). Through this primary production, the embedded diatoms and cyanobacteria contribute significantly to the matter and

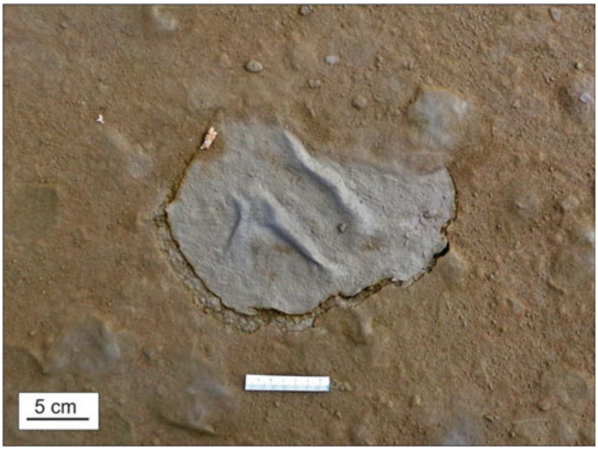


Fig. 8.3 A torn, cohesive biofilm which developed on top of underlying sediments. The crinkles of the biofilm show its characteristic cohesiveness. Photo DG Cuadrado, inner Bahia Blanca Estuary, Argentina.

energy flow of mudflats (Miller et al. 1996; Underwood and Kromkamp 1999; Pan et al. 2013); the primary remineralizers of organic matter are heterotrophic prokaryotes (Van Colen et al. 2014, and see Chaps. 2, 3).

The general formation and cycle of biofilms has been described by Hall-Stoodley and Stoodley (2002), Hall-Stoodley et al. (2004) and Stoodley (2016). On mudflats, biofilm formation initiates via the attachment of a variety of free-floating planktonic bacteria, or detached biofilm clumps, to sediment particles. The proteins of the secreted EPS play a critical role in the earliest stages of biofilm fixing to the substrate (Ubertini et al. 2015). The colonies then grow and mature into a structured community, from which the apical regions may detach under mechanical stress, continuing the cycle (Stoodley et al. 1999). The details of this evolution begin with the growth of microphytobenthos (MPB) around individual sediment grains (which become trapped in the EPS matrix), and continues with its expansion to the closest grains, ultimately forming a laterally-contiguous, cohesive organic layer (Fig. 8.3).

2.2.2 Microbial Mats and Microbially-Induced Sedimentary Structures (MISS)

In a nutrient-rich sediment environment (e.g. mudflats), the microbial consortia which evolve within biofilms form complex and multilayered microbial mats that grow by accumulation of EPS, empty cyanobacterial sheaths (which are resistant to degradation) and mineral deposition (Fenchel and Kühl 2000; de los Ríos et al. 2004; Kaźmierczak et al. 2015). In this way, a biologically-diverse laminated sedimentary community builds up. Biofilm morphology and behavior under different hydrodynamic conditions has been described by Stoodley et al. (1999), while the evolution of the physiological state of phototrophic biofilms has been documented by Wolf (2007), showing that a mature phase was reached after approximately 13 days.

Microbial mats are advanced biofilms, growing within the sediment, in which filamentous cyanobacteria have been recognized as the most successful components

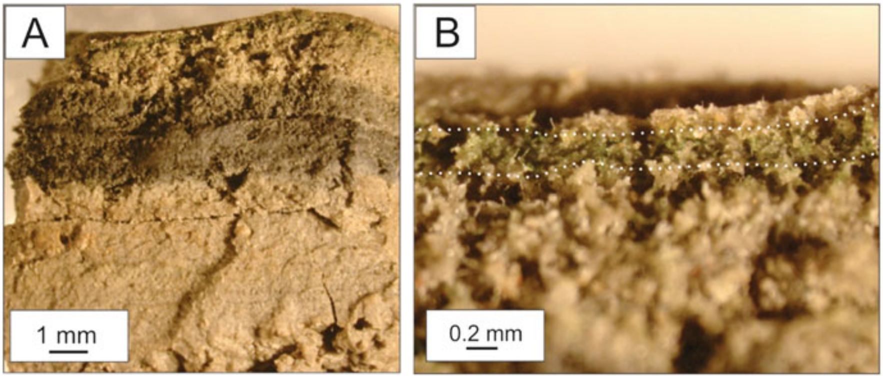


Fig. 8.4 Cross-section through tidal flat sediments from the inner Bahia Blanca Estuary. (**a**) Striation due to metabolic and sedimentation processes. The black color is probably due to sulfate-reducing bacteria. Note the cohesive aspect of the sediment at the bottom of the profile. (**b**) Detail of the top layer, composed of filamentous cyanobacteria (green) growing within the sediment, covered by a very thin biofilm of diatoms (brown). Photo DG Cuadrado, middle Bahia Blanca Estuary, Argentina.

(Neu 1994; Gerdes 2007). Horizontal physicochemical gradients allow the growth of different functional groups of bacteria and algae entangled within, and contributing to, the EPS matrix (Fig. 8.4). Consequently, a wide spectrum of metabolic processes, carried out by the large diversity of species within microbial mats, results in coupled reduction/oxidation reactions that support robust biogeochemical cycles (Visscher and Stolz 2005, and see Chaps. 2 and 3 for detailed account).

Epibenthic and endobenthic microbial mats develop under the particular tidal conditions of the mudflat. Epibenthic mats are dominated by the filamentous cyanobacterium *Microcoleus chthonoplastes*, which forms a coherent sedimentary microbial network, as well as a matrix of abundant EPS, covering the sediment surface (Cuadrado et al. 2011 and Fig. 8.5a). The high EPS production protects the underlying microbes during long periods of emersion. The dominant microbe in endobenthic microbial mats is the filamentous cyanobacterium *Oscillatoria* sp., forming a network that interweaves the grains like an organic carpet, developing in the sediment but not on top of it (Fig. 8.5b), in contrast to epibenthic mats. Sediment composition plays a dominant role: cyanobacteria-dominated microbial mats grow preferentially on quartz-rich fine sands.

Microbial mats do not occur in the almost continuously–inundated lower intertidal zone, although biofilms obviously colonize the sediment particles (Noffke 2010). These latter biofilms provide a degree of biostabilization, without forming true sedimentary structures.

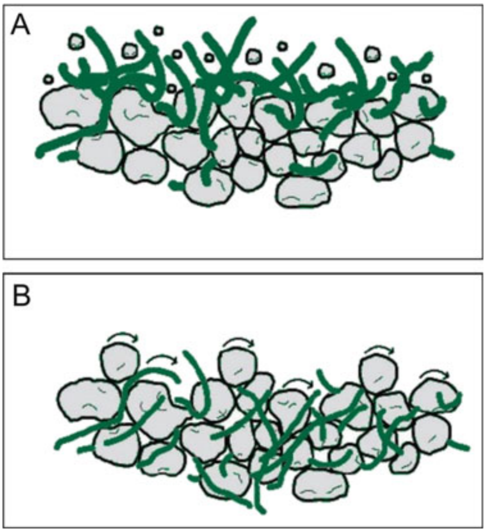


Fig. 8.5 Diagram showing the development of microbial mats, depending on degree of mudflat inundation [modified from Noffke (2010)]. (**a**) Epibenthic microbial mat. Coherent network covering grains on top of the sedimentary surface by the presence of filamentous cyanobacteria and abundant EPS secretion, forming a slippery surface. Sediment grains cannot be moved by ordinary water movement. (**b**) Endobenthic microbial mat. A network is formed by filaments extending through the sediment grains, forming a rough sedimentary surface. Water can move the sediment grains. When present, surficial biofilms grow atop these mats. Original schematic, D. Cuadrado.

Although benthic microorganisms can build several types of organo-sedimentary structures called *microbialites*, the ones that are most important for mudflats are the *microbially-induced sedimentary structures* (MISS; Noffke et al. 2001; Noffke and Awramik 2013). Microbial mats may generate MISS through the processes of baffling, trapping, and biostabilization, over long periods of time. Such structures are often laminar (Fig. 8.6), and may be created either through successful biostabilization of the sediment (perfectly laminar structures), or to the erosion and displacement of microbial mats. Although yet poorly-understood, what is known of these processes will be described below.

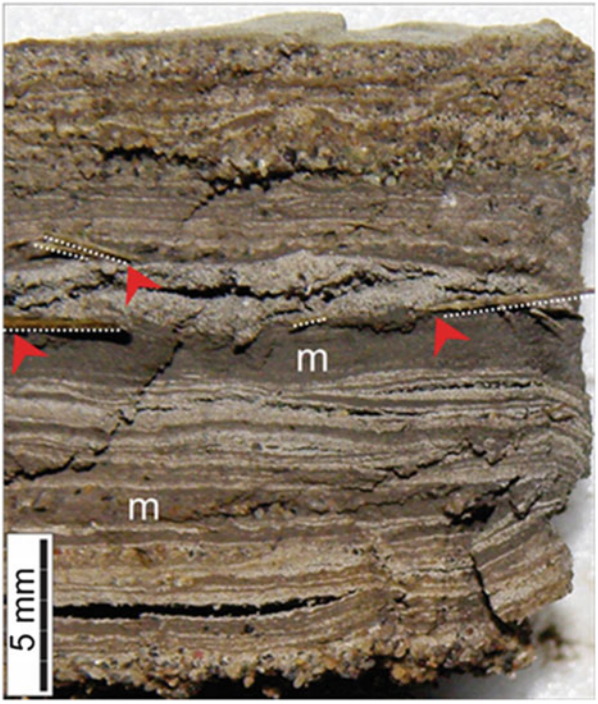


Fig. 8.6 Laminated microbial mats in a vertical sedimentary core, interpreted as different energy levels occurring in a modern tidal flat [modified from Cuadrado et al. (2013)]. Dark layers, "m", indicate the microbial mat colonization during latencies (calm conditions), while sand layers (lighter-coloured) indicate high-energy conditions. Note that vegetation (dashed lines) is located at the limits of the sand layer (stalks of *Spartina* sp. projecting from the sediment core at red arrows), above the microbial mat. The thickness of each layer is not proportional to the depositional interval; the microbial mats (m) form over several days or months, whereas the sand layers (representing storm events) require only a few days. Photo DG Cuadrado.

2.3 Water Flow, Shear Stress, and the Inhibition/Generation of Sedimentary Surface Structure

In the mid-1990s, it became evident that microbial mats played a role in stabilizing mudflat sediments (Yallop et al. 1994). In the following sections, we will describe how the opposing forces of water flow and microbe-induced sediment stabilization produce a cohesive sedimentary environment which provides infaunal protection from much of the wave- and tidal current energy, and how the first superficial sedimentary features are formed under high-energy conditions.

2.3.1 How Biofilms and Microbial Mats Stabilize Sediment

Microphytobenthos is an important biogeomorphological determinant of sediment stabilization, influencing the sediment erosion threshold and transport. *Erodibility* is defined as the erosion threshold or sediment bed shear stress needed to erode the surface of the bed (Andersen and Pejrup 2011); MPB has been shown to reduce erodibility and provide sediment stabilization (Neumeier et al. 2006), primarily through EPS secretion (Stal 2010). More recently, it has been proposed that organisms may "work together" in altering the erosion threshold of sediment habitats, giving rise to "cooperative ecosystem engineering" (Passarelli et al. 2014, and see Chap. 10). Such processes may be astonishingly rapid and effective (Stoodley et al. 2002; Lubarsky et al. 2010).

Experimental studies on intertidal mudflat biofilms have shown that the critical thresholds of biofilm resuspension differ for different groups of microorganisms (Dupuy et al. 2014). Free, unattached microorganisms (e.g. viruses, bacteria, and some nanoflagellates) are resuspended at weak flow speeds ($u^{*}_{\text{crit}} < 2$ cm s^{-1}), while microphytobenthos (i.e. phototrophic microbes, including nanoflagellates and attached bacteria) are resuspended at higher flow speeds ($u^{*}_{\text{crit}} > 3$ cm s^{-1}). Small diatoms (<60 µm) are resuspended at 3–5 cm s^{-1}, while speeds up to 5.5–6.5 cm s^{-1} are required for the resuspension of larger diatoms (>60 µm).

Several studies on sediment erodibility have been performed on homogeneous sandy (Friend et al. 2008) or muddy sediments (Tolhurst et al. 2008). However, under "real world" conditions, most sediments consist of a mixture of sand and mud; when the mud fraction is greater than 30%, the mixture behaves as fully cohesive. The biofilms formed on such high-mud sediments constitute a weaker stabilizing matrix, compared to those on more sandy sediments (sensu 'sandy mud', Folk et al. 1970); biofilm age also significantly affects the erosion critical threshold for resuspension (Ubertini et al. 2015).

It is common for paleo-hydraulic geologists to use Hjülstrøm's (1935) or Shields's (1936) diagrams in order to estimate the velocity needed to initiate grain movement in a unidirectional flow, as well as the development of sedimentary structures. However, a cautionary note when applying these models is that they are derived from experiments with sterile, unconsolidated sediments. Contemporary sediment transport studies take into account the significant influence of biofilms and microbial mats on the sediments. The inoculation of quartz sand with biofilm-forming cyanobacteria inhibits the production of ripples or dunes observed in sterile sediments. The microbial colonization of sediments affects the *critical shear stress* (the force necessary for the initiation of sediment motion), which initiates the erosion of the bed surface, and nearly doubles the flow velocity required to produce the traditional sequence of sedimentary bedforms (Hagadorn and McDowell 2012). This issue was also recently addressed by Fang et al. (2014) who experimentally calculated incipient motion and applied the mathematical theory of water waves to sediments colonized by biofilms, using dimensional- and force analysis, for sliding and rolling conditions, respectively.

Field studies have shown the effects of tidal currents acting on a sedimentary flat colonized by microbial mats, from erosion and deposition (mainly for suspended sediments), to latencies (i.e. periods with no- or very low rates of sediment reworking, Fig. 8.6).

2.3.2 Extent of Sediment Stabilization

During latencies, microbiota develop epibenthic and endobenthic mats, as discussed above. Low sedimentation (and thus low energy levels) are necessary for cyanobacteria to move upward towards the newly-deposited sedimentary surface. Once formed, however, the microbial mat can withstand increased energy levels during severe storms (Fig. 8.7). Microbial mats counteract erosion to varying extents, depending upon the type of mat that develops (Noffke 2010). Although both epibenthic and endobenthic microbial mats protect the sedimentary surface

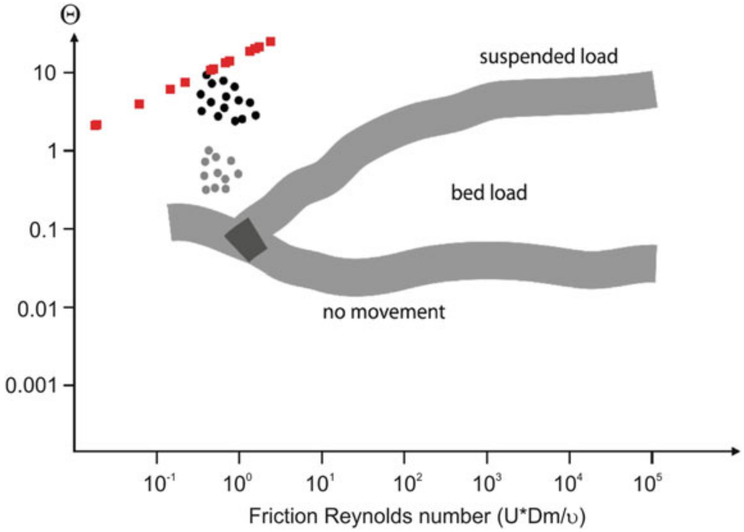


Fig. 8.7 Shield's diagram showing the shear stress (included in Θ) required to initiate sediment grain movement (U*Dm/v, i.e. sediment transport). Grey dots represent shear stress required to initiate sediment movement in endobenthic microbial mats; black dots correspond to the shear stress required to initiate sediment movement in epibenthic microbial mats. Red squares are the maximum values of shear stress generated by wave activity over epibenthic microbial mats. The force required to move the microbially-colonized sediments (points) is greater than that required for sterile sediment (curves). Modified from Cuadrado et al. (2014).

from erosion, their effects on water frictional forces are different. The epibenthic microbial mat has a *slippery* surface (probably due to abundant EPS, Fig. 8.2), which induces a ninefold increase in the erosion threshold, even reaching values up to 12 times in comparison to sterile sediments (Noffke 2010). Conversely, the endobenthic microbial mat produces a *rougher* sedimentary surface, turning the smooth, laminar water flow into a turbulent flow, increasing the sediment erosion threshold only 3–5 times (Cady and Noffke 2009). Re-deposition is also affected by the suspended sediment association with viscous EPS or biofilm, staying in suspension longer than unbound sediment grains due to their increased Reynold number (Jørgensen 1994; Noffke and Krumbein 1999; Noffke 2010).

The remarkable degree of sediment bed stabilization conferred by the presence of microbial mats was recently demonstrated for a storm event (Cuadrado et al. 2014). This study considered the calculated horizontal wave orbital velocity using linearized Airy wave theory, as well as the bed shear stress that was calculated for the wave data. The maximum values of wave orbital velocity ranged between 0.55 and 3.6 m s^{-1}, and bed shear stress produced by the waves (τ_w) ranged from 0.7 to 11.6 Nm^{-2}. The value of Shields' parameter (θ) generated by the waves was then compared with tidal current shear stress measured on endo- and epibenthic microbial mats (Fig. 8.7). The calculated storm-generated wave shear stress was greater than that recorded for tidal currents over biostabilized sediments, and this stress produced the overturned pieces of colonized sediments, called 'flip-over microbial sedimentary structures' (Fig. 8.8).

2.3.3 The Role of Microbial Mats in the Generation of Low-Grade Geomorphic Structures Under High-Energy Conditions

The study of microbial mats can yield important information about the sedimentary processes and hydraulic dynamics during storm events. Such a study was performed on the supratidal zone of a mudflat colonized by microbial mats in the Bahía Blanca estuary (Cuadrado et al. 2013). Evidence of the increased energy acting on the flat was left in the form of new microbial sedimentary structures, and the alteration or destruction of others. Due to prolonged aerial exposure of the supratidal zone between spring tides, and the subsequent desiccation of the microbial mats and the underlying sediment, shrinkage cracks may appear. Successive low-energy inundation may promote the covering of the polygonal cracks by mat overgrowth (Fig. 8.8a). Sometimes the cracks are re-filled with sediment before mat overgrowth occurs (Eriksson et al. 2007). In other cases, when the supratidal zone is inundated during storms, high wave- and tidal current-energy may rip the mat and create new sedimentary structures based on flipped-over mats (Fig. 8.8b). The same process can further fragment the mat into microbial chips that are transported by currents and scattered across the mudflat, where they may be recolonized (Fig. 8.8c). The erosion caused during transport may be inferred from the rounded edges of the microbial chips. Thick flipped-over mats are indicative of the highest energy levels generated by waves and currents over the mudflat (Fig. 8.8d).

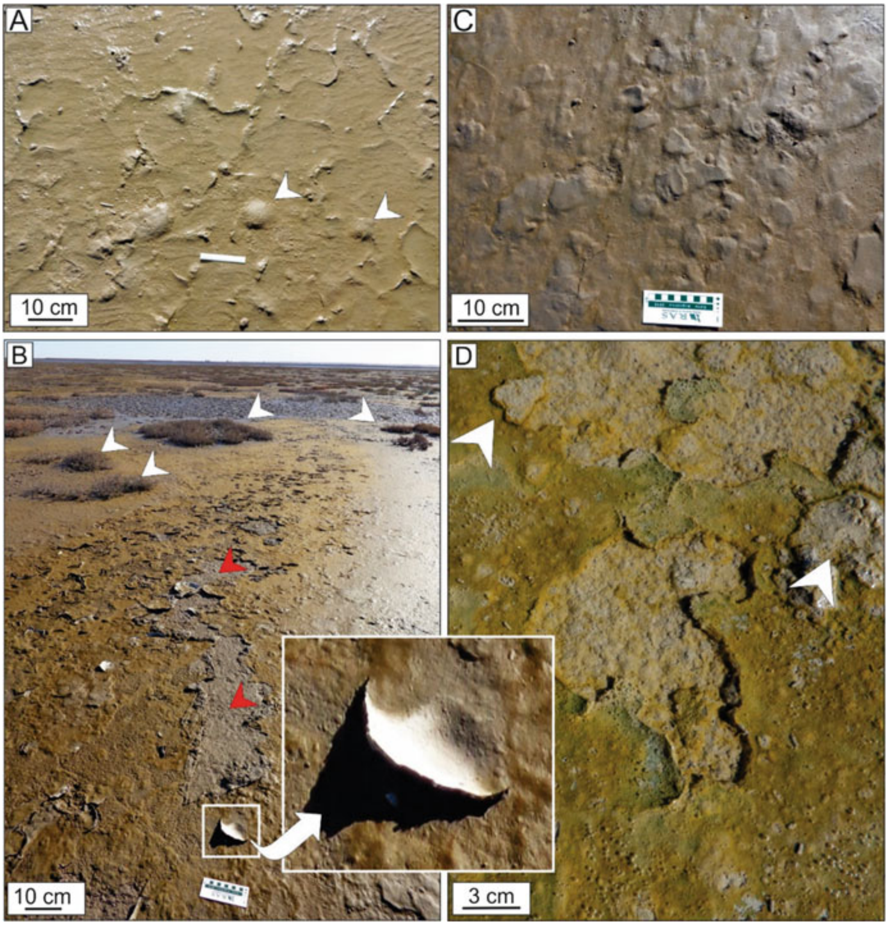


Fig. 8.8 Microbially-induced sedimentary structures (MISS) on a tidal flat in the inner Bahía Blanca Estuary, Argentina. (**a**) Sealed shrinkage cracks after inundation of the flat. Note bulging bubble (arrows), formed through microbial metabolic activity. (**b**) Epipelic diatom colonization on surface sediments in the supratidal zone; white arrows show typical halophyte angiosperms *Sarcocornia* spp. Wave action has ripped off parts of the mat, exposing the underlying sediment (red arrows). Note some borders upturned by desiccation (inset). (**c**) Microbial mat chips newly attached to the sediment, and recolonized by a thin biofilm. (**d**) Thick microbial mat dislodged by high wave-energy acting on the flat. Some flipped-over sedimentary structures were formed (arrows). These sedimentary structures reflect high energy events (storms) acting on the mudflat. Photos DG Cuadrado, inner Bahia Blanca Estuary, Argentina.

On mudflats with a high sand content, under prolonged high-energy and high-inundation conditions, such as during spring tide storms, microbial-mat sediment stabilization can also generate new sedimentary structures. Under such conditions, the supratidal zone may be inundated for several days during high tides, and the cohesive microbial mat may actually detach from the underlying sandy sediment,

Fig. 8.9 Liquefied sand beneath a microbial mat. The photograph was taken after a severe storm event during which the supratidal zone was inundated twice per day for several days (Cuadrado et al. 2014, photo DG Cuadrado).

which is so water-saturated that it behaves like a confined aquifer (Fig. 8.9). The water column and waves superimposed on the cohesive microbial mat increase the total pore water pressure on the sediment below, generating liquefied sand. Under these conditions, the microbial mat behaves like a flexible seal moving over liquefied sand, bearing the pressure of the water column and waves. Characteristic microbial sedimentary structures may be generated by such processes (Cuadrado et al. 2014).

2.3.4 'Deep Time' Understanding of MISS

Experiments in the modern and geological surveys in the fossil have shown that currents in the 'optimum' range for MISS formation are between 2 and 20 cm s^{-1}. Microbially-induced sedimentary structures may evenually fossilize, with the lithification of the organic components (Krumbein 1979; Schultze-Lam et al. 1996; Noffke 2010; Schieber et al. 2007).

Perhaps the most familiar fossil microbialites are the stromatolites, such as the emblematic structures exposed in the supratidal of Shark Bay, Australia. It is of the utmost importance to understand that, apart from being generated by microbial mats, stromatolites have nothing in common with mudflat MISS. The former are mainly warm-water structures formed from carbonate precipitation processes over many years; the latter are siliclastic, depositional structures which can form over the course of a single year or less and are found in cooler waters (Noffke et al. 2002; Noffke and Awramik 2013).

3 Genesis and Maintenance of Transitory Large-Scale Three-Dimensional Patterns

We have shown that superficial sedimentary structure is intimately related to the biological community within the mudflat. In addition to the micro-topographic structures detailed above, large-scale, transitory three-dimensional patterning may occur on mudflats though the interplay of sedimentary erosion caused by tidal currents and waves, and erosion resistance caused by microbial mats and surficial biofilms (Weerman et al. 2010). Such transitory sedimentary features, called *hummocks*, provide a three-dimensional complexity (Fig. 8.10), within which both geomorphological and biological patterns may emerge, as detailed below.

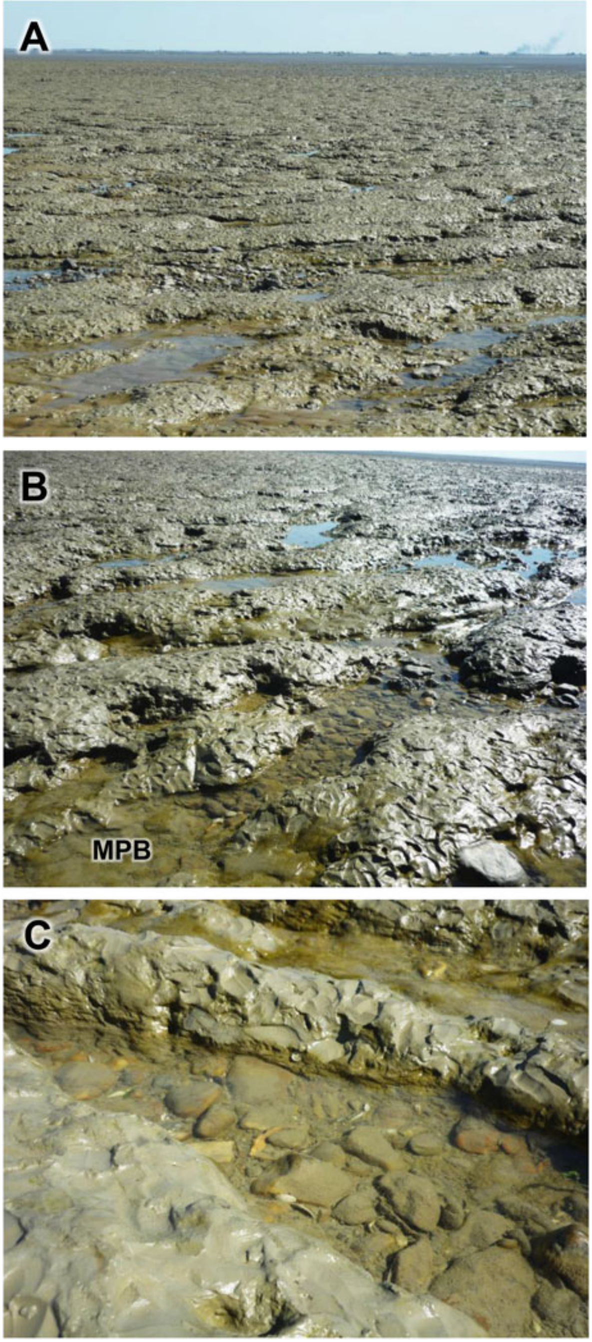
Transient epibenthic biofilms show a preference for the summits of mudflat topographical features, even on low-grade ripple marks (Fig. 8.11). Epipelic diatoms are also found in high densities on top of mudflat hummocks, dispersed over large mudflat areas (Noffke and Krumbein 1999; Blanchard et al. 2000; de Brouwer et al. 2000; Whitehouse et al. 2000; Lanuru et al. 2007, and Fig. 8.1, Chap. 1), while densities are much lower in the depressions (Weerman et al. 2010). These patterned landscapes can persist for months or years, showing seasonal variations corresponding to variations in the diatom biofilms atop the hummocks. The genesis and maintenance of such patterned mudflat landscapes are described below.

3.1 Hummock Formation

A number of recent studies on pattern formation in diatom biofilms provide insight into the mechanisms involved in the formation of mudflat hummock patterns (Weerman et al. 2010, 2011a, b). These studies highlight the emergence of spatial self-organization processes resulting from the interplay of diatom growth, reduction in sediment erosion, and drainage of tidal water (Noffke and Krumbein 1999; Carling et al. 2009; Weerman et al. 2010). As mentioned above, microphyobenthic biofilms grow preferentially on elevated sediment; by excreting EPS, microalgae and bacteria can both incorporate fine-grained particles into the biofilm matrix, and solidify the nascent three-dimensional structure (Yallop et al. 1994; Paterson 1995; de Brouwer et al. 2000; Lubarsky et al. 2010; Stal 2010). The formation of the biofilm also protects the diatoms themselves from (re)suspension, lowering their local losses, and can provide crucial nutrients for growth (Van de Koppel et al. 2001), thereby creating a positive feedback where increased diatom biomass leads to enhanced net sediment deposition.

The local accumulation of sediment beneath the diatom biofilms can have important implications for the drainage of seawater that remains on the mudflat at low tide. Diatom biofilms and epibenthic mats that are elevated above the average sediment

Fig. 8.10 Mixed-substrate mudflat, with hummocks and pools. (**a**) overview; (**b**) Detail showing microphytobenthos (MPB) in pool; (**c**) detail showing pool with exposed rocks. Note markings on hummock crests in (**b**) and (**c**). Photos PG Beninger, La Bernerie, France.



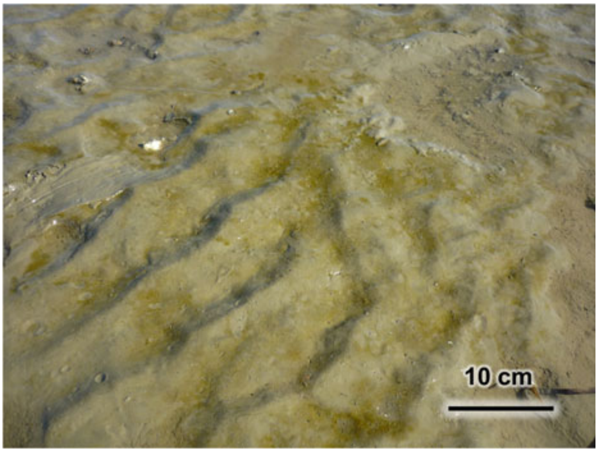


Fig. 8.11 Ripple marks on sediment surface with associated MPB surface biofilm. Foreground scale indicated. Photo P.G. Beninger, La Bernerie, France.

level will become slightly more dry compared to the biofilms that sit in local depressions. This reduction of the remaining water level will consolidate the mat, making it more resistant to erosion (Blanchard et al. 2000). Hence, an additional positive feedback is created where increased elevation improves drainage, stimulating diatom growth, further reducing erosion, and thus increasing elevation. More water remains in the depressions at low tide, which loosens the biofilm, dissolves EPS, and increases erosion, leading to an even deeper low-tide water layer. Using a mathematical model, Weerman et al. (2010) showed that this feedback can create a regularly patterned landscape of diatom-covered hummocks, and water-filled, bare depressions that form a typical drainage network. Similar morphological patterns, called erosional remnants and pockets, arise from the same sediment—microbiota interactions in sandy intertidal settings (Noffke and Krumbein 1999). The quantification of erosional remnants and pockets showed that such surface morpholgies are the result of biostabilizing microbial mats. The mats grow especially well in ripple valleys, where they baffle and trap sediment and bind it into the mat matrix. Consequently, the ripple marks appear smaller and the ripple index is modified. The sedimentary modifications generated by the microbiota in such sandy tidal settings are expressed as the modification index (MOD-I, Noffke and Krumbein 1999).

Increased erosion in the sediment depressions can lay bare underlying stones, resulting in a mixed-sediment, hummock-patterned mudflat (Fig. 8.10b). This self-organization process that emerges from the consolidating effect of the biofilms leads to the formation of a physical landscape of hummocks and hollows that not only allows for increased diatom biomass, but also promotes the capture of sediment throughout the mudflat (Weerman et al. 2010), affecting the entire mudflat landscape and ecosystem.

In mudflats with a higher sand content, the pattern of erosional remnants fluctuates in correspondence to the seasons: in summer the MOD-I (based on the surface morphologies) shows a high influence of microbial activities on the sedimentary processes; in winter, this influence is much less. However, in the lower supratidal

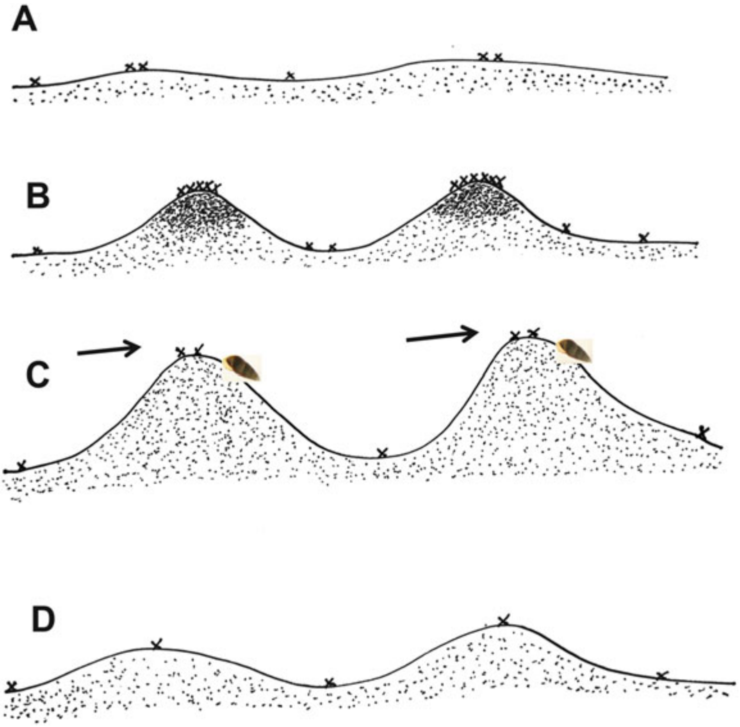


Fig. 8.12 Seasonal topographical mudflat patterning in the Westerschelde estuary and Wadden Sea (Netherlands). (**a**) winter, low MBP density (x), little effect on sediment topography; (**b**) Spring, proliferation of MBP on elevated sediments, enhancing sediment stabilization through EPS secretion; (**c**) summer grazing removes and fragments MBP, rendering it more susceptible to peeling from wave action (arrow); (**d**) less-stable sediment leads to recession of hummock formations in late summer-fall. Schematic PG Beninger.

zone, the MOD-I remains almost unaffected, proving that here the influence of epibenthic microbial mats remains strong through the entire year (Noffke and Krumbein 1999). Hummock patterns may persist for several years on these more sandy tidal flats, whereas those found in the finer-sediment Westerschelde estuary and Wadden Sea (Netherlands) are seasonally formed (Noffke and Krumbein 1999; de Brouwer et al. 2000; Weerman et al. 2011b). In winter, when diatom production is limited, there is little control by diatom biofilms on sediment properties, and the mudflat is bare and flat (Fig. 8.12a). Between April and June, a strongly patterned biofilm develops, with the accompanying hummock landscape Fig. 8.12b). When the temperatures increase during late spring, a sudden collapse in diatom densities is observed (Fig. 8.12c). This abrupt demise of the diatom population coincides with increased numbers of benthic grazers such as *Corophium volutator*, *Macoma baltica*, and *Hydrobia ulvae* (Weerman et al. 2011b). Although increased grazing certainly contributes to the collapse in the biofilms, calculations reveal that herbivore number may not be sufficient to consume all of the diatom biomass; field observations suggest the presence of a strong feedback between diatom growth and sedimentation. In April, when diatom densities are at their highest and the tidal flat is clearly patterned, there is a clear correlation between diatom densities and sediment elevation (Weerman et al. 2012). In May, this relation is greatly diminished, and the patterns rapidly degrade. This suggests that the loss of diatom-sedimentation feedback may amplify the disruption caused by benthic grazers, explaining both the dramatic decline of the diatom population, and the mismatch between potential grazing and observed diatom losses. Most of the epibenthic biofilms are likely dislodged by waves after the biofilms are fragmented by the epifaunal herbivores (Fig. 8.12d).

3.2 Seasonal Biofilm Spatial Dynamics

Weerman et al. (2012) highlighted that the epibenthic biofilm patterns changed from regular, at the peak of diatom densities, to increasingly fractal as biofilm degradation commenced. The term “fractal” here implies that patches do not have a characteristic size (as is the case with perfectly regular patterns), but follow a power law patch size distribution, in which small patches are very abundant, but patches become less numerous as their sizes increase. It appears that emerging epibenthic biofilm patches are abundant, but that most are lost before they can become a biofilm of any significant size. What are the underlying processes that create this bottleneck to epibenthic mat establishment? A clue was proposed by Seuront and Spilmont (2002). Similar to Weerman et al. (2012), they implicated power law patch size distributions, and proposed that these can be explained by the “self-organized criticality” concept (Bak et al. 1987; Pascual and Guichard 2005). Self-organized critical systems are governed by slow buildup of patches, increasing vulnerability of patches as they become bigger, followed by fast patch collapse. Although Seuront and Spilmont (2002) did not pinpoint a specific process of patch collapse, it is likely that once the biofilms become bigger, they become more vulnerable to wave action that peels the biofilms from the sediment (Fig. 8.8). When diatom growth is insufficient to overcome wave-induced losses, positive feedbacks between diatom growth and sediment accumulation fail, and very little diatom biomass can accumulate. Although this explanation is speculative, similar “criticality” processes linked to power law patch size distributions have been described for mussel beds on rocky shores (Guichard et al. 2003). Hence, power-law patch size distributions may be a general indicator of conditions where biofilms lose their grip on the ecosystem, and a more dynamic regime emerges.

It should be noted that bioturbators may also decrease the erosion threshold of mudflat sediments, as has been demonstrated for the cockle *Cerastoderma* edule (Li et al. 2017); such activity may be expected to facilitate the formation of geomorphological features. These observations once again underscore the interplay between physical and biological factors in patterning and unpatterning the mudflat landscape.

4 Higher-Level Biological Patterning

To date, few studies have focussed on fine-scale biological patterning on mudflats, although it is known that small scales are important sources of biological patterning (Findlay 1981, 1982; Murphy et al. 2008; Chapman et al. 2010). Indeed, such patterning is evident even on almost featureless mudflats. As noted above, microphytobenthos—dominated biofilms may develop preferentially on the slightest of elevations, such as on ripple marks (Fig. 8.11). Within the sediment, aggregated spatial distributions have been detected for every macro-infaunal species investigated to date (e.g. Boldina and Beninger 2013, 2014; Beninger and Boldina 2014), as well as for meiofauna (Boldina et al. 2014, and see Chap. 15). Because they tend to exclude each other within the perimeters of their feeding areas, deposit-feeders generally have thinner fine-scale distributions than suspensivores (Flach 1992; Flach and de Bruin 1993; Flach and Beukema 1994). Isotropic infaunal spatial patterning appears to be the rule (see Chap. 15); although this aspect has not yet been formally investigated, the spatial patterns of different infaunal species very probably overlap to varying extents (Fig. 8.13), depending on sedimentological (e.g. grain profile) and biological factors (e.g. bioturbation).

As described above, transient epibenthic biofilms grow rapidly on intertidal mudflat sediments, and epibenthic microbial mats grow in the humid supratidal sediments, which may be periodically submerged during spring tides. The idea that the biological patterning on mudflats is due to complex interactions between fauna, microflora, and sediment was posited by Murphy et al. (2008) with respect to the spatial variability of the microphytobenthos, and reiterated in Chap. 5. Considering the range of trophic

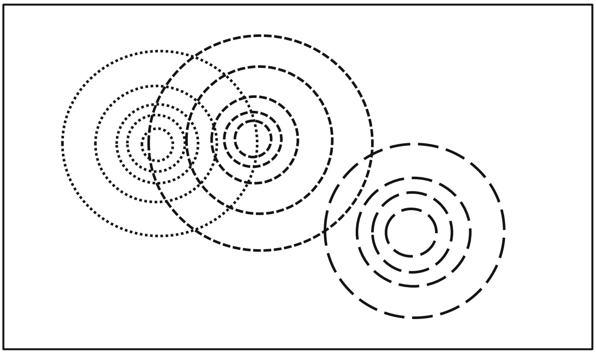
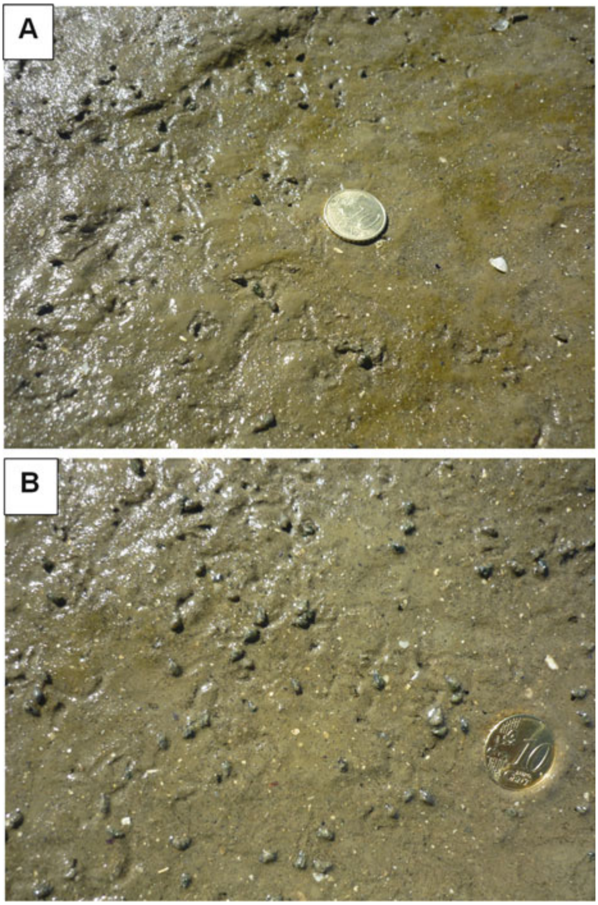


Fig. 8.13 Hypothetical juxtaposition of three isotropic patches belonging to three different infaunal species on a flat mudflat. Schematic PG Beninger.

Fig. 8.14 *Hydrobia ulvae* grazing on MPB. (**a**) note absence of MPB where the small gastropod *H. ulvae* are present; (**b**) detail of *H. ulvae*. Photos PG Beninger, Le Gois, France.



levels, it is likely that patterning is due to both 'bottom-up' and 'top-down' relations (van der Wal et al. 2008; Chapman et al. 2010). For example, the spatial distribution of the epibenthic biofilms influences that of infaunal biofilm consumers such as nematodes (Blanchard 1990). In mudflats with the complex hummock—depression spatial patterning described above, the consequent biological patterning of the epibenthic biofilms is even more striking. In turn, the spatial distribution of the microphytobenthos influences the biofilm-feeding distributions of such diverse fauna as the ubiquitous gastropods *Hydrobia* and *Nassarius* spp. (Cheverie et al. 2014 and Fig. 8.14), calidrid shorebirds (Jiménez et al. 2015, and see Chap. 12), mullets at high tide (Fig. 8.15) (Truslé 1981; Crosetti and Cataudella 1994; Carpentier et al. 2014 and Figs. 8.10b, c and 8.16), and their attendant parasite populations (Chap. 9). These relations are summarized in Fig. 8.16; they all make sense, but should be rigorously tested through future studies.

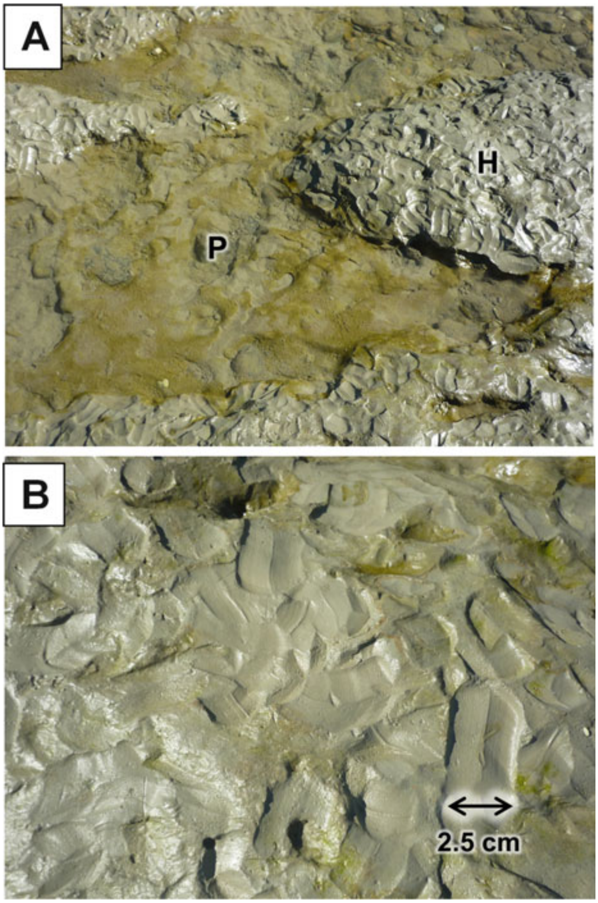


Fig. 8.15 Evidence of mullet (*Mullus* sp.) feeding on MPB. (**a**) totally denuded hummock crest (H) and partially-denuded pool (P). (**b**) Detail of mullet mouth-scrape marks (arrow) on hummock crest. Note absence of MPB wherever there are such marks. Photos PG Beninger, La Bernerie, France.

From the foregoing, as well as from the previous chapters, it is clear that microbial biofilms and mats are not mere passive constituents of mudflats; rather, both in contemporary and in paleontological eras, they form the basis of the mudflat ecosystem, allowing a host of organisms to persist and pattern in what otherwise could be a hostile, low-productive habitat. Beyond being the basis of the mudflat food web, biofilm-forming phytobenthic microbes model their habitat by altering sedimentation, hydrology, and nutrient availability, patterning both the physical and the biological landscapes in the process. Although understandably arduous, detailed study of the interplay between physical and biological patterning on mudflats represents an extremely interesting, and necessary, research goal (Chapman et al. 2010).

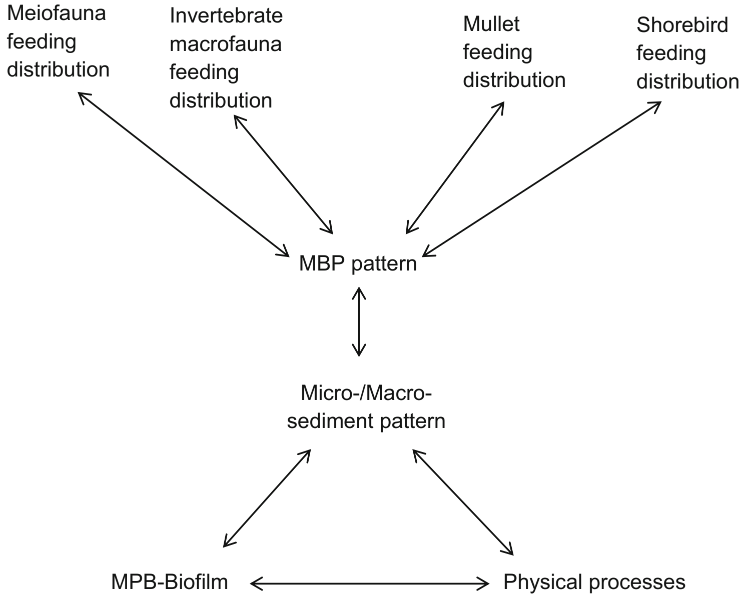


Fig. 8.16 Summary of relations between physical processes, MPB, mudflat topography, MPB spatial pattern, and consequences for the feeding distributions of MPB consumers. All of the animal taxa carry parasites, whose distribution will therefore also be influenced by the MBP pattern. Schematic PG Beninger.

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References

Andersen TJ, Pejrup M (2011) Biological influences on sediment behavior and transport. In: Wolanski E, McLusky DS (eds) Treatise on estuarine and coastal science, vol 2. Academic, Waltham, pp 289–309

Bak P, Tang C, Wiesenfeld K (1987) Self-organized criticality – an explanation of 1/f noise. Phys Rev Lett 59:381–384

Beninger PG, Boldina I (2014) Fine-scale spatial distribution of the temperate infaunal bivalve *Tapes (=Ruditapes) philippinarum* (Adams and Reeve) on fished and unfished intertidal mudflats. J Exp Mar Biol Ecol 457:128–134

Blanchard G (1990) Overlapping microscale dispersion patterns of meiofauna and rnicrophytobenthos. Mar Ecol Prog Ser 68:101–111

Blanchard GF, Paterson DM, Stal LJ, Richard P, Galois R, Huet V, Kelly J, Honeywill C, de Brouwer J, Dyer K, Christie M, Seguignes M (2000) The effect of geomorphological structures on potential biostabilisation by microphytobenthos on intertidal mudflats. Cont Shelf Res 20:1243–1256

Boldina I, Beninger PG (2013) Fine-scale spatial structure of the exploited infaunal bivalve *Cerastoderma edule* on the French Atlantic coast. J Sea Res 76:193–200

Boldina I, Beninger PG (2014) Fine-scale spatial distribution of the common lugworm *Arenicola marina*, and effects of intertidal clam fishing. Estuar Coast Shelf Sci 143:32–40

Boldina I, Beninger PG, Le Coz M (2014) Effect of long-term mechanical perturbation on intertidal soft-bottom meiofunal community spatial structure. J Sea Res 85:85–91

Bruslé J (1981) Food and feeding in grey mullets. In: Oren OH (ed) Aquaculture of grey mullets. Cambridge University Press, Cambridge, pp 185–217

Cady SL, Noffke N (2009) Geobiology: evidence for early life on earth and the search for life on other planets. GSA Today 19:4–10

Carling PA, Williams JJ, Croudace IW, Amos CL (2009) Formation of mud ridge and runnels in the intertidal zone of the Severn Estuary, UK. Cont Shelf Res 29:1913–1926

Carpentier A, Como S, Dupuy C, Lefrançois C, Feunteun E (2014) Feeding ecology of *Liza* spp. in a tidal flat: evidence of the importance of primary production (biofilm) and associated meiofauna. J Sea Res 92:86–91

Chapman MG (2000) Poor design of behavioural experiments gets poor results: examples from intertidal habitats. J Exp Mar Biol Ecol 250:77–95

Chapman MG, Tolhurst TJ, Murphy RJ, Underwood AJ (2010) Complex and inconsistent patterns of variation in benthos, micro-algae and sediment over multiple spatial scales. Mar Ecol Prog Ser 398:33–47

Cheverie AV, Hamilton DJ, Coffin MRS, Barbeau MA (2014) Effects of shorebird predation and snail abundance on an intertidal mudflat community. J Sea Res 92:102–114

Crosetti D, Cataudella S (1994) The mullets. In: Nash CE (ed) Production of aquatic animals: fishes. Elsevier, Amsterdam, pp 253–268

Cuadrado DG, Carmona NB, Bournod CA (2011) Biostabilization of sediments by microbial mats in a temperate siliciclastic tidal flat Bahía Blanca estuary (Argentina). Sediment Geol 237:95–101

Cuadrado DG, Bournod CN, Pan J, Carmonade NB (2013) Microbially-induced sedimentary structures (MISS) as record of storm action in supratidal modern estuarine setting. Sediment Geol 296:1–8

Cuadrado DG, Perillo GME, Vitale AJ (2014) Modern microbial mats in siliciclastic tidal flats: evolution, structure and the role of hydrodynamics. Mar Geol 352:367–380

de Brouwer JFC, Bjelic S, Deckere E, Stal LJ (2000) Interplay between biology and sedimentology in a mudflat (Biezelingse Ham, Westerschelde, the Netherlands). Cont Shelf Res 20:1159–1177

de los Ríos A, Ascaso C, Wierzchos J (2004) Microstructural characterization of cyanobacterial mats from the McMurdo Ice Shelf, Antarctica. Appl Environ Microbiol 70:569–580

Decho AW (2000) Microbial biofilms in intertidal systems: an overview. Cont Shelf Res 20:1257–1273

Dupuy C, Mallet C, Guizien K, Montanié H, Bréret M, Mornet F, Fontaine C, Nérota C, Orvainf F (2014) Sequential resuspension of biofilm components (viruses, prokaryotes and protists) as measured by erodimetry experiments in the Brouage mudflat (French Atlantic coast). J Sea Res 92:56–65

Eriksson PG, Porada H, Banerjee S, Bouougri E, Sarkar S, Bumby AJ (2007) Mat-destruction features. In: Schieber J, Bose P, Eriksson PG, Banerjee S, Sarkar S, Altermann W, Catuneanu O (eds) Atlas of microbial mat features preserved within the siliciclastic rock record. Elsevier, Amsterdam, pp 76–105

Fang H, Shang Q, Chen M, He G (2014) Changes in the critical erosion velocity for sediment colonized by biofilm. Sedimentology 61:648–659

Fenchel T, Kühl M (2000) Artificial cyanobacterial mats: growth, structure, and vertical zonation patterns. Microb Ecol 40:85–93

Fernández EM, Spetter CV, Martinez A, Cuadrado DG, Avena MJ, Marcovecchio JE (2016) Carbohydrate production by microbial mats communities in tidal flat from Bahía Blanca Estuary (Argentina). Environ Earth Sci 75:641

Findlay SEG (1981) Small-scale spatial distribution of meiofauna on a mud- and sandflat. Estuar Coast Shelf Sci 12:471–484

Findlay SEG (1982) Influence of sampling scale on apparent distribution of meiofauna on a sandflat. Estuaries 5:322–324

Flach EC (1992) Disturbance of benthic infauna by sediment-reworking activities of the lugworm *Arenicola marina*. Neth J Sea Res 30:81–89

Flach EC, Beukema JJ (1994) Density-governing mechanisms in populations of the lugworm *Arenicola marina* on tidal flats. Mar Ecol Prog Ser 115:139–149

Flach EC, de Bruin W (1993) Effects of *Arenicola marina* and *Cerastoderma edule* on distribution, abundance and population structure of *Corophium volutator* in Gullmarsfjorden, Western Sweden. Sarsia 78:105–118

Folk RL, Andrews PB, Lewis DW (1970) Detrital sedimentary rock classification and nomenclature for use in New Zealand. N Z J Geol Geophys 13:937–968

Friend PL, Lucas CH, Holligan PM, Collins MB (2008) Microalgal mediation of ripple mobility. Geobiology 6:70–82

Gerdes G (2007) Structures left by modern microbial mats in their host sediments. In: Schieber J, Bose P, Eriksson PG, Banerjee S, Sarkar S, Altermann W, Catuneanu O (eds) Atlas of microbial mat features preserved within the clastic rock record. Elsevier, Amsterdam, pp 5–38

Guichard F, Halpin PM, Allison GW, Lubchenco J, Menge BA (2003) Mussel disturbance dynamics: signatures of oceanographic forcing from local interactions. Am Nat 161:889–904

Hagadorn JW, McDowell C (2012) Microbial influence on erosion, grain transport and bedform genesis in sandy substrates under unidirectional flow. Sedimentology 59:795–808

Hall-Stoodley L, Stoodley P (2002) Developmental regulation of microbial biofilms. Curr Opin Biotechnol 13:228–233

Hall-Stoodley L, Costerton JW, Stoodley P (2004) Bacterial biofilms: from the natural environment to infectious diseases. Nat Rev Microbiol 2:95–108

Hjülstrøm F (1935) Studies of the morphological activity of rivers as illustrated by the river Fyris. Bull Geol Inst Univ Uppsala 25:221–528

Jiménez A, Elner RW, Favaro C, Rickards K, Ydenberg RC (2015) Intertidal biofilm distribution underpins differential tide-following behavior of two sandpiper species (*Calidris mauri* and *Calidris alpina*) during northward migration. Estuar Coast Shelf Sci 155:8–16

Jørgensen BB (1994) Diffusion processes and boundary layers in microbial mats. In: Stal LJ, Caumette P (eds) Microbial mats. NATO ASI series (Series G: Ecological sciences), vol 35. Springer, Berlin

Kaźmierczak J, Fenchel T, Kühl M, Kempe S, Kremer B, Łącka B, Małkowski K (2015) CaCO3 precipitation in multilayered cyanobacterial mats: clues to explain the alternation of micrite and sparite layers in calcareous stromatolites. Life 5:744–769

Krumbein WE (1979) Photolithotrophic and chemoorganotrophic activity of bacteria and algae as related to beach rock formation and degradation (Gulf of Aqaba, Sinai). Geomicrobiol J 1:139–203

Lanuru M, Riethmüller R, Bernem C, Heymann K (2007) The effect of bedforms (crest and trough systems) on sediment erodibility on a back-barrier tidal flat of the East Frisian Wadden Sea, Germany. Estuar Coast Shelf Sci 72:603–614

Li B, Cozzoli F, Soissons LM, Boumab TJ, Chen L (2017) Effects of bioturbation on the erodibility of cohesive versus non-cohesive sediments along a current-velocity gradient: a case study on cockles. J Exp Mar Biol Ecol 496:84–90

Lubarsky HV, Hubas C, Chocholek M, Larson F, Manz W, Paterson DM, Gerbersdorf SU (2010) The stabilisation potential of individual and mixed assemblages of natural bacteria and microalgae. PLoS One 5(11):e13794. https://doi.org/10.1371/journal.pone.0013794

Madsen KN, Nilson P, Sundbäck K (1993) The influence of benthic microalgae on the stability of a subtidal shallow water sediment. J Exp Mar Biol Ecol 170:159–177

Miller DC, Geider RJ, MacIntyre HL (1996) Microphytobenthos: the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats. II Role in sediment stability and shallow-water food webs. Estuaries 19:202–212

Murphy RJ, Tolhurst TJ, Chapman MG, Underwood AJ (2008) Spatial variation of chlorophyll on estuarine mudflats determined by field-based remote sensing. Mar Ecol Prog Ser 365:45–55

Neu TR (1994) Biofilms and microbial mats. In: Krumbein WE, Paterson D, Stal L (eds) Biostabilization of sediments. Oldenburg, BIS-Verlag, pp 9–17

Neumeier M, Weigert J, Schaffler A, Wehrwein G, Muller-Ladner U, Scholmerich J, Wrede C, Buechler C (2006) Different effects of adiponectin isoforms in human monocytic cells. J Leukoc Biol 79:803–808

Noffke N (2010) Microbial mats in sandy deposits from the Archean era to today. Springer, Berlin

Noffke N, Awramik SM (2013) Stromatolites and MISS—differences between relatives. GSA Today 23:4–9

Noffke N, Krumbein WE (1999) A quantitative approach to sedimentary surface structures contoured by the interplay of microbial colonization and physical dynamics. Sedimentology 46:417–426

Noffke N, Gerdes G, Klenke T, Krumbein WE (2001) Microbially induced sedimentary structures-a new category within the classification of primary sedimentary structures. J Sediment Res 71:649–656

Noffke N, Knoll AH, Grotzinger JP (2002) Sedimentary controls on the formation and preservation of microbial mats in siliciclastic deposits: a case study from the Upper Neoproterozoic Nama Group, Namibia. Palaios 17:533–544

Noffke N, Christian D, Wacey D, Hazen RM (2013a) Microbially induced sedimentary structures recording a complex microbial ecosystem in the 3.5 Ga Dresser Formation, Pilbara, Western Australia. Astrobiology 13:1–22

Noffke N, Decho AW, Stoodley P (2013b) Slime through time: the fossil record of prokaryote evolution. PALAIOS 28:1–5

Pan J, Bournod CN, Pizani NV, Cuadrado DG, Carmona NB (2013) Characterization of microbial mats from a siliciclastic tidal flat (Bahía Blanca estuary, Argentina). Geomicrobiol J 30:665–674

Pascual M, Guichard F (2005) Criticality and disturbance in spatial ecological systems. Trends Ecol Evol 20:88–95

Passarelli C, Olivier F, Paterson DM, Meziane T, Hubas C (2014) Organisms as cooperative ecosystem engineers in intertidal flats. J Sea Res 92:92–101

Paterson DM (1995) Biogenic structure of early sediment fabric visualized by low temperature scanning electron microscopy. J Geol Soc 152:131–140

Pierre G, Zhao J, Orvain F, Dupuy C, KleinGL GM, Maugard T (2014) Seasonal dynamics of extracellular polymeric substances (EPS) in surface sediments of a diatom-dominated intertidal mudflat (Marennes-Oléron France). J Sea Res 92:26–35

Rietkerk M, van de Koppel J (2008) Regular pattern formation in real ecosystems. Trends Ecol Evol 23:169–175

Rodrigues AM, Meireles S, Pereira T, Gama A, Quintino V (2006) Spatial patterns of benthic macroinvertebrates in intertidal areas of a Southern European estuary: the Tagus, Portugal. Hydrobiologia 555:99–113

Schieber J, Bose PK, Eriksson PG, Sarkar S (2007) Paleogeography of microbial mats in terrigenous clastic-environmental distribution of associated sedimentary features and the role of geologic time. In: Schieber J, Bose P, Eriksson PG, Bannerjee S, Sarkar S, Altermann W, Catuneau O (eds) Atlas of microbial mat features preserved within the siliciclastic rock record. Elsevier, Amsterdam, pp 267–275

Schultze-Lam S, Fortin D, Davis BS, Beveridge TJ (1996) Mineralization of bacterial surfaces. Chem Geol 132:171–181

Seuront L, Spilmont N (2002) Self-organized criticality in intertidal microphytobenthos patch patterns. Phys A Stat Mech Appl 313:513–539

Shields A (1936) Application of similarity principles and turbulence research to bed-load movement. Mitt Preussischen Versuchsanstalt fur Wasserbau und Schiffbau 26:5–24

Stal LJ (2010) Microphytobenthos as a biogeomorphological force in intertidal sediment stabilization. Ecol Eng 36:236–245

Stal LJ, de Brouwer JFC (2003) Biofilm formation by benthic diatoms and their influence on the stabilization of intertidal mudflats. Berichte-Forschungszentrum Terramare 12:109–111

Stal LJ, de Brouwer JFC (2005) Diatom biofilms and the stability of intertidal mudflats. Geophys Res Abstr 7:20–28

Steele DJ, Franklin DJ, Underwood JC (2014) Protection of cells from salinity stress by extracellular polymeric substances in diatom biofilms. Biofouling 30:987–998

Stolz J (2000) Structure of microbial mats and biofilms. In: Riding RE, Awramik SM (eds) Microbial sediments. Springer, Berlin, pp 1–8

Stoodley P (2016) Flow disrupts communication. Nat Microbiol 1:15012

Stoodley P, Dodds I, Boyle JD, Lappin-Scott HM (1999) Influence of hydrodynamics and nutrients on biofilm structure. J Appl Microbiol 85:19S–28S

Stoodley P, Cargo R, Rupp CJ, Wilson S, Klapper I (2002) Biofilm material properties as related to shearinduced deformation and detachment phenomena. J Ind Microbiol Biotechnol 29:361–367

Tolhurst TJ, Watts CW, Vardy S, Saunders JE, Consalvey MC, Paterson DM (2008) The effects of simulated rain on the erosion threshold and biogeochemical properties of intertidal sediments. Cont Shelf Res 28:1217–1230

Ubertini M, Lefebvre S, Rakotomalala C, Orvain F (2015) Impact of sediment grain-size and biofilm age on epipelic microphytobenthos resuspension. J Exp Mar Biol Ecol 467:52–64

Underwood GJC (1997) Microalgal colonization in a salt-marsh restoration scheme. Estuar Coast Shelf Sci 44:471–481

Underwood GJC, Kromkamp J (1999) Primary production by phytoplankton and microphytobenthos in estuaries. Adv Ecol Res 29:93–153

Underwood GJC, Paterson DM (2003) The importance of extracellular carbohydrate production by marine epipelic diatoms. Adv Bot Res 40:184–240

Underwood GJC, Smith DJ (1998) Predicting epipelic diatom exopolymer concentrations in intertidal sediments from sediment chlorophyll a. Microb Ecol 35:116–125

Underwood GJC, Paterson DM, Parkes RJ (1995) The measurement of microbial carbohydrate exopolymers from intertidal sediments. Limnol Oceanogr 40:1243–1253

Underwood GJC, Boulcott M, Raines CA, Waldron K (2004) Environmental effects on exopolymer production by marine benthic diatoms: dynamics, changes in composition, and pathways of production. J Phycol 40:293–304

Van Colen C, Underwood GJC, Serôdio J, Paterson DM (2014) Ecology of intertidal microbial biofilms: mechanisms patterns and future research needs. J Sea Res 92:2–5

Van de Koppel J, Herman PMJ, Thoolen P, Heip CHR (2001) Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. Ecology 82:3449–3461

van der Wal D, Herman PMJ, Forster RM, Ysebaert T, Rossi F, Knaeps E, Plancke YMG, Ides SJ (2008) Distribution and dynamics of intertidal macrobenthos predicted from remote sensing: response to microphytobenthos and environment. Mar Ecol Prog Ser 367:57–72

Van Gemerden H (1993) Microbial mats: a joint venture. Mar Geol 113:3–25

Visscher PT, Stolz JF (2005) Microbial mats as bioreactors: populations processes and products. Palaeogeogr Palaeoclimatol Palaeoecol 219:87–100

Wahl WK, Lok T, van der Meer J, Piersm T, Weissing J (2005) Spatial clumping of food and social dominance affect interference competition among ruddy turnstones. Behav Ecol 16:834–844

Weerman EJ, van de Koppel J, Eppinga MB, Montserrat F, Liu QX, Herman PMJ (2010) Spatial self-organization on intertidal mudflats through biophysical stress divergence. Am Nat 176:15–32

Weerman EJ, Herman PMJ, van de Koppel J (2011a) Macrobenthos abundance and distribution on a spatially patterned intertidal flat. Mar Ecol Prog Ser 440:95–103

Weerman EJ, Herman PMJ, van de Koppel J (2011b) Top-down control inhibits spatial self-organization of a patterned landscape. Ecology 92:487–495

Weerman EJ, Van Belzen J, Rietkerk M, Temmerman S, Kefi S, Herman PMJ, Van de Koppel J (2012) Changes in diatom patch-size distribution and degradation in a spatially self-organized intertidal mudflat ecosystem. Ecology 93:608–618

Whitehouse R, Bassoullet P, Dyer K, Mitchener H, Roberts W (2000) The influence of bedforms on flow and sediment transport over intertidal mudflats. Cont Shelf Res 20:1099–1124

Wolf G (2007) Kinetic modeling of phototrophic biofilms: the PHOBIA model. Biotechnol Bioeng 97:1064–1079

Yallop ML, de Winder B, Paterson DM, Stal LJ (1994) Comparative structure, primary production and biogenic stabilization of cohesive and non-cohesive marine sediments inhabited by microphytobenthos. Estuar Coast Shelf Sci 39:565–582

Zilber-Rosenberg I, Rosenberg E (2008) Role of microorganisms in the evolution of animals and plants: the hologenome theory of evolution. FEMS Microbiol Rev 32:723–735

Chapter 9
Ecology of Parasites in Mudflat Ecosystems

David W. Thieltges, Kim N. Mouritsen, and Robert Poulin

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Abstract Mudflats are not only home to large numbers of bivalves, polychaetes, crustaceans, fish and birds, but also to diverse communities of parasites. In this chapter, we illustrate and explore how the resulting parasite-host interactions can affect host populations, communities and food webs in mudflat ecosystems, equalling in importance the effects resulting from other species interactions, such as

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predation and competition. We first give an overview of the distribution and ecology of typical parasites occurring in mudflat ecosystems. Then we illustrate the main abiotic and biotic drivers of parasite infection levels in mudflat hosts. Following this, we conceptualise and illustrate the many direct and indirect effects of parasite-host interactions on host populations, communities and food webs in mudflat ecosystems. Finally, we highlight the potential impact of ongoing global changes such as increasing temperature and species introductions on parasite-host interactions in mudflat ecosystems. With this condensed overview of the presence and ecological role of parasites in mudflat ecosystems, we hope to increase the appreciation of the manifold ecological effects of parasite-host interactions on host populations, communities and food webs of mudflat ecosystems, and to spark further research in this field.

1 Parasites as Protagonists on Mudflat Ecosystems

1.1 Parasites and Biological Interactions

Species interactions such as competition and predation are well known drivers of the population dynamics and community structure of organisms inhabiting mudflats. While competition is mainly limited to high-density situations (Wilson 1991; Jensen 1993; Raffaelli and Hawkins 1999), predation by typical mudflat predators such as crabs, fish and birds seems to be a universal biotic structuring factor on mudflats (Reise 1985; Wilson 1991; Kaiser et al. 2011, see Chaps. 5, 6, 12). Although the power of species interactions in shaping mudflat community structure and dynamics is generally acknowledged, other species interactions have received much less attention in this respect. Among these are parasitic interactions, i.e. interactions between parasites and their hosts. In this type of interaction, one partner (the parasite) gains a benefit while the other (the host) suffers from negative effects. The benefit is usually a trophic one as parasites feed on their hosts' tissue or pre-digested gut content. The negative effects for hosts can be manifold and range from various sub-lethal effects to mortality.

With their positive-negative dichotomy, parasite-host interactions resemble predator-prey interactions in which the predator gains a benefit and the prey suffers from a negative effect in the interaction (Raffel et al. 2008; Lafferty and Kuris 2002). However, predators differ from parasites in respect to size (predators are usually larger than their prey while parasites are usually smaller) and the number of victims attacked (predators typically attack more than one victim over their life cycle, while parasites usually attack only a single victim per life-cycle stage; Lafferty and Kuris 2002). Under this definition, blood-sucking animals such as mosquitos, leeches or lampreys are considered to be micropredators as they feed on more than a single victim during a life cycle stage (Lafferty and Kuris 2002). However, broader definitions of parasitism would subsume them under parasites (Combes 2001). Further definitional distinctions into sub-categories of the term ‘parasite’ exist. Based on the impact on their hosts, some authors have suggested that typical parasites such as helminths feed on a single host without necessarily killing it while for parasitoids the killing of the host is an inevitable part of the life cycle (Lafferty and Kuris 2002). Finally, parasites are often divided into two groups, microparasites and macroparasites, which, apart from size, are distinguished by their reproductive dynamics: the descendants of microparasites (e.g. protozoans such as *Toxoplasma* and *Plasmodium* spp.) may continue to infect the host, as well as being transmitted to other hosts, whereas the descendants of macroparasites (usually successive larval stages, e.g. trematodes) leave the host to infect other hosts (Schmid-Hempel 2011). Although many microparasites may undoubtedly have strong effects on infected hosts in mudflat ecosystems, we will focus on macroparasites in this chapter, as their ecology and impacts on mudflat ecosystems are much better understood. We will also mainly focus on describing the distribution and various ecological effects of parasites on ‘wild’ hosts in mudflat ecosystems and thus exclude more applied issues of diseases in aquaculture settings such as mussel, oyster or shrimp culture in mudflat ecosystems. In general, we do not intend to provide an exhaustive review of the topic but instead we aim to sketch the broader picture and highlight some active current and future research fields.

1.2 Parasites Occurring in Mudflat Ecosystems

Mudflat ecosystems harbour a large variety of parasites (Fig. 9.1). Recent studies that include parasites in food web analyses give an idea about the typical composition of parasite communities in mudflat ecosystems (Table 9.1). These parasite-inclusive food webs do not cover all types of mudflats, but showcase a sub-set of mudflat ecosystems such as mudflats in estuarine salt marshes (Carpinteria, Bahia Falsa, Estero de Punta Banda) and shallow water ecosystems (Flensburg Fjord), mudflats behind back-barrier islands (Sylt tidal basin) and in large tidal inlets (Otago Harbour). The dominant parasite group in these mudflat ecosystems are trematodes, followed by other helminths such as nematodes, cestodes and acanthocephalans, and a variety of other parasitic groups (Table 9.1). The various parasite species in these food webs constitute between 16 and 76% of the richness of free-living (host) species, indicating that parasites contribute significantly to the biodiversity of mudflat ecosystems.

Although the parasite inventories from these six mudflat food webs give an idea about the general composition of parasite communities in mudflat ecosystems, they are far from being complete, since some host groups such as birds are notoriously

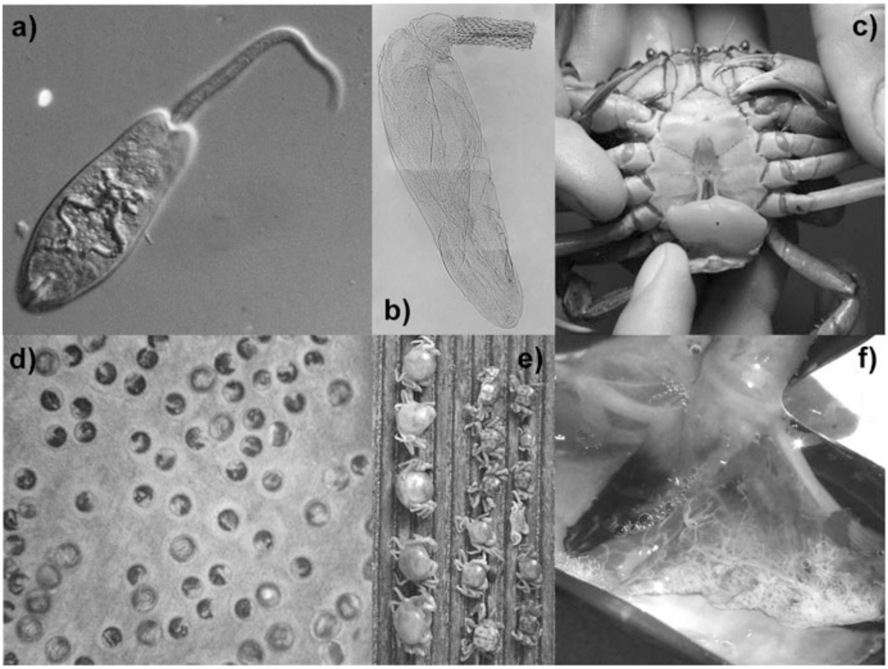


Fig. 9.1 Examples of metazoan parasites occurring in invertebrate hosts living on mudflats. (**a**) Free-living cercarial stage of the trematode *Maritrema subdolum* (length including tail ca. 340 μm); (**b**) cystacanth stage (with everted proboscis) of the acanthocephalan *Plagiorhynchus allisonae* (trunk length ca. 2.5 mm) from the amphipod *Transorchestia chiliensis*; (**c**) sac-like externa of the rhizocephalan barnacle *Sacculina carcini* underneath the pleon of an infected shorecrab *Carcinus maenas* (ca. 6 cm carapax width); (**d**) metacercarial stages of the trematode *Acanthoparyphium* sp. (380–470 μm diameter), encysted in the foot tissue of the New Zealand cockle *Austrovenus stutchburyi*; (**e**) pea crabs *Pinnotheres novaezelandiae* (ca. 8–16 mm carapax width) collected from inside green-lipped mussels *Perna canaliculus*; (**f**) white mesh-like structure of the sporocyst stages of the trematode *Prosorhynchus squamatus* infecting the gonads and hepatopancreas of a blue mussel *Mytilus edulis* (ca. 4 cm shell length) (Published with kind permission of (**a**), (**c**), (**e**): © Kim N. Mouritsen 2018; (**b**) © Bronwen Presswell 2018; (**d**) © Tommy Leung 2018; (**f**) © Tabea Stier 2018. All Rights Reserved).

understudied. Further complications arise from the fact that some host groups (e.g. fish and birds) are often transient components of the local food web that carry parasites acquired elsewhere, and therefore do not necessarily cycle within the local web. In addition, parasite-inclusive food web studies have so far mainly considered macroparasites; however, there is most likely also a large diversity of microparasites in mudflat ecosystems that awaits exploration (Thieltges et al. 2013a). Hence, the presently known diversity of parasites in mudflat ecosystems is likely to increase with future research efforts.

Table 9.1 Composition of parasite communities in six functionally different mudflat ecosystems based on parasite richness of typical taxonomic groups

	Sylt Tidal Basin	Otago Harbour	Flensburg	Carpinteria Salt Marsh	Bahia Falsa	Estero de Punta Banda
Total host richness	116	117	60	92	101	123
Invertebrates	66	93	48	39	47	59
Fish	21	7	12	11	13	19
Birds	29	17	8	42	41	45
Total parasite richness	35	19	46	60	53	76
Trematodes	27	13	27	30	34	39
Nematodes	1	2	10	5	4	7
Cestodes	1		3	6	4	8
Acanthocephalans	1	2	2	2	2	4
Monogeneans				1	1	2
Crustaceans	4	2	1	4	3	4
Rhabdocoelans	1					1
Myxozoans				1		
Nemerteans				1		1
Microsporidians			1			
Protists			2	7	5	9
Viruses				1		1
Parasitic plants				2		

For comparison, total species richness of free-living (metazoan) host species and of major taxonomic groups are also given for each food web (excluding basal groups and bacteria, zooplankton and meiofauna). Data based on Hechinger et al. (2011), Mouritsen et al. (2011), Thieltges et al. (2011), and Zander et al. (2011)

1.3 Parasite Life Cycles

A common feature of many parasites occurring in mudflat ecosystems are their complex life cycles, i.e. they sequentially infect several different host species over their life cycle. For example, the dominant trematodes typically have a three-host life cycle (Figs. 9.1 and 9.2; Galaktionov and Dobrovolskij 2003). Fish, birds or marine mammals, depending on the trematode species, serve as definitive hosts of the adult stages of the parasites. Here, the parasites reproduce sexually and release eggs that leave the host via its faeces. From the eggs, ciliated larvae called miracidia hatch and infect a first intermediate host, which is usually a gastropod and sometimes a bivalve. In the first intermediate host, clonal reproduction by asexually reproducing intramolluscan stages (sporocysts and rediae) leads to the production of a second

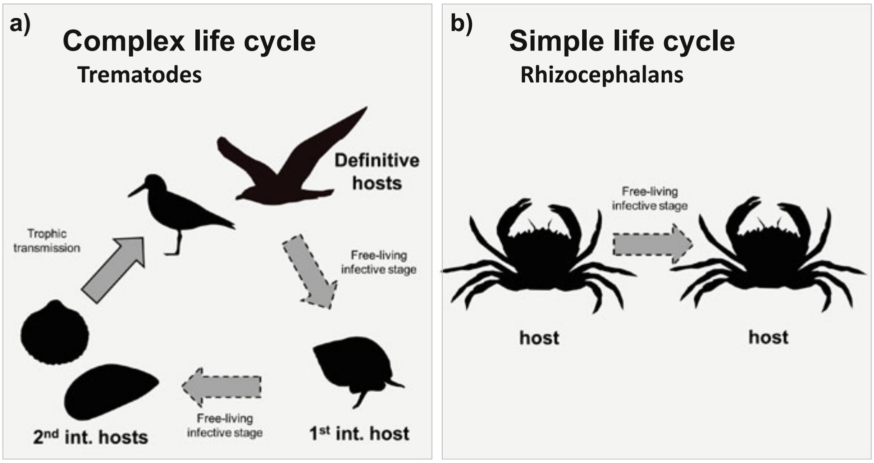


Fig. 9.2 Examples of typical life cycles of parasites occurring on mudflats. (**a**) Complex life cycle of a trematode parasite, including three sequential host species (one definitive host and two intermediate hosts). Host specificity is usually highest in 1st intermediate hosts and lower in 2nd intermediate and definitive hosts. Transmission occurs via a free-living infective stage or via trophic transmission when definitive hosts consume infected prey. (**b**) Simple life cycle of rhizocephalan parasites (e.g. *Sacculina carcini)* infecting other crabs horizontally via a free-living infective stage, released by infected crabs (Published with kind permission of © David Thieltges 2018. All Rights Reserved).

free-living stage, the cercariae, which are released into the environment in large numbers. After a short free-living dispersal period of usually less than 24 h, the cercariae infect a second intermediate host, an invertebrate or fish, depending on the trematode species. Here, most cercariae encyst as metacercariae, and await ingestion of the second intermediate host by a definitive host, before closing the life cycle via trophic transmission. While the standard trematode life cycle consists of three consecutive hosts, variations on the theme exist, with abbreviations as well as extensions of the life cycle (Poulin and Cribb 2002; Galaktionov and Dobrovolskij 2003). Complex life cycles, including the use of one or several intermediate hosts, and a definitive host, also exist in other types of marine parasites such as nematodes, cestodes and acanthocephalans (see Rhode 1993, 2005). The existence of this complexity of life cycles is puzzling and their selective benefits are still debated; increased transmission and survival are, among other benefits, thought to underlie the evolution of these complex life cycles (Poulin 2007).

Although complex life cycles prevail in mudflat ecosystems, there are also parasites that have simple life cycles in which a free-living infective stage released from infected hosts infects another host individual of the same species. For example, the rhizocephalan parasite *Sacculina carcini* infects shore crabs *Carcinus maenas*, in which it grows internally and develops a visible external sac-like structure below the abdomen of the host (the so-called externa), from which infective stages are released and infect a new crab host (Figs. 9.1 and 9.2; Høeg 1995; Høeg and Lützen 1995).

Other marine parasites with simple life cycles are shell-boring polychaetes such as *Polydora ciliata*, or monogenean flatworms infecting fish (Buschbaum et al. 2007; Rhode 2005).

1.4 Hosts Affected in Mudflat Ecosystems

Due to the complex life cycles of many parasites, a single parasite species usually affects several very different host taxa during its life, ranging from invertebrates to vertebrates. In addition, if host specificity is low, the same parasite species can infect several different host species at a given life cycle stage. Overall, this results in most free-living species inhabiting mudflats being infected by at least one parasite species. However, not all of these free-living species will serve as hosts to parasites to the same degree, due to host specificity issues or other ecological processes. For example, at the host species level, the mean number of trematode species that can be found in populations of snail first intermediate hosts in mudflat ecosystems varies widely among host species from 1 to 12.7 (Poulin and Mouritsen 2003). There may also be gastropod species that do not serve as hosts for trematodes at all (Pechenik et al. 2001). Likewise, the mean infection prevalence (the proportion of hosts infected) of the same trematodes in populations of gastropods varies widely among gastropod host species (Poulin and Mouritsen 2003), indicating varying general suitability as hosts among gastropod species.

The same pattern can also be observed within single mudflat ecosystems. For example, the number of parasite species infecting gastropods and bivalves varies widely among host species in a back-barrier islands mudflat ecosystem in German/ Danish coastal waters (Fig. 9.3a). Similarly, the number of parasite species infecting crustaceans in a large tidal inlet in New Zealand varies among host species (Fig. 9.3b). In addition, the mean infection intensity (no. of parasites per infected host) of individual parasite species also differs strongly among and within host species (Fig. 9.3b), indicating that not all hosts are evenly suitable to all parasite species. In general, this suggests that some host species will be more likely to be affected by specific parasite species than others. In addition to among-host species differences in parasite richness and infection levels, there is often also considerable within-host species variation, since the spatial heterogeneity of infections is frequently high in hosts inhabiting mudflats, even within the same mudflat ecosystem (e.g. Hechinger and Lafferty 2005; Fredensborg et al. 2006; Thieltges and Reise 2007). This heterogeneity extends to even smaller scales, as not all individuals of the same host species in the same locality will be equally infected, leading to the almost universal phenomenon of parasite aggregation among hosts, generally observed in parasite-host interactions (Shaw and Dobson 1995). This suggests that not only different host species will be affected by parasitism to a different degree, but also that single host individuals may experience very different exposure to parasites, depending on the locality and other factors. We further discuss some of the underlying mechanisms below.

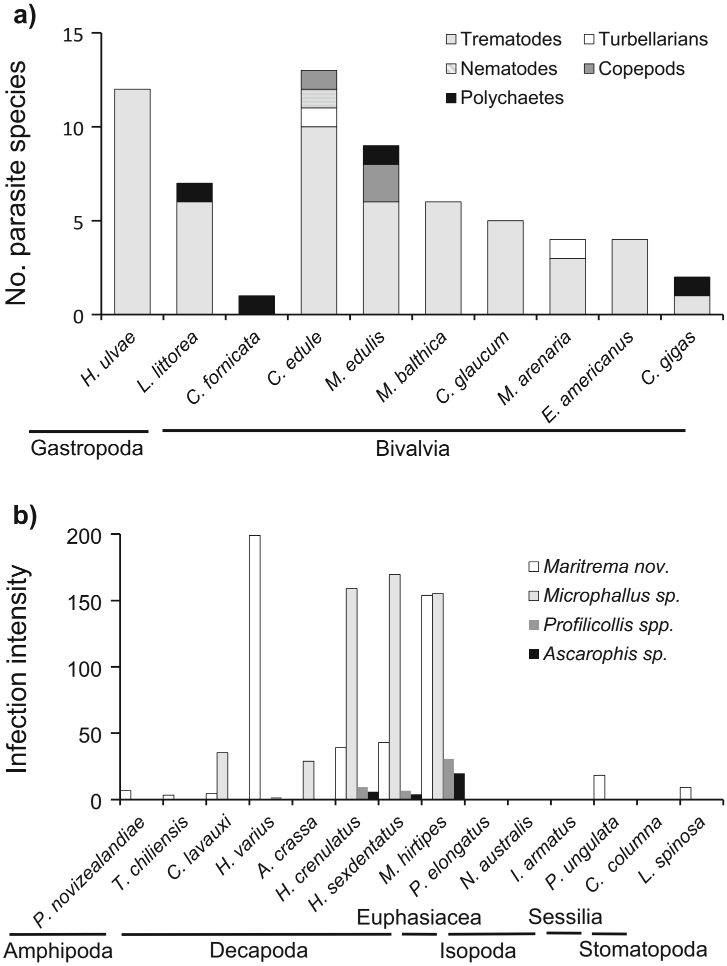


Fig. 9.3 Examples of parasite richness and infection intensities among typical host groups inhabiting mudflat ecosystems. (**a**) Parasite richness of different groups of parasites (shell boring polychaetes, intestinal copepods, nematodes and turbellarians, and trematodes in their first or second intermediate host life cycle stages) in gastropods and bivalves from a back-barrier island mudflat ecosystem in German/Danish coastal waters (Thieltges et al. 2006). (**b**) Mean infection intensity (no. of parasites per infected hosts) of four parasite taxa (two trematodes: *Maritrema novaezealandensis* and *Microphallus* sp., one acanthocephalan species group: *Profilicollis* spp. and one nematode: *Ascarophis* sp.) infecting crustaceans of different taxa in a large tidal inlet in New Zealand (Koehler and Poulin 2010). Redrawn from Thieltges et al. (2006) and Koehler and Poulin (2010).

While the general degree to which molluscs and crustaceans are affected by parasites in mudflat ecosystems is relatively well known (Lauckner 1980, 1983; Poulin and Mouritsen 2003; Thieltges et al. 2009a, b, c), we know much less about parasite infection levels in other host groups. Polychaetes are one of the dominant taxa on mudflats, but have not been studied intensively with respect to parasites. They are known to serve as intermediate hosts, not only for trematodes, but also for nematodes and cestodes (see Peoples 2013 for a recent review); however, little is known about infection levels of polychaetes in mudflat ecosystems (but see Peoples et al. 2012). Fish inhabiting mudflats serve as intermediate and definitive hosts for parasites with complex life cycles such as trematodes and other helminths, which are acquired via trophic transmission from intermediate hosts (Thieltges and Poulin 2016). Although the parasitology of marine fishes is relatively well known, the specific parasite communities and infection intensities of fishes inhabiting mudflats are less well studied, apart from scattered reports on specific fish host or parasite species (e.g. Groenewold et al. 1996), and from a very limited number of broader studies on entire mudflat ecosystems such as Californian estuarine salt marshes (Kuris et al. 2008). This results from the fact that fish parasitological studies usually focus on offshore or deeper coastal waters, and rather on commercially than ecologically relevant species. In addition, it can be difficult to link parasites found in fish with specific habitats, because many coastal fish species often only occur temporarily on mudflats (Horn et al. 1999). Hence, besides being infected with parasites locally acquired via trophic transmission, fish hosts caught on mudflats will also harbour other parasites such as parasitic copepods (e.g. Koch et al. 2014) that they acquired elsewhere, which complicates linking parasites to specific mudflat habitats. Finally, the least-studied host group with respect to parasites (mainly due to ethical constraints in conducting invasive parasitological surveys) are birds, which use mudflats mainly as feeding grounds (Chap. 12). They serve as definitive hosts to the majority of trematode parasites occurring in mudflat ecosystems, and they acquire them via trophic transmission (Thieltges and Poulin 2016). However, little is known about the actual infection levels in birds in specific mudflat ecosystems, apart from local studies on single host and/or parasite species (e.g. Latham and Poulin 2002; Kuris et al. 2008). In addition, like fish, most birds also use mudflats only temporarily, e.g. at stop-overs during their annual migrations, so that their parasite faunas are likely to be composed of parasite species acquired in different habitats (Gutiérrez et al. 2017).

2 Drivers of Infection Levels

2.1 Biotic Factors

Because parasites, by the nature of their life style, depend on their hosts for a living, the presence of parasites depends on the presence of their hosts. Hence, host diversity and abundance usually drive parasite richness and infection levels. This relationship can be observed on large regional, as well as on small local spatial scales. For example, the diversity and prevalence of trematodes infecting a common gastropod species (serving as first intermediate host) which inhabits mudflats depends on the presence and abundance of bird definitive hosts (which are the upstream hosts in the parasites' life cycles) on regional scales (Fredensborg et al. 2006). Likewise, the same relationship can also be observed on small local spatial scales such as in intertidal mud channels and pans within a single estuarine salt marsh ecosystem (Hechinger and Lafferty 2005). Similar relationships have also been observed in second intermediate hosts of trematodes. For example, the infection intensity of metacercarial stages of trematodes in cockles (*Cerastoderma edule),* which serve as second intermediate hosts for the parasites, is positively correlated with the abundance of snail first intermediate hosts in the field (Thieltges and Reise 2007), and with densities of infected snails in field experimental settings (Thieltges 2007).

It is not just the upstream hosts in the complex life cycles of parasites, but also the receiving hosts themselves which can affect parasite richness and infection intensities. Host body size is a host trait that is generally positively correlated with both parasite diversity and infection intensity, as larger hosts provide more space and niches for parasites (Poulin 2007; Kamiya et al. 2014). In addition, larger hosts are also often older hosts, and may thus have accumulated parasite infections over a longer exposure period, resulting in higher infection levels in larger and older host individuals. In some cases, the effect of age or exposure time may be a stronger factor than host body size. For example, experimental exposure of cockles (*Cerastoderma edule*) of different body size, showed that exposure time was a much stronger determinant of trematode infection levels than body size (Thieltges 2008). Host body size can also be important in cases where it co-varies with the general infection suitability of the host. For example, trematodes that use gastropods as first intermediate hosts mainly infect mature snails, since they depend on the gonadal tissue of the snails (Galaktionov and Dobrovolskij 2003). This results in infection thresholds in snails, with small juvenile snails usually being uninfected, and thus produces a typical skewed size-class distribution of infections in gastropod hosts (see e.g. review by Lauckner 1980). Besides the traits of individual hosts, it can also be the density of all conspecific hosts at a specific location that can affect parasite infection levels. Usually, parasite infection intensities and host density are positively correlated, as a result of basic epidemiological mechanisms (Poulin 2007; Kamiya et al. 2014). However, in mudflat ecosystems, host density can also have a negative effect on infection intensities of individual hosts, in cases where free-living infective stages are diluted by conspecific downstream hosts. This can, for example, be observed in second intermediate hosts of trematodes where high densities of hosts lead to lower infection intensities in individual hosts in field observational and experimental settings (Mouritsen et al. 2003; Thieltges and Reise 2007).

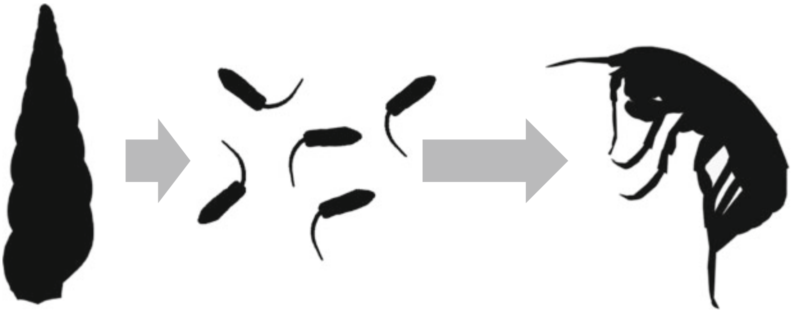
Besides the upstream hosts and the hosts themselves, organisms that do not serve as hosts can also affect parasite infection levels. At first sight, this sounds counterintuitive, but there are various ways by which non-hosts can affect parasite infection levels. A particularly well-studied mechanism in this respect is the interference of non-hosts with the transmission of infective stages of parasites (Thieltges et al. 2008a; Johnson and Thieltges 2010). For example, many organisms inhabiting mudflats are capable of interfering with the transmission of the free-living infective cercarial stages of trematodes, either by preying on cercariae (e.g. crabs, shrimps, amphipods, anemones, bivalves) or by constituting a physical obstacle such as algae

(Thieltges et al. 2008b; Hopper et al. 2008; Welsh et al. 2014). This transmission interference does not only reduce the number of infective stages in the environment, but also leads to reduced infection intensities in the downstream hosts in experimental settings (Thieltges et al. 2008b, 2009d). Such a transmission interference by non-hosts may be common in mudflat ecosystems, as recent food web studies using parasite-inclusive webs indicate that predation on free-living infective stages accounts for 10–20% of the total number of trophic links in the six food webs mentioned above (Table 9.1; Thieltges et al. 2013b).

2.2 Abiotic Factors

Infection levels in mudflat hosts are further mediated by a variety of abiotic factors. They affect both parasites and hosts, as well as their interactions, often resulting in complex net effects of environmental drivers on infection levels. Best studied in this respect is the effect of temperature on trematode infections in second intermediate hosts, such as bivalves and crustaceans, which are infected via free-living cercarial stages released from first intermediate gastropod hosts (Fig. 9.4). The production and release of cercarial stages is generally strongly positively correlated with temperature (Poulin 2006), a pattern also commonly observed in parasites occurring on mud flats (e.g. Mouritsen 2002a; Thieltges and Rick 2006; Studer et al. 2010; see also Chap. 15). At the same time, infectivity of cercariae (i.e. the successful infection of the down-stream second intermediate host) increases with temperature, while the longevity of cercarial stages decreases (e.g. Thieltges and Rick 2006; Studer et al. 2010). Temperature can also influence infection levels of host species, e.g. by stressing hosts and compromising immunity and thus increasing susceptibility, or by increasing parasite-induced host mortality (Lafferty et al. 2004; Harvell et al. 2009). Finally, temperature may also affect the development and survival of parasites in their second intermediate hosts, potentially compromising future infectivity with respect to the definitive hosts.

Potentially, temperature can have very different effects at different stages of parasite transmission. This is illustrated by a study from Studer et al. (2010) on temperature effects on the transmission of the trematode *Maritrema novaezealandensis* from its first intermediate host, the mud snail *Zeacumantus subcarinatus*, to its second intermediate host, the amphipod *Paracalliope novizealandiae* (Fig. 9.4). A series of laboratory experiments that decomposed the different transmission stages, showed that parasite transmission and host mortality were very slight at low temperatures (<20 °C), while at intermediate temperatures (20–25 °C), parasite transmission peaked, and amphipod hosts showed increased mortality. Finally, at the highest temperatures (≥30 °C), amphipod mortality was very high while parasite transmission was strongly reduced, due to both low numbers of infective stages being released, and low infectivity. Hence, temperature had very different effects on the different stages of the infection process, and the second intermediate amphipod host turned out to be the particularly vulnerable part. Similar complex temperature



T	Parasite Production	Parasite Survival	Parasite Infectivity	Host Susceptibility	Host Survival	Parasite Development
16°C	+	+++	+	+	+++	+
20°C	++	++	++	+	++	++
25°C	+++	++	+++	+	++	+++
30°C	++	+	++	+	-	-
34°C		+	+	+	-	-

Fig. 9.4 Conceptual illustration of the effect of temperature on different stages in the transmission process of a trematode species from its first intermediate gastropod host over the free-living cercarial stages to the second intermediate host and subsequent parasite development in the host. The table shows the direction and strength of temperature (T) effects on the different stages of the transmission process in laboratory experiments with the trematode *Maritrema novaezealandensis*, which uses the mud snail *Zeacumantus subcarinatus* as its first and the amphipod *Paracalliope novizealandiae* as its second intermediate hosts. Data based on Studer et al. (2010). (Published with kind permission of © David Thieltges 2018. All Rights Reserved).

effects probably exist in other parasite-host systems on mudflats (and elsewhere), but this largely remains to be studied.

Independent of temperature, the presence of water is of high importance for the dispersal of the free-living infective stages of trematodes. Hence, on mudflats transmission will generally take place only during high tide, or in the residual water of pools and puddles remaining at low tide. Such small water bodies probably serve as hotspots for infections, since they may warm up considerably during low tide in the summer, and trigger the temperature-induced mechanisms discussed above (Studer and Poulin 2012). The resulting positive effect on transmission is exemplified by experimental observations that cockles (*Cerastoderma edule*) exposed over several months in shallow tidal pools on a mudflat in the German Wadden Sea showed 43–73% higher infection intensities with trematode metacercarial stages, compared to cockles exposed outside the pools (Thieltges and Reise 2007).

In addition to the presence of water, the chemical properties of water can affect parasite transmission. Waterbody salinity is known to vary considerably on mudflats due to riverine freshwater input, surface runoff, or rainfall. Experimental studies in

New Zealand with the trematode *Philophthalmus* sp., which uses the snail *Zeacumantus subcarinatus* as first intermediate host, showed that cercarial production, encystment success (the parasite has a resting stage in the environment), and the survival of cysts were reduced under long-term (6–12 weeks) exposure to lower salinities of 25 or 30 psu, compared to the normal salinity of 35 psu (Lei and Poulin 2011). Such effects of salinity on trematode transmission may further be mediated by temperature. For example, Mouritsen (2002a) reported that salinity effects in the trematode *Maritrema subdolum*, which infects the mud snail *Hydrobia ulvae*, only occurred at certain temperatures in short-term (12 h) exposure experiments.

Another chemical property of water that can affect parasite transmission in mudflat ecosystems is the pH of the water, a property that has gained increasing interest in the contest of the expected future ocean acidification (MacLeod and Poulin 2012, see also below), but that can also vary considerably in the coastal waters of today (Melzner et al. 2013). Experimental studies with the trematode *Martitrema novaezealandense* have shown that cercarial survival decreases with decreasing pH of the seawater medium (MacLeod and Poulin 2015). However, the infection success in second intermediate amphipod hosts (*Paracalliope novizealandiae*) is actually highest under low pH conditions, which may result from negative effects of low pH on the hosts, leading to increased susceptibility (Harland et al. 2015). These examples show that we are far from understanding the full range of effects of biotic and abiotic drivers on parasite infections levels in hosts inhabiting mudflats. However, they illustrate that these effects may often differ between different stages of the transmission process, and also between parasites and hosts, and that the different biotic and abiotic drivers may often interact.

2.3 Large-Scale Drivers and Biogeography

Some of the biotic and abiotic factors discussed above also act on larger spatial scales and shape biographical patterns of parasites inhabiting mudflats. Like on smaller spatial scales, the presence and abundance of hosts is pivotal for the existence of parasites on large biogeographical scales, as illustrated by a study that investigated metacercarial trematode infections in the New Zealand cockle *Austrovenus stutchburyi* along the entire coastline of New Zealand (Studer et al. 2013b). The prevalence of parasites in the first intermediate host at the respective sampling sites proved to be the strongest determinant of infection intensities, besides the size of the cockle's foot (the parasites encyst mainly in the foot tissue).

Temperature is also expected to drive large-scale distributional patterns of parasites, resulting in latitudinal gradients in parasite species richness and infection intensity (Kamiya et al. 2014). Given the strong effects of temperature on trematode transmission, one would expect higher infection levels at higher average temperatures occurring at lower latitudes. However, this pattern may actually not be very strong in hosts inhabiting mudflat ecosystems. For example, Studer et al. (2013b) did not find a significant latitudinal gradient in trematode infection intensity in the New Zealand cockle *Austrovenus stutchburyi* along the coast of New Zealand, although there was a strong seawater temperature gradient from the North to the South. Large-scale patterns in parasite richness also do not universally follow the expectation. For example, when aggregating local host population data into larger geographical regions, Galaktionov (2017) found a decrease in trematode richness with increasing latitude in gastropod hosts (*Littorina* spp. and *Hydrobia* spp.). However, on the scale of local host populations, Thieltges et al. (2009a) did not find a latitudinal gradient in trematode infections of mud snails *Hydrobia ulvae* along the European Atlantic coast, nor did they find any robust latitudinal gradient in the infection prevalence of periwinkles *Littorina littorea.* Other studies have even reported latitudinal patterns opposite to the expectation. For example, Torchin et al. (2015) found that trematode species richness and prevalence actually increased with latitude in the Pacific horn snail *Cerithideopsis californica* and the Atlantic horn snail *Cerithideopsis pliculosala* along the coasts of North and Central America. These examples suggest that infection levels in individual hosts are more strongly affected by local factors, such as those emphasised above, than by large-scale temperature gradients.

This rule of thumb may also be true for latitudinal gradients involving across-species comparisons, i.e. studies based on data of parasite richness and infection intensity from different host species. In this case, latitude is not only a correlate for temperature but also serves as a general proxy for evolutionary rates which are considered to be higher at lower latitude due to increased solar influx (Willig et al. 2003; Turner et al. 1987; Cardillo 1999). Based on this, one would expect not only higher infection intensities, but also higher parasite species richness at lower latitudes. Indeed, in some cases, this pattern has been observed. For example, trematode species richness, mean prevalence, and mean intensity in marine amphipod hosts decrease with increasing latitude (Thieltges et al. 2009c). However, other across-species comparisons have failed to find such a latitudinal pattern. For example, Poulin and Mouritsen (2003) did not detect an effect of latitude across gastropod host species (but they found an effect at the sample level, i.e. when individual samples from locations were analysed). Likewise, Gutiérrez et al. (2017) did not detect any effect of latitude on parasite richness across shorebird species which often use mudflats as feeding grounds. These findings are in line with a recent meta-analysis on drivers of parasite richness, including terrestrial and freshwater environments (Kamiya et al. 2014), which emphasises that drivers of large-scale patterns in parasites of mudflats still remain to be identified.

3 Effects of Parasites on Mudflat Hosts and Ecosystems

3.1 Direct Effects on Individual Hosts and Host Populations

By definition, parasite-host interactions result in negative effects on infected hosts. These direct negative effects are inflicted on individual hosts, but they can also have knock-on effects on host populations. This is best illustrated in the case of parasite-

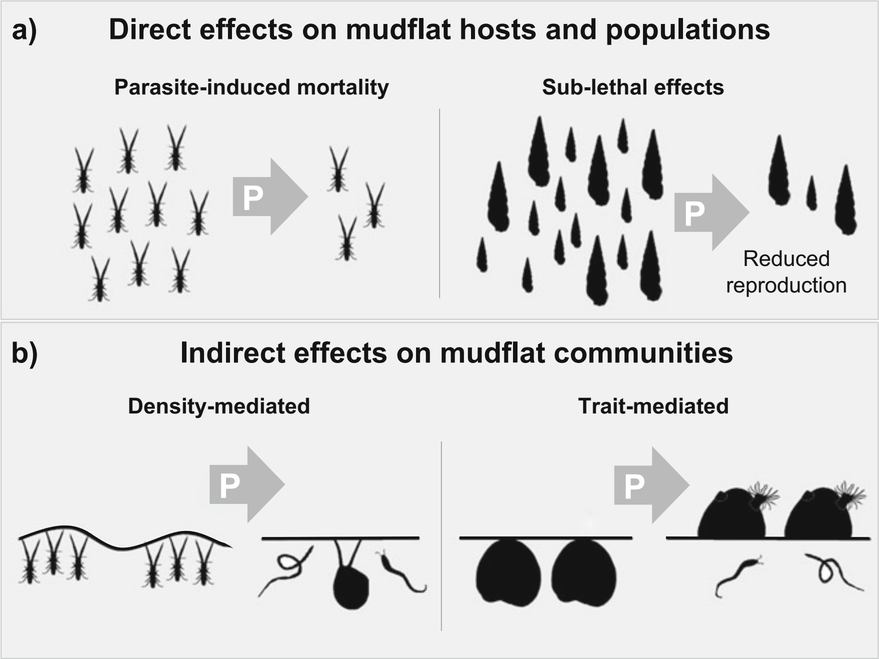


Fig. 9.5 Conceptual diagram illustrating direct and indirect effects of parasites on mudflat hosts, populations and communities. (**a**) Direct effects of parasites (P) include parasite-induced mortality and sub-lethal fitness effects such as reduced host reproduction on infected individual hosts which can have knock-on effects on host population sizes. (**b**) Indirect effects of parasites on mudflat communities occur when parasites alter the density (density-mediated indirect effects) or morphological, physiological or behavioural traits (trait-mediated indirect effects) of infected hosts such as the burrowing ability of cockles. In turn, this can affect other organisms living on mudflats, and ultimately affect community composition. For details, see text (Published with kind permission of © David Thieltges 2018. All Rights Reserved).

induced mortalities of infected hosts (Fig. 9.5a). Mortality induced by many parasites is intensity-dependent, i.e. host mortality increases with the infection intensity of a parasite (Fredensborg et al. 2004). If parasite infection levels are relatively high in a host population, this can result in the mortality of many infected hosts, and this in turn can affect the size and dynamics of the host population. For example, heavy trematode infections in populations of the amphipod *Corophium volutator* on mudflats have been reported to lead to significant decreases in population size, or even local extinction (Meissner and Bick 1997; Jensen and Mouritsen 1992). Such parasite-induced mortalities often coincide with other environmental stressors. In particular, temperature stress has been reported to be associated with mass mortalities of infected hosts. For example, in the amphipod *C. volutator*, mass mortalities of amphipods in the field have been associated with coinciding high temperatures, and elevated infection levels with trematode metacercariae (Jensen and Mouritsen 1992). In addition, laboratory experiments have confirmed the link between temperature stress and increased host mortality in infected amphipods (Mouritsen and Jensen 1997; Jensen et al. 1998; Meissner and Bick 1999; Larsen and Mouritsen 2014). Temperature stress does not only elevate host mortality in crustaceans, but has also been reported to increase mortality in infected gastropod (McDaniel 1969; Tallmark and Norrgren 1976) and bivalve hosts (Thieltges 2006a). However, in some cases, the resistance of trematode-infected gastropods to temperature stress and prolonged exposure is not different from that of non-infected ones, or is even higher (Riel 1975; Sousa and Gleason 1989; Berger et al. 2001; Bates et al. 2011). Besides temperature, other environmental stressors may also elevate parasite-induced mortality. For example, oxygen depletion reduces the survival of juvenile bivalves infected with metacercarial stages of trematodes (Wegeberg and Jensen 1999). Likewise, desiccation can lead to higher mortality in hydrobiid snails infected with trematodes (Jensen et al. 1996).

Instead of inducing direct host mortality, parasites can also have more subtle sub-lethal effects on hosts living on mudflats. Such sub-lethal effects on individual hosts may also have knock-on effects on host populations, just like the ones observed in the case of parasite-induced mortality. A good illustration for this is provided by the ubiquitous trematodes that can be found in many gastropods living on mudflats (Fig. 9.5a). These trematodes infect the gonadal tissue of their hosts and usually lead to partial or total castration, which strongly reduces the life-time fitness of infected individuals (Lauckner 1980; Huxham et al. 1993; Mouritsen and Jensen 1994). In host species that have pelagic larvae for dispersal, even the castration of the majority of individual hosts in a local population may not affect the size of the population much, since larval stages originating from elsewhere can supply the local recruitment. However, in host species that have direct development, parasitic castration of a large proportion of the host population may significantly lower local population size. Indeed, such population-level effects of parasite infections have been observed in several gastropod species with direct development (Lafferty 1993; Sokolova 1995; Fredensborg et al. 2005). Similar population-level effects have also been suggested in the case of the direct-developing amphipod *C. volutator*, in which metacercarial stages of trematodes reduce the brood size of infected females, which in turn likely reduces local abundance of the amphipods (Bick 1994; McCurdy et al. 1999).

Besides host castration and reduced reproduction, other sub-lethal effects of parasites that have been observed in typical mudflat hosts include, among others, changes in growth rates of molluscs, both in a positive (Mouritsen and Jensen 1994; Probst and Kube 1999) and negative direction (Mouritsen et al. 1999; Thieltges 2006b; O'Connell-Milne et al. 2016), reduced condition of bivalves (Wegeberg and Jensen 2003; Stier et al. 2015; O'Connell-Milne et al. 2016), reduced filtration rates in bivalves (Stier et al. 2015), morphological changes such as the shape and ornamentation of shells in gastropods (Hay et al. 2005; Thieltges et al. 2009e), behavioural changes such as impaired burrowing ability in bivalves (Lauckner 1983; Thomas and Poulin 1998) and potential changes in animal personality such as reduced boldness in infected snails (Seaman and Briffa 2015). Many of these sub-lethal direct effects may also trigger knock-on effects on host population sizes and dynamics, and some of them may also trigger further indirect effects on other organisms and eventually affect entire mudflat communities, as discussed below.

3.2 Indirect Effects on Host Communities

Many of the direct effects that parasites inflict on their hosts can also lead to indirect effects on other species living next to the infected hosts, and ultimately affect entire mudflat communities. These indirect effects occur when parasites either alter the density of infected hosts (density-mediated indirect effects), or change morphological, physiological or behavioural traits of infected individuals (trait-mediated indirect effects; see Hatcher et al. (2006) and Hatcher and Dunn (2011) for a detailed account of indirect effects of parasites in general).

Density-mediated indirect effects of parasites are closely linked to the parasite-mediated mortalities discussed above. These mortalities can trigger indirect effects, particularly in host species that have strong impacts on local habitats and communities themselves. For example, parasites that affect ecosystem engineers (organisms that create or modify habitat for other organisms—Jones et al. 1997; see Chap. 10) may trigger particularly strong indirect effects on local communities (Thomas et al. 1999). A good example for this is the parasite-induced mortality of the amphipod *Corophium volutator* discussed above (Fig. 9.5b). With their tube-building activity, these amphipods can stabilise the sediment and lead to a typical mudflat topography of subtle hummocks and shallow puddles (Mouritsen and Poulin 2002). A parasite-induced mass mortality event of the amphipods on a mudflat in the Danish Wadden Sea lead to increased erosion, which altered the sediment grain size composition, and ultimately turned the mudflat topography into a flat surface (Mouritsen et al. 1998; Mouritsen and Poulin 2002). In turn, this change in habitat condition affected other organisms on the mudflat, leading to altered composition and abundance of macrofauna (Jensen and Mouritsen 1992; Larsen et al. 2011, and see Chap. 10). Similar indirect effects are likely to result from other parasite-induced host mortalities, but to date we lack information on the extent of such density-mediated indirect effects of parasites in mudflat ecosystems.

Examples for the other type of indirect effects induced by parasites, the so-called trait-mediated indirect effects, are also known from mudflat ecosystems. One of the prime examples comes from mudflats in New Zealand where the New Zealand cockle *Austrovenus stutchburyi* is infected by the trematode *Curtuteria australis* and other closely-related trematode species (Fig. 9.5b). These parasites infect the foot of the cockles, and compromise the burrowing ability of infected individuals, which normally live 1–2 cm beneath the sediment surface, so that infected cockles end up laying on the sediment surface (Thomas and Poulin 1998; Mouritsen 2002b). This behavioural alteration of the cockle is considered to be adaptive for the parasites, as it increases predation by birds, which serve as definitive host for the trematodes (Thomas and Poulin 1998). Besides increasing transmission for the parasites, the parasite-induced surfacing of cockles also indirectly affects other organisms. The cockles laying on the sediment surface change the local near-bed hydrodynamics and sedimentation rates by being obstacles, and they no longer act as bioturbators of the sediment. Together, these effects lead to an increase in general macrobenthic species richness and a higher abundance of many macrobenthic taxa and functional groups (Mouritsen and Poulin 2005). The parasite-induced surfacing of cockles has further been linked with changes in primary and secondary production on mudflats (Mouritsen and Poulin 2006). Similar trait-mediated effects have been observed in the mudsnail *Hydrobia ulvae* which serves as first intermediate host to a range of trematode species. Field experiments indicated that infected snails indirectly alter the abundance and composition of primary and secondary producers via direct effects of parasite infections on the snails' grazing behaviour (Mouritsen and Haun 2008). Other morphological, physiological or behavioural traits of hosts that are induced by parasites in infected hosts are likely common in mudflat ecosystems but, as in the case of density-mediated indirect effects, the extent and relevance of these indirect effects for mudflat ecosystems have yet to be determined.

3.3 Effects on Food Chains, Food Webs and Ecosystem Energetics

The various impacts of parasites on their hosts can also affect food chains, food webs and ecosystem energetics in mudflat ecosystems (Lafferty et al. 2008). One way of doing so is that parasites can mediate the strength of trophic interactions and thus alter the flow of energy in food chains. For example, trematode infections in periwinkles (*Littorina littorea*) can reduce the grazing activity of infected snails, so that they consume only about 2/3 of the macroalgal biomass compared to uninfected snails, thus altering the interaction strength between primary and secondary consumers (Clausen et al. 2008). Likewise, parasites can also mediate the interaction strength between secondary and tertiary consumers. Periwinkles (*L. littorea*) are often infected with the shell-boring polychaete *Polydora ciliata*. Infected snails have weaker shells caused by the burrowing activity of the worms, and this affects predation of snails by shore crabs (*Carcinus maenas*), a typical predator on mudflats along the North East Atlantic coast. Experiments have revealed that crab predation rates on infected snails are almost five times higher than on uninfected individuals (Buschbaum et al. 2007). Similar effects of increased predation by crabs on *P. ciliata*-infected hosts have also been observed in blue mussels *Mytilus edulis* (Ambariyanto and Seed 1991; Kent 1981). In some cases, such increased predation on infected individuals is associated with increased transmission of parasites to down-stream hosts if the predator serves as a host for the parasite. If the increased predation on infected hosts results from behavioural or other trait changes induced by the parasite, this is often considered to be an adaptive host manipulation by the parasite, as it increases its transmission (Poulin 2010). As parasite manipulation of host behaviour may be common in tropically transmitted parasites such as the ubiquitous trematodes occurring on mudflats, parasites may often alter the interaction strength between predators and infected prey in typical mudflat food chains. However, such parasite—mediated alterations of trophic interactions and energy flows are not well-studied in mudflat ecosystems to date.

Besides mediating trophic interaction strength between predators and their resources in food chains, parasites may also act as a resource themselves (Johnson et al. 2010). One of the ways in which this can occur, is that the many free-living infective stages produced by parasites may be utilised by non-hosts as a resource. In particular, the production of cercarial stages of trematodes is known to be substantial in mudflat ecosystems (Kuris et al. 2008; Thieltges et al. 2008c), and many organisms that do not serve as host for these parasites are known to prey on these stages (Thieltges et al. 2008a, b; Welsh et al. 2014). Studies on parasite-inclusive food webs indicate that this predation on infective stages may be common, as this link type comprises 10–20% of the total number of trophic links in food webs of mudflat ecosystems (Thieltges et al. 2013b). However, whether the consumption of infective stages significantly contributes to the diet of consumers in mudflat ecosystems is largely unknown. Another mechanism through which parasites can become a resource themselves, is when parasites are consumed by a predator together with their host but when the predator is not a suitable host for the co-ingested parasites. This so-called concomitant predation of parasites is not well understood but studies on parasite-inclusive food webs indicate that it may actually be very common, as about 60–70% of the trophic links in food webs of mudflat ecosystems are concomitant predation links (Thieltges et al. 2013b). Besides potentially contributing additional nutritional value to predators in some cases, this type of predation on parasites may also have important consequences for parasite population dynamics (Lafferty et al. 2008). However, the magnitude and relevance of parasites as resources in mudflat food webs remain to be investigated.

Besides affecting predation strength and potentially serving as a resource to predators, parasites can also affect the general structure and topology of entire food webs (Lafferty et al. 2008; Dunne et al. 2013). When parasites are integrated into topological food webs, i.e. food webs that denote the presence or absence of trophic interactions but do not include information on interaction strength or energy flow, they generally increase food web size and the density of trophic interaction links (connectivity; Lafferty et al. 2008; Dunne et al. 2013). Many of these topological changes are probably not unique to parasites, but simply result from the addition of species to the webs (Dunne et al. 2013). However, the predation on parasites by predators discussed above seems to result in unique contributions to food web motifs, i.e. patterns of small interactive units of food webs (Dunne et al. 2013; Cirtwill and Stouffer 2015). However, it is largely unknown whether these changes in food web structure in topological webs, that denote only absence or presence of trophic interactions, also affect energy flows in food webs. The standing stock of some parasite groups can be high in mudflat food webs, e.g. the biomass of trematodes in gastropods equals that of birds in Californian estuaries (Kuris et al.

2008). However, the contribution of parasites to the flow of energy through entire food webs remains to be unravelled.

4 Parasites and Global Change

4.1 Species Invasions

Mudflats face a multitude of challenges in the course of ongoing global changes which also have repercussions for parasites and their hosts in mudflat ecosystems. Among these challenges are biological invasions. In marine ecosystems such as mudflats, species are mainly introduced via ballast water from large ships and by aquaculture practices such as oyster farming (Grosholz 2002; Bax et al. 2003, see also Chap. 14). Many introduced species do not spread much and remain at relatively low population levels, whereas others become invasive, disperse widely and cause considerable impacts on native ecosystems (Grosholz 2002, see also Chap. 11). Parasites can have various roles in the invasion process, and on the impacts of invasive species in mudflats and other marine ecosystems (see Goedknegt et al. 2016 for a recent review). First of all, invasive species are often released from parasite infection pressure in their recipient ecosystems and this may facilitate the establishment and spread of invasive species. Such a release from parasites results from the fact that introduced species often lose all or most of their own native parasites in the course of the introduction, due to various invasion barriers. For example, parasites may not survive the transport stage or do not find suitable intermediate and definitive hosts in the new environment (Torchin et al. 2003; Blakeslee et al. 2013). The resulting low parasite burden may give the invader a competitive benefit over native competitors, and thus facilitate its establishment and spread (Torchin et al. 2003; Blakeslee et al. 2013). However, once arrived in a new environment, invasive species may acquire local native parasite species. This may reduce their initial competitive advantage, but it may also affect native hosts of the parasites if the parasite species' population size is amplified by the invasive species, resulting in greater infection levels in native species (parasite spillback—Kelly et al. 2009). Invasive species may also co-introduce parasites which can affect native host species as well (parasite spillover—Prenter et al. 2004; Kelly et al. 2009). For example, Pacific oysters (*Crassostrea gigas*) that have been introduced to Europe for aquaculture purposes have co-introduced an intestinal parasitic copepod (*Mytilicola orientalis*) which has spilled over to native mussels, cockles and Baltic tellins (Goedknegt et al. 2017) and which has negative effects on host condition (Goedknegt et al. in review).

While such parasite spillover effects have negative effects for native host species, invasive species such as the Pacific oyster can also have positive effects on native hosts, by reducing their infection levels with native parasites. They can do so by the transmission interference mechanisms discussed above. For example, Pacific oysters are very efficient filter feeders, and can remove cercarial stages of trematodes from the water above mudflats (without becoming infected themselves), and thus reduce infection levels in native hosts such as mussels (Thieltges et al. 2009d). Other invasive species can also interfere with parasite transmission on mudflats (Welsh et al. 2014), but our understanding of the full range and magnitude of the effects of invasive species on parasites and their hosts in mudflat ecosystems is still very limited. With the globally increasing number of species introductions to coastal ecosystems, this will be an important future research field.

4.2 CO_2 Double Trouble: Temperature Increase and Ocean Acidification

Other global challenges affecting mudflat ecosystems include the effects of anthropogenic emissions of carbon dioxide (CO_2) which have increased atmospheric CO_2 levels by nearly 40% since the beginning of the industrial revolution (Salomon et al. 2007). The resulting effect on marine ecosystems is twofold: an increase in seawater temperature, and an increase in pH, due to the dissolution of CO_2 in seawater, leading to a phenomenon called ocean acidification (Doney et al. 2009; Orr et al. 2005; Hoegh-Guldberg and Bruno 2010). Based on the strong temperature-dependency of many parasite transmission processes such as in trematodes, a potential increase in infection levels under increasing water temperatures has been suggested (Poulin 2006; Poulin and Mouritsen 2006). For some host species that are sensitive to temperature stress and parasite infections, future temperature increases may thus have strong impacts on host population dynamics. For example, population dynamic modelling of trematode infections in amphipod hosts suggest strong population declines, and even local extinction at future elevated temperatures in mudflat ecosystems in Europe and New Zealand (Mouritsen et al. 2005; Studer et al. 2013a; Fig. 9.6).

However, in other host species increased temperatures may offset negative effects of infections. For example, periwinkles (*Littorina littorea*) show reduced feeding rates when infected with trematodes at normal summer water temperatures (18 °C), but at elevated temperatures that are predicted to occur under climate change (21 °C), feeding rates did not differ between infected and uninfected periwinkles (Larsen and Mouritsen 2009). In other cases, increased temperatures may not lead to elevated infections levels in hosts in the first place as, for example, observed in cockles infected with trematode metacercariae where cercarial emergence is limited during hot days (de Montaudouin et al. 2016). Many trematode species may also exhibit a relatively high acclimation capacity, so that cercarial development, emergence and survival, as well as the survival of miracidia, will not be much influenced by temperature across a rather broad range of optimal temperatures (Morley 2011, 2012; Morley and Lewis 2013, 2015). Hence, the actual effects of climate change on parasites and their hosts will not be universal, but will most likely be parasite- and host-specific.

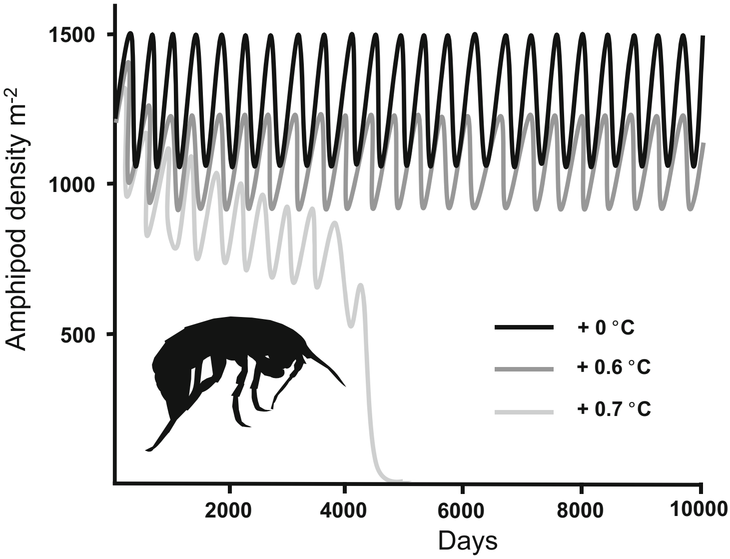


Fig. 9.6 Model simulation output of annual population fluctuations (density m^{-2}) of the amphipod *Paracalliope novizealandiae* infected with the trematode *Maritrema novaezealandensis* under various climate change scenarios: current conditions (+0 °C; black line), an increase in the mean temperature of 0.6 °C (dark grey line), and an increase of 0.7 °C (light grey line). Shown are the simplified population trajectories predicted for the first 10,000 days (≈27 years) of 80-year model runs. Data based on Studer et al. (2013a).

Parasites and hosts will not only be affected by temperature, but also by other environmental stressors, which may result in complex interactions. For example, a multifactorial experiment on the survival of cercariae of the intertidal trematode *Maritrema novaezealandensis* identified significant interactions among temperature, salinity and ultraviolet radiation (Studer and Poulin 2013), suggesting that the effects of future temperature increases on parasite-host interactions on mudflats will most likely be driven by a complex interplay of factors, rather than by simple temperature effects. Similar caveats with respect to predictions of future parasite infection levels on mudflats also apply to the effect of ocean acidification on marine parasites and their hosts. Here, the effects of increased seawater pH on parasites and their hosts also seem to be species-specific, and also interacting with other factors, such as temperature and salinity (Koprivnikar et al. 2010; MacLeod and Poulin 2015, 2016). Hence, more research will be necessary to characterize the complex interplay of major drivers of infection levels, and the resulting impacts on hosts in specific parasite-host interactions, to allow realistic predictions of changes in parasite infection levels under future temperature increases and ocean acidification.

Besides invasive species, temperature increases and ocean acidification, coastal mudflat ecosystems face other human-induced challenges such as habitat degradation, eutrophication and overfishing (see Chaps. 13 and 14). We do not know much about the impact of these various stressors, and more research will be needed to identify and quantify their effects on parasite-host interactions in mudflat ecosystems.

5 Conclusion and Outlook

In this chapter, we have illustrated and explored the many ways in which parasite-host interactions can affect host populations, communities and food webs in mudflat ecosystems, equalling in importance similar effects resulting from other species interactions such as predation and competition. However, although our knowledge of the ecology of parasites in mudflat ecosystems has grown considerably during the last two decades, there are still many aspects that await further investigation, as we have pointed out throughout the chapter. Possibly the greatest challenge preventing the full inclusion of parasites in ecological studies of mudflat ecosystems is, as we also stressed with respect to meiofauna in Chap. 5, the reluctance of marine ecologists to investigate small organisms whose identification and quantification have traditionally required expert taxonomical expertise. However, modern tools can facilitate rigorous studies of parasite diversity and abundance for non-parasitologists. For example, environmental DNA, or eDNA, approaches can allow the detection of parasite species and the estimation of their relative abundance with a non-invasive method based on samples of water or sediment (Bass et al. 2015). Similarly, in the future, the establishment of DNA barcode databases could be used for the quick and easy identification of multiple parasite taxa by non-experts, without the need for detailed morphological examinations (Leung et al. 2009). The rapidly-decreasing costs of gene sequencing should make such new technologies very attractive for future parasite-inclusive studies of mudflat ecosystems.

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References

Ambariyanto A, Seed R (1991) The infestation of *Mytilus edulis* Linnaeus by *Polydora ciliata* (Johnston) in the Conwy Estuary, North Wales. J Mollusc Stud 57:413–424

Bass D, Stentiford GD, Littlewood DTJ, Hartikainen H (2015) Diverse applications of environmental DNA methods in parasitology. Trends Parasitol 31:499–513

Bates AE, Leiterer F, Wiedeback ML, Poulin R (2011) Parasitized snails take the heat: a case of host manipulation? Oecologia 167:613–621

Bax N, Williamson A, Aquero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: a threat to global biodiversity. Mar Policy 27:313–323

Berger VJ, Galaktionov KV, Prokofiev VV (2001) Influence of parasites on host adaptations to environmental factors: host-parasite system molluscs-trematode parthenitae. Parazitologiya 35: 192–200

Bick A (1994) *Corophium volutator* (Corophiidae: Amphipoda) as an intermediate host of larval Digenea – an ecological analysis in a coastal region of the southern Baltic. Ophelia 40:27–36

Blakeslee AMH, Fowler AE, Keogh CL (2013) Marine invasion and parasite escape: updates and new perspectives. Adv Mar Biol 66:87–169

Buschbaum C, Buschbaum G, Schrey I, Thieltges DW (2007) Shell-boring polychaetes affect gastropod shell strength and crab predation. Mar Ecol Prog Ser 329:123–130

Cardillo M (1999) Latitude and rates of diversification in birds and butterflies. Proc R Soc B Biol Sci 266:1221–1225

Cirtwill AR, Stouffer DB (2015) Concomitant predation on parasites is highly variable but constrains the ways in which parasites contribute to food-web structure. J Anim Ecol 84:734–744

Clausen KT, Larsen MH, Iversen NK, Mouritsen KN (2008) The influence of trematodes on the macroalgae consumption by the common periwinkle *Littorina littorea*. J Mar Biol Assoc U K 88:1481–1485

Combes C (2001) Parasitism: the ecology and evolution of intimate interactions. The University of Chicago Press, Chicago

de Montaudouin X, Blanchet H, Bazairi H, Nazik A, Desclaux-Marchand C, Bachelet G (2016) Cockle infection by *Himasthla quissetensis* – II. The theoretical effect of climate change. J Sea Res 113:108–114

Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean acidification: the other CO_2 problem. Annu Rev Mar Sci 1:169–192

Dunne JA, Lafferty KD, Dobson AP, Hechinger RF, Kuris AM, Martinez ND, McLaughlin JP, Mouritsen KN, Poulin R, Reise K, Stouffer DB, Thieltges DW, Williams RJ, Zander C-D (2013) Parasites affect food web structure primarily through increased diversity and complexity. PLoS Biol 11:e1001579

Fredensborg BL, Mouritsen KN, Poulin R (2004) Intensity-dependent mortality of *Paracalliope novizealandiae* (Amphipoda: Crustacea) infected by a trematode: experimental infections and field observations. J Exp Mar Biol Ecol 311:253–265

Fredensborg BL, Mouritsen KN, Poulin R (2005) Impact of trematodes on host recruitment, survival and population density in the intertidal gastropod *Zeacumantus subcarinatus*. Mar Ecol Prog Ser 290:109–117

Fredensborg BL, Mouritsen KN, Poulin R (2006) Relating bird host distribution and spatial heterogeneity in trematode infections in an intertidal snail: from small to large scale. Mar Biol 149: 275–283

Galaktionov KV (2017) Patterns and processes influencing helminth parasites of Arctic coastal communities during climate change. J Helminthol 91:38–408

Galaktionov KV, Dobrovolskij AA (2003) The biology and evolution of trematodes: an essay on the biology, morphology, life cycles, transmission, and evolution of digenetic trematodes. Kluwer Academic, Dordrecht

Goedknegt MA, Feis ME, Wegner KM, Luttikhuizen PC, Buschbaum C, Camphuysen KCJ, van der Meer J, Thieltges DW (2016) Parasites and marine invasions: ecological and evolutionary perspectives. J Sea Res 113:11–27

Goedknegt MA, Schuster A-K, Buschbaum GR, Jung AS, Luttikhuizen PC, van der Meer J, Troost K, Wegner KM, Thieltges DW (2017) Spillover but no spillback of two invasive parasitic copepods from invasive Pacific oysters (*Crassostrea gigas*) to native bivalve hosts. Biol Invasions 19:365–379

Groenewold S, Berghahn R, Zander CD (1996) Parasite communities of four fish species in the Wadden Sea and the role of fish discarded by the shrimp fisheries in parasite transmission. Helgländer Meeresun 50:69–85

Grosholz E (2002) Ecological and evolutionary consequences of coastal invasions. Trends Ecol Evol 17:22–27

Gutiérrez JS, Rakhimberdiev E, Piersma T, Thieltges DW (2017) Migration and parasitism: habitat use, not migration distance, influences helminth species richness in Charadriiform birds. J Biogeogr 44:1137–1147

Harland H, MacLeod CD, Poulin R (2015) Non-linear effects of ocean acidification on the transmission of a marine intertidal parasite. Mar Ecol Prog Ser 536:55–64

Harvell D, Altizer S, Cattadori IM, Harrington L, Weil E (2009) Climate change and wildlife diseases: when does the host matter the most? Ecology 90:912–920

Hatcher MJ, Dunn AM (2011) Parasites in ecological communities: from interactions to ecosystems. Cambridge University Press, Cambridge

Hatcher MJ, Dick JT, Dunn AM (2006) How parasites affect interactions between competitors and predators. Ecol Lett 9:1253–1271

Hay KB, Fredensborg BL, Poulin R (2005) Trematode-induced alterations in shell shape of the mud snail *Zeacumantus subcarinatus* (Prosobranchia: Batillariidae). J Mar Biol Assoc U K 85: 989–992

Hechinger RF, Lafferty KD (2005) Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. Proc R Soc B 272:1059–1066

Hechinger RF, Lafferty KD, McLaughlin JP, Fredensborg BL, Huspeni TC, Lorda J, Sandhu PK, Shaw JC, Torchin ME, Whitney KL, Kuris AM (2011) Food webs including parasites, biomass, body sizes, and life stages for three California/Baja California estuaries. Ecology 92:791

Høeg JT (1995) The biology and life cycle of the Rhizocephala (Cirripedia). J Mar Biol Assoc U K 75:517–550

Høeg JT, Lützen J (1995) Life cycle and reproduction in the Cirripedia Rhizocephala. Oceanogr Mar Biol Annu Rev 33:427–485

Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. Science 328:1523–1528

Hopper JV, Poulin R, Thieltges DW (2008) Buffering role of the intertidal anemone *Anthopleura aureoradiata* in cercarial transmission from snails to crabs. J Exp Mar Biol Ecol 367:153–156

Horn MH, Martin KLM, Chotkowski MA (1999) Intertidal fishes: life in two worlds. Academic Press, London

Huxham M, Raffaelli D, Pike A (1993) The influence of *Cryptocotyle lingua* (Digenea: Plathyhelminthes) infections on the survival and fecundity of *Littorina littorea* (Gastropoda: Prosobranchia); an ecological approach. J Exp Mar Biol Ecol 168:223–238

Jensen KT (1993) Density-dependent growth in cockles (*Cerastoderma edule*): evidence from interannual comparisons. J Mar Biol Assoc U K 73:333–342

Jensen KT, Mouritsen KN (1992) Mass mortality in two common soft-bottom invertebrates, *Hydrobia ulvae* and *Corophium volutator* – the possible role of trematodes. Helgoländer Meeresun 46:329–339

Jensen KT, Latama G, Mouritsen KN (1996) The effect of larval trematodes on the survival rates of two species of mud snails (Hydrobiidae) experimentally exposed to desiccation, freezing and anoxia. Helgoländer Meeresun 50:327–335

Jensen T, Jensen KT, Mouritsen KN (1998) The influence of the trematode *Microphallus claviformis* on two congeneric intermediate host species (*Corophium*): infection characteristics and host survival. J Exp Mar Biol Ecol 227:35–48

Johnson PTJ, Thieltges DW (2010) Diversity, decoys and the dilution effect: how ecological communities affect disease risk. J Exp Biol 213:961–970

Johnson PTJ, Dobson A, Lafferty KD, Marcogliese DJ, Memmott J, Orlofske SA, Poulin R, Thieltges DW (2010) When parasites become prey: ecological and epidemiological significance of eating parasites. Trends Ecol Evol 25:362–371

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957

Kaiser MJ, Attrill MJ, Jennings S, Thomas DN, Barnes DKA (2011) Marine ecology: processes, systems, and impacts. Oxford University Press, Oxford

Kamiya T, O'Dwyer K, Nakagawa S, Poulin R (2014) What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. Biol Rev 89:123–134

Kelly DW, Paterson RA, Townsend CR, Poulin R, Tompkins DM (2009) Parasite spillback: a neglected concept in invasion ecology? Ecology 90:2047–2205

Kent RML (1981) The effect of *Polydora ciliata* on the shell strength of *Mytilus edulis*. J Cons Int Explor Mer 39:252–255

Koch W, Boer P, Witte JIJ, van der Veer HW, Thieltges DW (2014) Inventory and comparison of abundance of parasitic copepods on fish hosts in the western Wadden Sea (North Sea) between 1968 and 2010. J Mar Biol Assoc U K 94:547–555

Koehler AV, Poulin R (2010) Host partitioning by parasites in an intertidal crustacean community. J Parasitol 96:862–868

Koprivnikar J, Lim D, Fu C, Brack SHM (2010) Effects of temperature, salinity, and pH on the survival and activity of marine cercariae. Parasitol Res 106:1167–1177

Kuris AM, Hechinger RF, Shaw JC, Whitney KL, Aguirre-Macedo L, Boch CA, Dobson AP, Dunham EJ, Fredensborg BL, Huspeni TC, Lorda J, Mababa L, Mancini FT, Mora AB, Pickering M, Talhouk NL, Torchin ME, Lafferty KD (2008) Ecosystem energetic implications of parasite and free-living biomass in three estuaries. Nature 454:515–518

Lafferty KD (1993) Effect of parasitic castration on growth, reproduction and population dynamics of the marine snail *Cerithidea californica*. Mar Ecol Prog Ser 96:229–237

Lafferty KD, Kuris AM (2002) Trophic strategies, animal diversity and body size. Trends Ecol Evol 17:507–513

Lafferty KD, Porter JW, Ford SE (2004) Are diseases increasing in the ocean? Annu Rev Ecol Evol Syst 35:31–54

Lafferty KD, Allesina S, Arim M, Briggs CJ, De Leo G, Dobson AP, Dunne JA, Johnson PTJ, Kuris AM, Marcogliese DJ, Martinez ND, Memmott J, Marquet PA, McLaughlin JP, Mordecai EA, Pascual M, Poulin R, Thieltges DW (2008) Parasites in food webs: the ultimate missing links. Ecol Lett 11:533–546

Larsen MH, Mouritsen KN (2009) Increasing temperature counteracts the impact of parasitism on periwinkle consumption. Mar Ecol Prog Ser 383:141–149

Larsen MH, Mouritsen KN (2014) Temperature–parasitism synergy alters intertidal soft-bottom community structure. J Exp Mar Biol Ecol 460:109–119

Larsen MH, Jensen KT, Mouritsen KN (2011) Climate influences parasite-mediated competitive release. Parasitology 138:1436–1441

Latham ADM, Poulin R (2002) New records of gastrointestinal helminths from the southern black-backed gull (Larus *dominicanus*) in New Zealand. N Z J Zool 29:253–257

Lauckner G (1980) Diseases of mollusca: gastropoda. In: Kinne O (ed) Diseases of marine animals, General aspects, protozoa to gastropoda, vol I. Wiley, New York, pp 311–424

Lauckner G (1983) Diseases of mollusca: Bivalvia. In: Kinne O (ed) Diseases of marine animals, Introduction, Bivalvia to Scaphopoda, vol 2. Biologische Anstalt Helgoland, Hamburg, pp 477–961

Lei F, Poulin R (2011) Effects of salinity on multiplication and transmission of an intertidal trematode parasite. Mar Biol 158:995–1003

Leung TLF, Donald KM, Keeney DB, Koehler AV, Peoples RC, Poulin R (2009) Trematode parasites of Otago Harbour (New Zealand) soft-sediment intertidal ecosystems: life cycles, ecological roles and DNA barcodes. N Z J Mar Freshw Res 43:857–865

MacLeod CD, Poulin R (2012) Host–parasite interactions: a litmus test for ocean acidification? Trends Parasitol 28:365–369

MacLeod CD, Poulin R (2015) Differential tolerances to ocean acidification by parasites that share the same host. Int J Parasitol 45:485–493

MacLeod CD, Poulin R (2016) Parasitic infection alters the physiological response of a marine gastropod to ocean acidification. Parasitology 143:1397–1408

McCurdy DG, Forbes MR, Boates JS (1999) Testing alternative hypotheses for variation in amphipod behaviour and life history in relation to parasitism. Int J Parasitol 29:1001–1009

McDaniel JS (1969) *Littorina littorea*: lowered heat tolerance due to *Cryptocotyle lingua*. Exp Parasitol 25:13–15

Meissner K, Bick A (1997) Population dynamics and ecoparasitological surveys of *Corophium volutator* in coastal waters in the Bay of Mecklenburg (southern Baltic Sea). Dis Aquat Org 29: 169–179

Meissner K, Bick A (1999) Mortality of *Corophium volutator* (Amphipoda) caused by infestation with *Maritrema subdolum* (Digenea, Microphallidae) ± laboratory studies. Dis Aquat Org 35: 47–52

Melzner F, Thomsen J, Koeve W, Oschlies A, Gutowska MA, Bange HW, Hansen HP, Körtzinger A (2013) Future ocean acidification will be amplified by hypoxia in coastal habitats. Mar Biol 160:1875–1888

Morley NJ (2011) Thermodynamics of cercarial survival and metabolism in a changing climate. Parasitology 138:1442–1452

Morley NJ (2012) Thermodynamics of miracidial survival and metabolism. Parasitology 139: 1640–1651

Morley NJ, Lewis JW (2013) Thermodynamics of cercarial development and emergence in trematodes. Parasitology 140:1211–1224

Morley NJ, Lewis JW (2015) Thermodynamics of trematode infectivity. Parasitology 142:585–597

Mouritsen KN (2002a) The *Hydrobia ulvae-Maritrema subdolum* association: influence of temperature, salinity, light, water-pressure and secondary host exudates on cercarial emergence and longevity. J Helminthol 76:341–347

Mouritsen KN (2002b) The parasite-induced surfacing behaviour in the cockle *Austrovenus stutchburyi*: a test of an alternative hypothesis and identification of potential mechanisms. Parasitology 124:521–528

Mouritsen KN, Haun SCB (2008) Community regulation by herbivore parasitism and density: trait-mediated indirect interactions in the intertidal. J Exp Mar Biol Ecol 367:236–246

Mouritsen KN, Jensen KT (1994) The enigma of gigantism: effect of larval trematodes on growth, fecundity, egestion and locomotion in *Hydrobia ulvae* (Pennant) (Gastropoda: Prosobranchia). J Exp Mar Biol Ecol 181:53–66

Mouritsen KN, Jensen KT (1997) Parasite transmission between soft-bottom invertebrates: temperature mediated infection rates and mortality in *Corophium volutator*. Mar Ecol Prog Ser 151: 123–134

Mouritsen KN, Poulin R (2002) Parasitism, community structure and biodiversity in intertidal ecosystems. Parasitology 124:S101–S117

Mouritsen KN, Poulin R (2005) Parasite boosts biodiversity and changes animal community structure by trait-mediated indirect effects. Oikos 108:344–350

Mouritsen KN, Poulin R (2006) A parasite indirectly impacts both abundance of primary producers and biomass of secondary producers in an intertidal benthic community. J Mar Biol Assoc U K 86:221–226

Mouritsen KN, Mouritsen LT, Jensen KT (1998) Changes of topography and sediment characteristics on an intertidal mud-fat following mass-mortality of the amphipod *Corophium volutator*. J Mar Biol Assoc U K 78:1167–1180

Mouritsen KN, Gorbushin A, Jensen KT (1999) Influence of trematode infections on in situ growth rates of *Littorina littorea*. J Mar Biol Assoc U K 79:425–430

Mouritsen KN, McKechnie S, Meenken E, Toynbee JL, Poulin R (2003) Spatial heterogeneity in parasite loads in the New Zealand cockle: the importance of host condition and density. J Mar Biol Assoc U K 83:307–310

Mouritsen KN, Tompkins DM, Poulin R (2005) Climate warming may cause a parasite-induced collapse in coastal amphipod populations. Oecologia 146:476–483

Mouritsen KN, Poulin R, McLaughlin JP, Thieltges DW (2011) Food web including metazoan parasites for an intertidal ecosystem in New Zealand. Ecological Archives E092–173. Ecology 92:2006

O'Connell-Milne SA, Poulin R, Savage C, Rayment W (2016) Reduced growth, body condition and foot length of the bivalve *Austrovenus stutchburyi* in response to parasite infection. J Exp Mar Biol Ecol 474:23–28

Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, Feely RE, Gnanadesikan A, Gruber N, Ishida A, Joos F, Key RM, Lindsay K, Maier-Reimer E, Matear R, Monfray P, Mouchet A, Najjar RG, Plattner G-K, Rodgers KB, Sabine CL, Sarmiento JL, Schlitzer R, Slater RD, Totterdell IJ, Weirig M-F, Yamanaka Y, Yool A (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681–686

Pechenik JA, Fried B, Simpkins HL (2001) *Crepidula fornicata* is not a first intermediate host for trematodes: who is? J Exp Mar Biol Ecol 261:211–224

Peoples RC (2013) A review of the helminth parasites using polychaetes as hosts. Parasitol Res 112:3409–3421

Peoples RC, Randhawa HS, Poulin R (2012) Parasites of polychaetes and their impact on host survival in Otago Harbour, New Zealand. J Mar Biol Assoc U K 92:449–455

Poulin R (2006) Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. Parasitology 132:143–151

Poulin R (2007) Evolutionary ecology of parasites. Princeton University Press, Princeton

Poulin R (2010) Parasite manipulation of host behavior: an update and frequently asked questions. Adv Study Behav 41:151–186

Poulin R, Cribb TH (2002) Trematode life cycles: short is sweet? Trends Parasitol 18:176–183

Poulin R, Mouritsen KN (2003) Large-scale determinants of trematode infections in intertidal gastropods. Mar Ecol Prog Ser 254:187–198

Poulin R, Mouritsen KN (2006) Climate change, parasitism and the structure of intertidal ecosystems. J Helminthol 80:183–191

Prenter J, MacNeil C, Dick JTA, Dunn AM (2004) Roles of parasites in animal invasions. Trends Ecol Evol 19:385–390

Probst S, Kube J (1999) Histopathological effects of larval trematode infections in mudsnails and their impact on host growth: what causes gigantism in *Hydrobia ventrosa* (Gastropoda: Prosobranchia). J Exp Mar Biol Ecol 238:49–68

Raffaelli D, Hawkins SJ (1999) Intertidal ecology. Springer, Berlin

Raffel TR, Martin LB, Rohr JR (2008) Parasites as predators: unifying natural enemy ecology. Trends Ecol Evol 23:610–618

Reise K (1985) Tidal flat ecology. Springer, Berlin

Rhode K (1993) Ecology of marine parasites: an introduction to marine parasitology. CAB International, Wallingford

Rhode K (ed) (2005) Marine parasitology. CSIRO Publishing, Melbourne and Wallingford

Riel A (1975) Effect of trematodes on survival of *Nassarius obsoletus* (Say). Proc Malacol Soc Lond 41:527–528

Schmid-Hempel P (2011) Evolutionary parasitology: the integrated study of infections, immunology, ecology, and genetics. Oxford University Press, Oxford

Seaman B, Briffa M (2015) Parasites and personality in periwinkles (*Littorina littorea*): infection status is associated with mean-level boldness but not repeatability. Behav Process 115:132–134

Shaw DJ, Dobson AP (1995) Patterns of macroparasite abundance and aggregation in wildlife populations: a quantitative review. Parasitology 111:S111–S127

Sokolova IM (1995) Influence of trematodes on the demography of *Littorina saxatilis* (Gastropoda: Prosobranchia: Littorinidae) in the White Sea. Dis Aquat Org 21:91–101

Solomon S, Quinn D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) (2007) Climate change 2007: the physical science basis: contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

Sousa WP, Gleason M (1989) Does parasitic infection compromise host survival under extreme environmental conditions? The case for *Cerithidea californica* (Gastropoda : Prosobranchia). Oecologia 80:456–464

Stier T, Drent J, Thieltges DW (2015) Trematode infections reduce clearance rates and condition in blue mussels Mytilus edulis. Mar Ecol Prog Ser 529:137–144

Studer A, Poulin R (2012) Seasonal dynamics in an intertidal mudflat: the case of a complex trematode life cycle. Mar Ecol Prog Ser 455:79–93

Studer A, Poulin R (2013) Cercarial survival in an intertidal trematode: a multifactorial experiment with temperature, salinity and ultraviolet radiation. Parasitol Res 112:243–249

Studer A, Thieltges DW, Poulin R (2010) Parasites and global warming: the net effect of temperature on an intertidal host-parasite system. Mar Ecol Prog Ser 415:11–22

Studer A, Poulin R, Tompkins DM (2013a) Local effects of a global problem: modelling the risk of parasite-induced mortality in an intertidal trematode-amphipod system. Oecologia 172: 1213–1222

Studer A, Widmann M, Poulin R, Krkošek M (2013b) Large scale patterns of trematode parasitism in a bivalve host: no evidence for a latitudinal gradient in infection levels. Mar Ecol Prog Ser 491:125–135

Tallmark B, Norrgren G (1976) The influence of parasitic trematodes on the ecology of *Nassarius reticulatus* (L.) in Gullmar Fjord (Sweden). Zoon 4:149–154

Thieltges DW (2006a) Parasite induced summer mortality in common cockles *Cerastoderma edule* by the trematode *Gymnophallus choledochus*. Hydrobiologia 559:455–461

Thieltges DW (2006b) Effect of infection by the metacercarial trematode *Renicola roscovita* on growth in intertidal blue mussel *Mytilus edulis*. Mar Ecol Prog Ser 319:129–134

Thieltges DW (2007) Habitat and transmission – effect of tidal level and upstream host density on metacercarial load in an intertidal bivalve. Parasitology 134:599–605

Thieltges DW (2008) Effect of host size and exposure on metacercarial infection levels in the intertidal cockle *Cerastoderma edule*. J Mar Biol Assoc U K 88:613–616

Thieltges DW, Poulin R (2016) Food-web-based comparison of the drivers of helminth parasite species richness in coastal fish and bird definitive hosts. Mar Ecol Prog Ser 545:9–19

Thieltges DW, Reise K (2007) Spatial heterogeneity in parasite infections at different scales in an intertidal bivalve. Oecologia 150:569–581

Thieltges DW, Rick J (2006) Effect of temperature on emergence, survival and infectivity of cercariae of the marine trematode *Renicola roscovita* (Digenea: Renicolidae). Dis Aquat Org 73:63–68

Thieltges DW, Krakau M, Andresen H, Fottner S, Reise K (2006) Macroparasite community in molluscs of a tidal basin in the Wadden Sea. Helgol Mar Res 60:307–316

Thieltges DW, Jensen KT, Poulin R (2008a) The role of biotic factors in the transmission of free-living endohelminth stages. Parasitology 135:407–426

Thieltges DW, Donas-Botto Bordalo M, Hernández C, Prinz K, Jensen KT (2008b) Ambient fauna impairs parasite transmission in a marine parasite-host system. Parasitology 135:1111–1116

Thieltges DW, de Montaudouin X, Fredensborg BL, Jensen KT, Koprivnikar J, Poulin R (2008c) Production of marine trematode cercariae – a potentially overlooked path of energy flow in benthic systems. Mar Ecol Prog Ser 372:147–155

Thieltges DW, Ferguson MAD, Jones CS, Noble LR, Poulin R (2009a) Biogeographical patterns of marine larval trematode parasites in two intermediate snail hosts in Europe. J Biogeogr 36: 1493–1501

Thieltges DW, Fredensborg BL, Poulin R (2009b) Geographical variation in metacercarial infection levels in marine invertebrate hosts–parasite species character versus local factors. Mar Biol 156:983–990

Thieltges DW, Fredensborg BL, Studer A, Poulin R (2009c) Large-scale patterns in trematode richness and infection levels in marine crustacean hosts. Mar Ecol Prog Ser 389:139–147

Thieltges DW, Reise K, Jensen KT (2009d) Invaders interfere with native parasite-host interactions. Biol Invasions 11:1421–1429

Thieltges DW, Saldanha I, Leung TLF, Poulin R (2009e) Contribution of parasites to intra- and inter-site variation in shell morphology of a marine gastropod. J Mar Biol Assoc U K 89: 563–568

Thieltges DW, Reise K, Mouritsen KN, McLaughlin JP, Poulin R (2011) Food web including metazoan parasites for a tidal basin in Germany and Denmark. Ecological Archives E092–172. Ecology 92:2005

Thieltges DW, Engelsma MY, Wendling CC, Wegner KM (2013a) Parasites in the Wadden Sea food web. J Sea Res 82:122–133

Thieltges DW, Amundsen P-A, Hechinger RF, Johnson PTJ, Lafferty KD, Mouritsen KN, Preston DL, Reise K, Zander C-D, Poulin R (2013b) Parasites as prey in aquatic food webs: implications for predator infection and parasite transmission. Oikos 122:1473–1482

Thomas F, Poulin R (1998) Manipulation of a mollusc by a trophically transmitted parasite: convergent evolution or phylogenetic inheritance? Parasitology 116:431–436

Thomas F, Poulin R, de Meeus T, Guegan J-F, Renaud F (1999) Parasites and ecosystem engineering: what roles could they play? Oikos 84:167–171

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. Nature 421:628–630

Torchin ME, Miura O, Hechinger RFG (2015) Parasite species richness and intensity of interspecific interactions increase with latitude in two wide-ranging hosts. Ecology 96:3033–3042

Turner JRG, Gatehouse CM, Corey CA (1987) Does solar-energy control organic diversity—butterflies, moths and the British climate. Oikos 48:195–205

Wegeberg AM, Jensen KT (1999) Reduced survivorship of *Himasthla* (Trematoda, Digenea)-infected cockles (*Cerastoderma edule*) exposed to oxygen depletion. J Sea Res 42:325–331

Wegeberg AM, Jensen KT (2003) In situ growth of juvenile cockles, *Cerastoderma edule*, experimentally infected with larval trematodes (*Himasthla interrupta*). J Sea Res 50:37–43

Welsh JE, van der Meer J, Brussaard CPD, Thieltges DW (2014) Inventory of organisms interfering with transmission of a marine trematode. J Mar Biol Assoc U K 94:697–702

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annu Rev Ecol Evol Syst 34:273–309

Wilson WH (1991) Competition and predation in marine soft-sediment communities. Annu Rev Ecol Syst 21:221–241

Zander CD, Josten N, Detloff KC, Poulin R, McLaughlin JP, Thieltges DW (2011) Food web including metazoan parasites for a brackish shallow water ecosystem in Germany and Denmark. Ecological Archives E092–174. Ecology 92:2007

Chapter 10
Mudflat Ecosystem Engineers and Services

Claire Passarelli, Cédric Hubas, and David M. Paterson

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Abstract Ecosystem engineers play a fundamental role in the creation, maintenance and transformation of habitats in tidal flats. Highly diverse in terms of size, phylogeny, and effect on their environment, they can facilitate or hinder a number of organisms, but generally have a positive influence on both the abundance and the

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diversity of mudflat organisms. The magnitude of the engineering effect is, however, largely dependent on the biotic and abiotic environment of the engineer. In particular, stressful habitats such as mudflats host a large number of ecosystem engineers; understanding interactions between them, and how they vary with abiotic variables, is therefore of crucial importance, to evaluate how ecosystem engineers affect benthic communities and ecosystem functioning. Such understanding will also help human populations which benefit from mudflat organisms and/or functioning (i.e. which derive ecosystem services from them), to maintain and manage the sustainably of tidal flats, in a way which maintains human health and well-being.

1 Introduction

Despite being stressful environments, with little apparent complexity, tidal flats host a large diversity of organisms, in the sediment, on the sediment and above the sediment. Along with morphological, physiological, and behavioural adaptations necessary to survive in such systems, numerous organisms benefit from facilitative interactions with other organisms. These non-trophic interactions promote the settlement or development of at least one species, without negatively affecting the other; for instance, through modification of habitat or reduction of an environmental stress. Facilitation is being increasingly recognised as an important mechanism that explains assemblage formation and composition and ecosystem functioning, especially in stressful habitats such as the intertidal. (Bertness and Leonard 1997).

Research on facilitation by habitat modification was stimulated in 1994, when Jones and colleagues proposed the concept of ecosystem engineering to describe the creation, maintenance and transformation of habitat by organisms (Jones et al. 1994). This concept has received considerable attention since then, with more than 2600 papers citing this founding article, 1100 of them published in the last 4 years (Web of Science 2017). Research has focussed on the identification of ecosystem engineers and the characterisation of their effects, the modelling of engineering effects, the interactions of engineers with their biotic and abiotic environment, or between several engineers, as well as the implications of engineering effects in terms of ecosystem functioning, goods, services, and management.

Sediment reworking organisms were suggested to be a good example of ecosystem engineers, due to their strong impact on sediment properties, and therefore on associated communities and ecosystem functioning (Jones et al. 1994). In intertidal flats, the exclusion of one bioturbator species such as the lugworm *A. marina* has indeed been shown to have diverse sediment-mediated effects on benthic communities (Volkenborn et al. 2009). Coastal systems host a striking diversity of ecosystem engineers (see e.g. Passarelli et al. 2014), most of them affecting the sediment (Reise 2002), either directly (e.g. construction and maintenance of burrows by *Hediste diversicolor*) or indirectly (e.g. modification of hydrodynamics by surface-protruding tubes built by the sandmason worm *Lanice conchilega*). In addition to their effects on sediments, ecosystem engineers of tidal flats also constitute a major source of hard substrate, necessary for the recruitment of several species (such as algae, Thomsen et al. 2010), and as the main provider of habitat complexity (Zühlke et al. 1998; Bouma et al. 2009). Therefore, ecosystem engineers are key drivers of the diversity and functioning of mudflats.

Human populations derive numerous benefits from tidal flats, some quite obvious, such as the provision of fish and shellfish, and some less known, such as nutrient recycling. However, these services may be altered when the biotic and/or abiotic environment of ecosystem engineers change, leaving the system in a different functioning state that it used to be. Understanding how ecosystem engineers modify biodiversity and ecosystem functioning, how they interact with their environment, and what are the consequences of such interactions on mudflats, is thus essential in order to maintain the provision of ecosystem services to human populations.

In this review, we will first analyse how the diverse ecosystem engineers that inhabit mudflats influence their diversity and functioning, at different time and space scales. We will then assess how the biotic and abiotic environment of ecosystem engineers alter their abundance and effects on ecosystems, with a special focus on interactions between ecosystem engineers. Finally, we will review the variety of ecosystem services provided by mudflats and their ecosystem engineers, and discuss consequences for coastal management.

2 Diversity of Ecosystem Engineers in Mudflats

2.1 Engineers vs. Non-engineers

Ecosystem engineering may have a longer history than many other ecological interactions, such as predation or competition. The early and abiotic conditions on the newly formed planet Earth did not last for long and in geological terms life evolved very rapidly (Dodd et al. 2017) with the first evidence of life almost 4 billion years before present, not long, geologically speaking, after the formation of the planet (4.6 billion years). Life immediately began to have an effect on the new planet, and while it took some time for the complete change in atmospheric conditions (from anoxic to oxic) as a result of microbial metabolism (Catling and Claire 2005), much earlier indications of life are present. Early microbes created structures, laminations in sediments, akin to modern day biofilms, and those laminations were preserved in the fossil record as stromatolites (Krumbein et al. 2003, see Chap. 8). This may be the first organismal engineering activity (Paterson et al. 2008) that we can recognise.

This example highlights two issues: (1) ecosystem engineering is not new; and (2) an organism does not have to be large and charismatic to influence the environment; a large number of small ones may be equally, or more, important (Boogert et al. 2006). However, that is not to say that a single isolated bacterium does not influence its surroundings, but is this ecosystem engineering? This is a

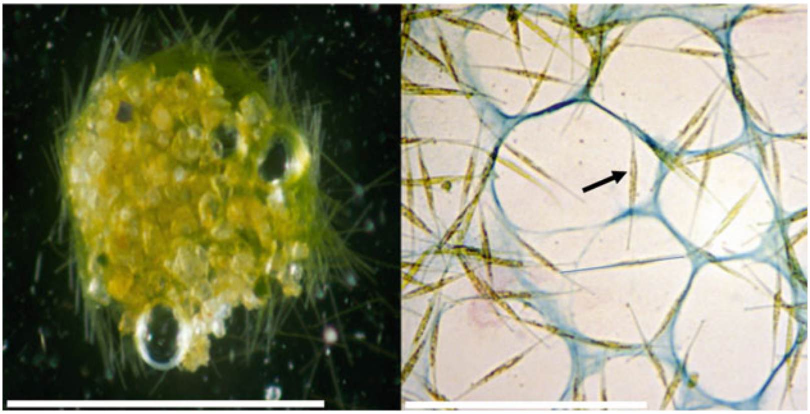

Fig. 10.1 Small-scale ecosystem engineering by cyanobacteria *Oscillatoria* spp. (left) and the polymers produced by diatoms *Cylindrotheca gracilis* (right, black arrow to diatom, polymers stained with Alcian blue; from culture: f/2 Guillard in artificial seawater at 25 PSU). Scale bars: 100 μm.

question of scale and so it is to some extent arbitrary to decide "how much effect must be created before the effect is recognised as ecosystem engineering", which may be very much a question of context and perspective. A relevant example is the secretion of extracellular polymeric substances (EPS) from bacteria and microphytobenthos. A microbial mat is easily recognised as having an engineering impact whereas a single diatom cell may not, but the single cells still secrete polymer and will stick local grains together, albeit the effect is on a very small scale (Fig. 10.1). However, since the effect is measurable, is it ecosystem engineering? The reality is that all living organisms alter their environment to some extent; it would be incredible if they did not, but there is a wide variety of impact ranging from almost quiescent "deep bacteria" (Whitman et al. 1998) with extremely slow metabolism, to the obvious and rapid activity of bowerbirds. We apply the term ecosystem engineering to those cases where the effect is deemed significant from a human perspective. This may recognise very large-scale effects more easily, beaver dams and coral reefs, but may miss less obvious examples such as biogeochemical pathways supplying nutrients. All organisms are capable of ecosystem engineering; the recognition of the process is a function of scale, knowledge and perceived importance.

Some examples of commonly recognised ecosystem engineers in mudflat can be found in Passarelli et al. (2014).

2.2 *Classification of Ecosystem Engineers*

When Jones and colleagues proposed the concept of ecosystem engineering in 1994, they immediately defined 2 types of ecosystem engineers: on one hand, autogenic engineers that transform the environment through their own physical structure,

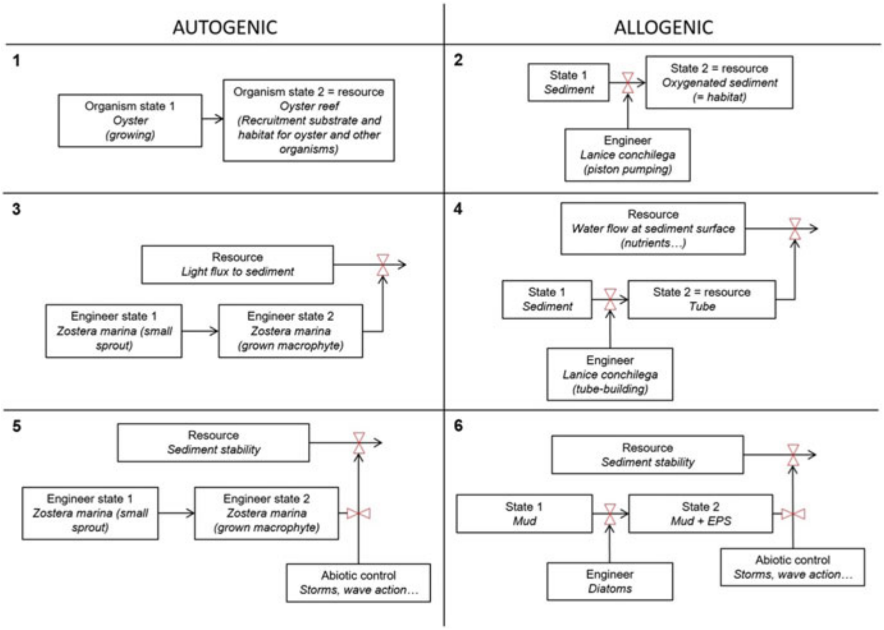

Fig. 10.2 Autogenic and allogenic ecosystem engineering: diverse mechanisms of action. Figure adapted from Jones et al. (1994), with examples from mudflats. The hourglass symbol shows potential point of modulation. Case 1 was initially excluded from ecosystem engineering by Jones et al. (1994), but subsequently proposed to be included (Jones et al. 1997); it is however worth noting that the provision of trophic resource (organism in state 2 as a food source) is not ecosystem engineering.

where the engineer remains part of the engineered environment; e.g. submerged macrophytes, such as *Zostera* species, whose leaves modify hydrodynamics (Fonseca et al. 1982), sedimentation (Ganthy et al. 2013), light (van der Heide et al. 2007), and many other parameters (Lee et al. 2001). On the other hand, allogenic engineers alter their environment by transforming other material from one state to another; e.g. burrowing macrofauna rework sediment (Meadows and Meadows 1991), alter its stability (Meadows et al. 1990), and pump oxygen into the sediment (Forster and Graf 1995).

Jones and colleagues also proposed subcategories, as illustrated in Fig. 10.2 with examples from tidal flats; an ecosystem engineer can alter its environment by different actions and therefore belong to different categories and subcategories. Ecosystem engineers can directly create a habitat for other organisms, either by their own growth (autogenic engineers, case 1) or by transforming a living or non-living material (allogenic engineers, case 2); for instance, the sand mason worm *Lanice conchilega* oxygenates sediments by piston pumping (Forster and Graf 1995). Oxygenated subsurface sediment can thereafter be colonised by diverse organisms (Reise 2002). Another mechanism of action of ecosystem engineers is the modulation of resource flow to other organisms (cases 3 and 4). For instance, tube-building polychaetes modify, through their tubes, water flow at sediment surface, and therefore access to nutrients for benthic organisms (Luckenbach 1986; Zühlke et al. 1998). Seagrasses, shells, and faecal casts of *Arenicola marina* have similar effects (Friedrichs et al. 2009). Finally, Jones et al. (1994) separate in different categories engineers that modulate the effect of "powerful abiotic control", such as fires or hurricanes. Organisms which stabilise the sediment either directly or indirectly (case 5 and 6), therefore preventing sediment erosion by storms, can be attributed to these categories.

Beyond their interest to illustrate the diverse possible mechanisms of ecosystem engineering, these categories serve to illustrate general patterns for certain groups of ecosystem engineers. For example, organisms modifying water flow at the sediment surface are highly diverse in terms of phylogeny; examples include tube-building polychaetes (Zühlke et al. 1998) and amphipods (Rigolet et al. 2014), seagrasses (Fonseca et al. 1982), kelps (Eckman et al. 2003), snails and shells, and even faecal casts by the lugworm *Arenicola marina* (Friedrichs et al. 2009). Yet, their actions on sediment have been shown to be primarily dependent on the density of the structures (Friedrichs et al. 2000), with an increase of the flow toward the sediment and sediment destabilisation by the turbulent flow at low density; while a higher density of structures limits water flux into sediment, and therefore increases sediment stability. The size and shape of the structures still influence the exact flow (Friedrichs et al. 2009). Functional classes of ecosystem engineers have been proposed to take these similarities into account (Berke 2010).

The different mechanisms of ecosystem engineering also have consequences on the persistence of the effect after the death of the engineer. For example, following the same case of organisms building biogenic structures, leaves of *Zostera marina* will stop having an effect on water fluxes as soon as the leaves die, are carried away, or eaten. On the other hand, tubes built by polychaetes can survive the worms themselves (Zühlke 2001). On a larger spatial and temporal scale, oyster reefs can become accreted, and deeply modify the assemblages of organisms in the surrounding environment (Lejart and Hily 2011), even after the death of the oysters (Summerhayes et al. 2009). The persistence of the engineering effect after the engineer's death is dependent upon the persistence of its remains for autogenic engineers; for allogenic engineers, which modify other materials, the effects are more likely to last after the death of the engineer (Hastings et al. 2007). However, because the maintenance of the "engineered" state might require constant action from the engineer, the persistence of the effect might be short-lived (Reise 2002).

In the specific case of mudflats and coastal sediment, Bouma et al. (2009) proposed that autogenic and allogenic ecosystem engineers have inverse effects on epibenthic (which live on the mud or near the mud surface) and endobenthic communities (which live in the mud; e.g. *A. marina*). Autogenic, principally epibenthic ecosystem engineers, such as *Spartina anglica*, create a complex epibenthic habitat, increasing the density of organisms in this habitat at the expense of endobenthic organisms. On the other hand, the numerous allogenic engineers that rework the sediment (see e.g. Meadows et al. 2012), creating burrows and oxygenating otherwise anoxic habitats, facilitate other infauna, and therefore increase the diversity of endobenthic organisms.

The diversity and composition of infaunal assemblages are largely controlled by the sediment stability, itself being strongly dependent of biofilm-forming microorganisms (see Chap. 8).

2.3 Case Study: Biofilms and Sediment Stabilisation

A careful review of the literature would unearth a number of relevant studies that expand knowledge on the effects of biofilms on sediment behaviour, but the general realisation that biological mediation must be considered when working with, or predicting or modelling natural sediment behaviour (Black et al. 2002; Murray et al. 2002), has been slow to take hold. This might seem surprising, since the early studies of biogenic stabilisation were often quite clear and convincing (Manzenrieder 1983; Paterson and Black 1999). Perhaps the real problem was how to communicate this research in a way that was meaningful to different interest groups. For example, a physical modeller might ask for the erosion threshold of an intertidal flat, in order to prepare a suitable model. The standard way of deriving this would be to measure grain size and then predict an erosion threshold from a known relationship developed in the laboratory (e.g. Shields criterion, Shields 1936, and see Chap. 8). This is almost always wrong; even ignoring the sedimentological context of the natural spatial variability of sediment distribution and particle mixing, the biology is missing. Using hydrodynamics and sediment geotechnics in an ecological context can create inroads to further development between the two disciplines.

An early study by Dade et al. (1990) was prescient. These workers incubated bacteria on sand, and measured their effect on the erosion threshold; in addition, they also extracted the polymer they considered to be the "active" agent of the biological stabilisation, from a similar culture of bacteria, and tested the effect of this polymer on sand behaviour. The results were informative. The bacteria stabilised the bed more effectively than the polymer on its own but both tests were more stable than the control sand (Fig. 10.3). From this, we might expect that it would be possible to incorporate in the model a "proxy" for biological stabilisation, perhaps by determining the concentration of extracellular polymeric substances (EPS); however, this has proven difficult.

Dade's early results may also help explain why this is the case. The natural population of bacteria is more effective than the polymer on its own. There may be several reasons for this. The extracted polymer is no longer in the same molecular conformation as the EPS mixture formed under natural conditions. In addition, the bacteria may secrete some polymers randomly, but also some in a much more targeted manner, such as attached to surfaces, essentially creating networks of polymer strands and bridges, which are unlike the extracted material being added uniformly to a clean substratum. It is therefore unsurprising that the growth of a

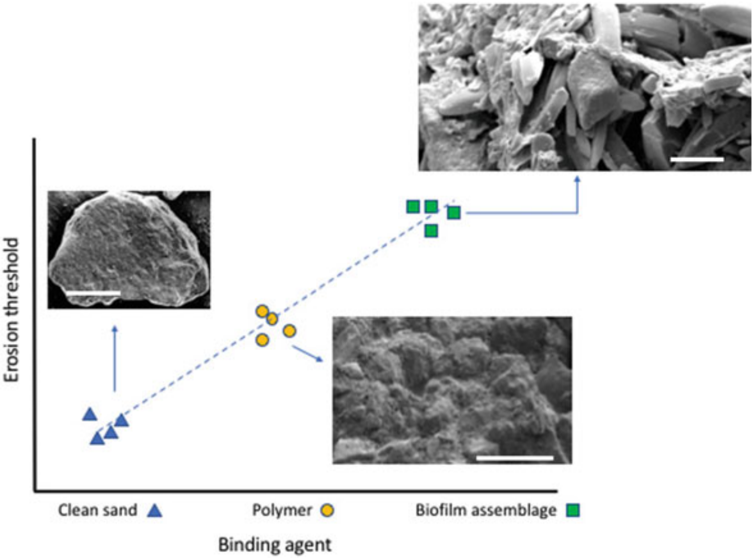

Fig. 10.3 Schematic representation of the effect of clean sand, extracted polymer, and biofilm development on sediment erosion threshold (after Dade et al. 1990). Scale bars: clean sand 50 μm; others 100 μm.

biofilm imparts more structure and is more effective at binding material. Even if this were not a limitation, biogenic effects would still be subject to the natural variability of biological systems; moreover, the spatial patchiness and variability of biofilm formation is well-known, and also applies to other EPS producers such as diatoms (Jesus et al. 2005). Defew et al. (2003) showed that a multivariate and often site-specific approach would be required to predict the influence of biogenic effects of sediment stability, and while developments in spatial analysis, molecular tools and advances in remote sensing may all offer new opportunities, there is still a void in terms of communication and research using natural systems to address this shortcoming. This requires an interdisciplinary approach (Malarkey et al. 2015), to better integrate increasing knowledge of biogenic stabilisation with modelling platforms capable of incorporating biogenic effects.

2.4 Influence of Ecosystem Engineers on Biodiversity and Ecosystem Functioning

Ecosystem engineers influence both the abundance, and, because their effects are species-specific, the composition of surrounding assemblages. For example, species which stabilise sediment tend to facilitate the recruitment and growth of organisms that rely on sediment stability, while they exclude organisms having a contrary effect

(Woodin and Jackson 1979). Also, a single ecosystem engineer species can affect assemblages of organisms of very different sizes and habitats; for instance in mudflats, *Lanice conchilega* influences the recruitment and development of microorganisms, meiofauna, and macrofauna (Passarelli et al. 2012b), as well as associated epibenthic and fish populations (Rabaut 2009).

A good example of an effect at multiple levels comes from the experiments of Volkenborn and colleagues, who excluded the lugworm *Arenicola marina* from 400 m^2 plots during 3 years. This exclusion led to the accumulation of fine particles and organic matter in the sediment, eventually modifying its chemical and physical properties, and also altering the growth of microphytobenthos, as measured by chlorophyll concentrations (Volkenborn et al. 2007). Exclusion also increased the abundance of ragworms *Hediste diversicolor*, which benefited from reduced competition, while *Scoloplos armiger* were negatively affected by the change of sediment chemistry (Volkenborn and Reise 2006). Exclusion of *A. marina* also benefitted other macrofaunal species such as clams and tube-building polychaetes, as well as some algal species who settled on the tubes (Volkenborn and Reise 2007; Volkenborn et al. 2009). These authors pointed out that such engineering effects were highly dependent on time, space, and on the recruitment success of *A. marina* (Volkenborn and Reise 2007).

For individual species, the effect of ecosystem engineers can be either positive or negative, so there is no reason to assume that the net effect of an engineer on biodiversity will always be positive at a patch scale (Jones et al. 1997). However, ecosystem engineers who increase the complexity of a habitat tend to have a positive effect on the diversity, while those who render the habitat more homogenous decrease it (Crooks 2002; Cruz Sueiro et al. 2011). This is because transforming simple habitats into complex ones creates additional niches (Bell 1985), and can also provide refuge from predators (Woodin 1978; Bouma et al. 2009).

Given that engineering effects are highly dependent on time and space, non-engineered habitats, engineered habitats and previously engineered habitat will coexist at a larger temporal and spatial scale. By increasing the patchiness of habitats, the engineer will generally increase diversity at a landscape scale (Jones et al. 1997; Volkenborn and Reise 2007). This is especially true since the effect of engineers on associated assemblages can change after their death and during the degradation of their structures (Summerhayes et al. 2009).

Ecosystem engineers usually facilitate their own recruitment, especially beyond a given threshold (Bouma et al. 2009). When settled, organisms then modify their environment, which attracts new species. Mudflats are highly dynamic systems, and as such they are stressful for many organisms. Ecosystem engineers can reduce the magnitude of variations of physical and chemical parameters, facilitating the settlement and growth of other species, therefore acting as foundation species (Altieri et al. 2007). The creation of this new habitat, however, can be made at the expense of another (Bertness 1984).

Indeed, the combination of thresholds and positive feedback mechanisms make possible the coexistence of several stable states (Wilson and Agnew 1992; van der Heide et al. 2007; Bouma et al. 2009). This can be illustrated by the seagrass *Zostera* *marina*, which reduces nutrient concentration in the water column, and softens the current and wave action. Both mechanisms decrease turbidity, which facilitates the development of the seagrass, and its associated assemblages. If the population of *Z. marina* decreases, e.g. following a disease, the turbidity will remain high; this will hinder the development of the seagrass. The threshold for the survival of a population seems to be around 1000 shoots per square meter (van der Heide et al. 2007).

Any biotic or abiotic variable able to modify the abundance of an ecosystem engineer is therefore likely to have a large influence on the abundance, composition and diversity of the communities.

2.5 Evolutionary Perspective of Ecosystem Engineering

Since Charles Darwin first presented the theory of evolution to the world (Darwin 1859) evolutionary science has itself evolved considerably (Laland et al. 2014). The mechanisms of evolution are under increasing scrutiny as the science of molecular genetics increases in sophistication, allowing the interrogation of genes and genomes at a speed and resolution that was until recently unthinkable (Hall 2007). There are also many discussions in terms of evolutionary theory trying to explain how the pressures that lead to evolutionary change can be classified and modelled. Ecosystem engineering is a relevant example. It is understood that the activity of ecosystem engineers alters the environment, and one school of evolutionary thought, presented under the "Extended Evolutionary Synthesis" (EES) theory (Extended Evolutionnary Synthesis 2016), suggests that the activity of the engineer in changing the environment should in itself be recognised as a distinct evolutionary pressure. EES proposes that engineering activity significantly alters the evolutionary trajectory of organisms exposed to the effect (Fig. 10.4). A classic example would be bacteria evolving in a soil that has been bioturbated by earthworms, but there are many other examples. This hypothesis is described under the theory of "niche construction" (Odling-Smee et al. 2003), an evolutionary partner to ecosystem engineering.

Even greater complexity can be imagined when aspects such as "cooperative ecosystem engineering" as proposed by Passarelli et al. (2014) are considered. There is no restriction on this activity that suggests cohorts of organisms may provide similar pressures or effects. In addition, species may also interfere with one another diluting selective pressures. As noted earlier, the first evidence of life on earth are laminated structures preserved in rock arising from the activity of bacterial biofilm assemblages. This early ecosystem engineering creates more stable sedimentary gradients, potentially driving evolutionary change (Paterson et al. 2017). Although this hypothesis is contested by many evolutionary biologists (Laland et al. 2014), it is clear that ecosystem engineering does have a significant impact on the local environment of both the engineers and of cohabiting species, and the theory of

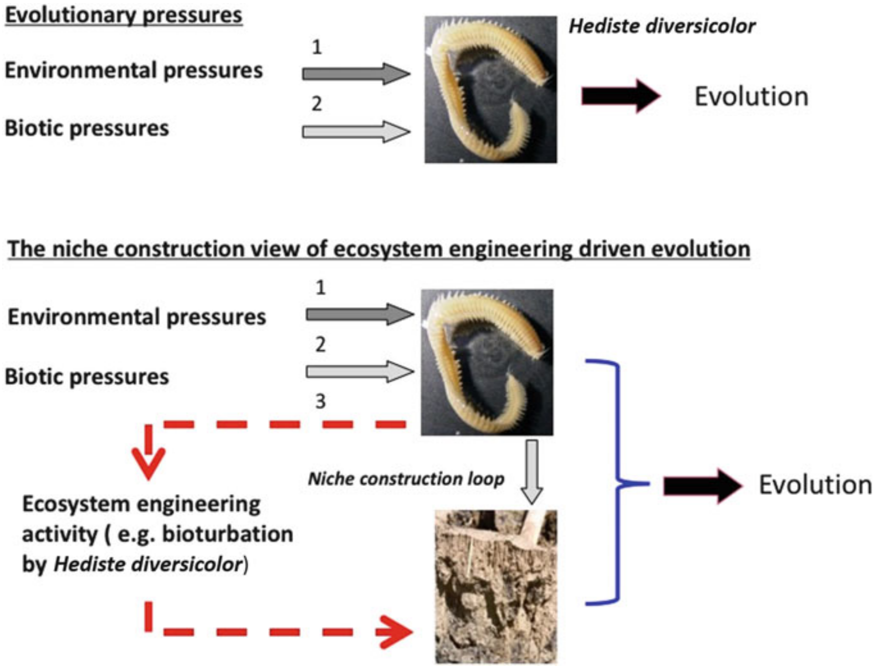

Fig. 10.4 Simplified schematic representation of the niche construction theory. 1: environmental pressures. 2: biotic pressures. 3: alteration of local environment by ecosystem engineering. Engineering activity (e.g. bioturbation by *Hediste diversicolor*) alters the local environment for other organisms, altering their evolutionary trajectory.

niche construction is worthy of consideration, emphasising the evolutionary importance of ecosystem engineering.

3 Mudflat Ecosystem Engineers in Their Biotic and Abiotic Environment

3.1 Ecosystem Engineers and Interaction Webs: Example of Sediment Stabilisation by Biofilms

Shortly after proposing the concept of ecosystem engineers, Lawton and Jones (1995) suggested that engineering effects have their place in larger interaction webs, which would combine both trophic and non-trophic interactions. Engineers are indeed themselves organisms which undergo variations of their biotic and abiotic environment, which can influence their abundance and densities, and thus their engineering effect. More recently, Hastings et al. (2007) proposed that integrating non-trophic, engineering interactions into food webs was especially important when

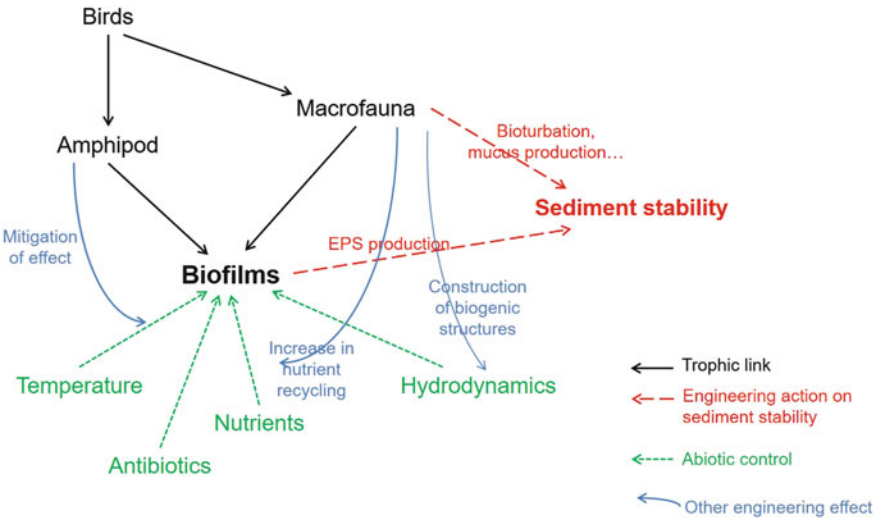

Fig. 10.5 Interaction networks around biofilms and sediment stability, detailing trophic (black arrows) and non-trophic (through action on abiotic factors) interactions in the examples discussed in Sect. 3.1.

the time and spatial scale at which these interactions occur is very different from the scale at which trophic interactions occur. Our previous example of biofilms and sediment stabilisation, illustrates the need to build interaction webs when trying to assess the magnitude or dynamics of an engineering effect (Fig. 10.5).

A first point is that biofilms are a trophic resource for consumers, such as the amphipod *Corophium volutator* (Daborn et al. 1993; Hagerthey et al. 2002) and the common mud snail *Hydrobia ulvae* (Andersen et al. 2002; Hagerthey et al. 2002). The selective-feeding *C. volutator* has a strong influence on biofilms, both reducing biomass and altering the composition of the microphytobenthic assemblage; on the other hand, the unselective grazer *H. ulvae* reduces microphytobenthic biomass but does not affect the composition of the assemblage (Hagerthey et al. 2002). These consumers are therefore likely to have contrasting effects on the biofilm's engineering capacity (Andersen et al. 2002). Also, Daborn et al. (1993) demonstrated that, when *C. volutator* is consumed by migratory birds, an "ecological cascade" takes place where birds, by feeding on the amphipods, decrease the consumption of biofilms and therefore increase sediment stabilisation. The development of biofilms is also controlled by various abiotic parameters, such as nutrients or light. A good example is the bioadvective gardening by the lugworm *A. marina*, i. e. the transport of nutrients from depth to surface, where they become available for microphytobenthos (Chennu et al. 2015).

To complicate the picture even more, diverse types of interactions can take place between the same two engineers. For example, *C. volutator* feeds on biofilms, but also mitigates the effect of temperature on biofilm development (Hagerthey et al. 2002). The ragworm *Hediste diversicolor* feeds on biofilms as well, but this worm also reworks sediment and potentially increases the recycling of nutrients, therefore stimulating the growth of biofilm (Passarelli et al. 2012a). Therefore, considering the trophic links alone might lead to conclude that *H. diversicolor* will have a negative impact on sediment stabilisation by biofilms (Passarelli et al. 2014), while in fact the worms can stimulate biofilm growth and the engineering effect (Passarelli et al. 2012a). With that in mind, it seems necessary to understand the various trophic and non-trophic interactions on ecosystem engineers with their environment if we are to estimate the magnitude of engineering effects and their variability in space and time.

3.2 Effects of Abiotic Parameters on Ecosystem Engineers, and Consequences for Mudflats

Numerous environmental variables alter the development of ecosystem engineers, and through them their associated communities. This can be a seasonal effect in the case of *Lanice conchilega*, as these sand-mason worms can suffer massive mortalities in winter, causing a change in sediment properties (Alves et al. 2017). Bateman and Bishop (2017) used a meta-analysis to decipher the factors contributing to the variations of the engineering effects of bivalves on the assemblages of epifauna and infauna. They conclude that even if some engineers, such as oysters, generally had a large effect compared to others, the magnitude of the engineering effect was very variable, and also deeply affected by environmental context. Human actions can also modify habitat, and through them the development of engineers. For example, recreational clam-digging activities deeply alter the distribution of the lugworm *Arenicola marina* (Boldina and Beninger 2014), an ecosystem engineer known to have major effect on sediment properties and macrofaunal communities (Volkenborn and Reise 2006; Volkenborn et al. 2009). Global changes in temperature will also affect the biogeographic range of engineers (Wethey et al. 2011) and therefore the functioning of ecosystem. Finally, massive pollution events can have in-depth consequence for the composition and functioning of coastal systems: for example, the *Deepwater Horizon* oil spill in US led to large loss of oysters *Crassostrea virginica*, which in turn led in the destruction of fish habitat, reduced nutrient recycling and increased sediment erosion (Powers et al. 2017).

Ecosystem engineers modify the abiotic parameters of the habitat in which they live, therefore potentially facilitating their own development (positive feedback; Bruno et al. 2003). These mechanisms will influence the population dynamics of the engineers, either keeping the population below a certain density in the case of negative feedbacks, or increasing densities above a certain threshold, which then facilitates the survival of the population. These feedbacks also mean that “switches” between two alternative states can happen, following a perturbation (Wilson and Agnew 1992). For example, diatom biofilm development on mudflats enhances the accumulation of silt, which stabilises the sediment and further stimulates diatom development (Van De Koppel et al. 2001). If the biofilm is disturbed by an external perturbation, the sediment might be eroded, which will further reduce diatom development. Such switches have been demonstrated with *Zostera marina*, whose recovery after a disease was hindered by the increase of turbidity prompted by their own death (van der Heide et al. 2007).

The action of ecosystem engineers on their habitat can also facilitate the recruitment of better competitors, which will then tend to limit the development of these ecosystem engineers (negative feedback; Bruno et al. 2003). This can lead to stable equilibrium between ecosystem engineers and better competitors, which highlights the possible interplay between abiotic and biotic variables in explaining the magnitude of engineering effects.

3.3 Interactions Between Ecosystem Engineers

Ecosystem engineers are involved in numerous interactions with other organisms, such as trophic links. Engineering and trophic interactions are starting to be integrated in models (Kéfi et al. 2012; Sanders et al. 2014), showing that the net effect of one engineer species will depend on its direct engineering effects, its direct trophic influence, and any positive or negative feedback on the engineer itself (Sanders et al. 2014). Ecosystem engineers are also involved in other types of interactions such as parasitism and competition (Jones et al. 1997), such as the mutual exclusion of sediment stabilising and sediment destabilising species (Woodin and Jackson 1979). Also, the trophic interactions in which ecosystem engineers are engaged are themselves dependent on abiotic factors; for example, shade alters the predation of the clam *Macomona liliana* by eagle rays, and therefore their engineering effect on the meiofaunal community (Van Colen et al. 2015).

Ecosystem engineers can also interact among themselves, which can deeply modify their effects on communities. Such interactions can happen when ecosystem engineers act as foundation species, creating habitat for other organisms (Altieri et al. 2007), including other ecosystem engineers. Thomsen et al. (2010) proposed the concept of habitat cascade to describe these interactions where a basal habitat former, by its engineering effect, stimulates the development of an intermediate habitat user and former, which in turn engineers habitat for a focal group of organisms. For example, hard substrate for algal settlement is rare in soft-bottom tidal flats; yet, shellfish and tube-forming polychaetes, such as *Diopatra cuprea* (basal habitat formers), provide suitable substrate for the recruitment of seaweeds, such as *Gracilaria* spp. (intermediate habitat former), which will provide habitat to epibionts (Thomsen et al. 2010). Similarly, the modification of the habitat of the clam *Anadara trapezia* by *Caulerpa taxifolia* influences the burial depth of the clam, which increases the substrate available for epibionts, thereby enhancing their diversity (Gribben et al. 2009). Also, tube-building polychaetes can take advantage of the absence of the bioturbator *A. marina* following an experimental exclusion; their tubes then provide substrate for algae, which in turn increases the settlement of byssus-drifting bivalves (Volkenborn et al. 2009).

Species facilitated by engineers can also associate with them, further modifying the environment (Alvarez et al. 2015). And in non-hierarchical interactions, the net effect of two species of ecosystem engineers might differ from the sum of individual effects. For example, Boyer and Fong (2005) manipulated, in a saltmarsh, the density of the snail *Cerithidea californica*, which tends to increase microalgal cover, and that of the crab *Pachygrapsus crassipes*, which slightly decreases it. When these two engineers were put together, surprisingly, the microalgal cover disappeared. More recently, Eklöf et al. (2011) investigated the counteracting effects of *Zostera noltii,* which stabilises sediment, and the lugworm *Arenicola marina*, which destabilises sediment by bioturbation. They cleared patches of *Z. noltii* and added lugworms to some of the cleared patch, expecting *A. marina* to reduce recolonization by the seagrass. They did not observe such an effect, until an unplanned disturbance (possibly strong hydrodynamics) increased the size of the cleared patches; then, they demonstrated that the presence of the worm decreased the threshold-size of the patch necessary to prevent the recolonization by the seagrass. They concluded that the interaction between counteracting engineers could influence the response of ecosystems to disturbance.

The effect of two ecosystem engineers can also be synergistic, meaning that their combined effect will exceed the sum of their individual effect. For example, we investigated the effect of *Lanice conchilega* and microphytobenthos on sediment stability (Passarelli et al. 2012b). At high tube density, the tube-building polychaete modifies sediment properties (e.g. grain size) by altering water flow at the sediment surface. Microphytobenthos produces extracellular polymeric substances (EPS) that bind and stick the sediment particles together. The resulting effect of both engineers together is a significant increase in sediment surface adhesion, a proxy for sediment stability (Passarelli et al. 2012b). We proposed the term of cooperative ecosystem engineering to describe this synergistic interaction (Passarelli et al. 2014).

Caliman et al. (2011) demonstrated similar synergistic effects of three bioturbators on nutrient fluxes at the sediment/water interface, mainly driven by complementarity between the species (nymphs of *Campsurus melanocephalus*, adults of *Heteromastus similis* and *Heleobia australis*). However, synergistic effects were only apparent when the volume of sediment available for bioturbation was above a certain threshold. This shows that interactions between ecosystem engineers can themselves be dependent on other factors, which makes the picture even more complex. Eklöf et al. (2015) demonstrated that interactions between ecosystem engineers (seagrass and lugworm), in concert with abiotic conditions, dictate the distribution of engineers and associated communities.

Understanding these interactions is of crucial importance if we are to understand how ecosystem engineers will influence their environment in the future, and what the consequences for human populations are.

4 Importance of Mudflats Ecosystem Engineers for Human Populations: Ecosystem Services

4.1 *Definition and Examples of Ecosystem Services*

The most commonly-accepted definition of ecosystem services (or ecological services) is that of the Millennium Ecosystem Assessment (MEA 2003), which states that it refers to the benefits that humans derive from ecosystems. The idea that notions such as biodiversity and ecosystem services could be assessed in environmental and economic terms emerged in the 1970s–1980s, and was further popularized by the MEA. The main postulate was clearly anthropocentric, as it stated that monetary valuation should help society to familiarise itself with abstract ecological concepts of biodiversity that are mostly regarded as meaningless or non-understandable by the general public. Since then, policy makers have increasingly recognised the role of environmental valuation for environmental management and conservation purposes; and the number of economic studies seeking to value biodiversity has increased simultaneously. Research effort has increased in all fields, including the marine environment; numerous marine habitats, species, or ecosystems services have been studied, and it has been shown that a decline in biodiversity could result in a change in the provision of goods and services by marine ecosystems, including reduced resilience and resistance to environmental change, declining marine environmental health, reduced fisheries potential, and loss of recreational opportunities (Beaumont et al. 2008).

At around the same time period, mudflats were largely regarded as "unvegetated" habitats, and therefore considered non-productive, compared with vegetated mudflats, such as salt marshes or seagrass beds. It is likely that this restrictive view contributed to diverting the attention of numerous scientists and economists toward apparently more diverse and/or endangered habitats/species, until the profile of its "secret garden" (i.e. microphytobenthos) was raised (MacIntyre et al. 1996; Miller et al. 1996). In addition, the relationship between diversity of microphytobenthos and ecosystem function was recognised only relatively recently (Forster et al. 2006).

In the terrestrial ecosystem, vegetative cover is widely considered to play a key role in regulating and supporting services related to soil retention and prevention of landslides (Millenium Ecosystem Assessment 2003). *De facto*, it is difficult to believe that bare mud contributes to erosion control and therefore coastal protection, even though microphytobenthos is now considered a major biogeomorphological player in mudflats (see Chaps. 2, 4 and 8). Its ability to enhance sediment stability and influence erosion threshold of intertidal sediments, as well as sediment transport, has been studied extensively (Paterson 1989; Black et al. 2002; Tolhurst et al. 2008; Gerbersdorf et al. 2009; Lubarsky et al. 2010), and is well recognised (Stal 2010). Coastal protection is an important ecosystem service, as the cost of coastal erosion is estimated to reach hundreds of millions of dollars each year in the USA alone (Heinz Centre for Science Economics and the Environment 2000).

Table 10.1 Ecosystem services in the mudflat, and links to ecosystem engineers

Type of ES	Ecosystem service (ES)	Example from the mudflat	Example of mudflat ecosystem engineers directly or indirectly involved in ES
Provisioning	Food production	Fishing, seafood gathering by hand, aquaculture (oysters, mussels, shellfish production) See also Chap. 13	Microphytobenthos (Passarelli et al. 2014) directly as a food source or indirectly at the base of the food web
	Genetic resources: Sources of biological material and products	Genetic variability between individuals within a population	All ecosystem engineers
	Biochemicals	Bioactive compounds	Benthic microalgae and bacteria and their EPS (Lubarsky et al. 2010)
Regulating	Climate regulation	Greenhouse gas regulation	All ecosystem engineers, for instance diatoms
	Waste treatments/ water purification; recovery or removal of nutrients	Nitrogen fixation and removal, P, Fe, Sulphate and methane cycle. See also Chap. 4	Bacterial assemblages of the sediment
Cultural	Recreational activities	Eco-tourism, fishing (see Chap. 12), seafood gathering, seabird watching	Emblematic ecosystem engineers. Ex: honeycomb worm
	Cultural	Educational, scientific value	Emblematic ecosystem engineers
Supporting	Erosion control and sediment retention; coastal protection	Biostabilisation of sediments by microbes	Benthic microalgae and bacteria and their EPS (Lubarsky et al. 2010), engineers forming biogenic structures
	Primary production		Benthic microalgae, seaweeds
	Nutrient cycling	See Chap. 4	Examples include sulphate-reducing bacteria, nitrifying/ denitrifying bacteria. . .

Based on the framework given by the MEA (Millenium Ecosystem Assessment 2003), we identified the following ecosystem services provided by mudflats (Table 10.1; Costanza et al. 1997; Markov and Nedkov 2016).

4.1.1 Food Production

Food production includes the vast range of food products derived from plants, animals, and microbes, as well as materials derived from mudflats. The trophic input of mudflat benthic invertebrates (meiofauna, macrofauna) is largely based on microphytobenthic production. The diet of mudflat fishes (including important commercial species) depends on their life cycle. In general, larvae and/or juveniles feed on zooplankton or harpacticoid copepods (Kanou et al. 2004), later switching to other prey items (e.g. gammaridean amphipods, mysids, polychaetes, detritus, bivalves and fishes). In some cases, mudflat fishes' food webs may be supported predominantly via carbon from adjacent habitats (e.g. macroalgae, seagrasses) and not *in situ* meiofauna or MPB (Project 1997; Melville and Connolly 2005). For more detail on food production, see Chaps. 13 and 14.

4.1.2 Genetic Resources

The genetic variability between individuals within a population of a given species, corresponds to the diversity of genetic resources for that species. Alternatively, the genetic variability within a given population in a biological community forms the genetic resources for an ecosystem. Mudflats are tidally-influenced ecosystems, that are naturally characterised by strong physical and geochemical gradients, under varied geomorphological settings, which give rise to a multitude of habitats and niches. Environment fluctuations can indeed have a direct influence on genetic interactions among traits, as well as the genetic variance in traits themselves (Hedrick et al. 1976; Sgrò and Hoffmann 2004). For instance, the diatoms as a group are characterized by a large variety of sizes and shapes among species, which allows them a large spectrum of interactions with the environment and of niche exploitations. Environmental fluctuations in mudflats are thus a potential source of genome variability; however, few studies have dealt with this issue.

4.1.3 Biochemicals, Natural Medicines, and Pharmaceuticals

Many medicines, bioactive molecules for human health and plant health, biocides, food additives such as alginates, and biological materials are derived from marine ecosystems. Marine polysaccharides have been exploited for many years, and are mainly used as texturing agents in the agri-food and cosmetics industries (principally hydrocolloids, which increase viscosity and give a gel-like texture; Agasse et al. 2015). For example, those extracted from macroalgae represent 40% of the global market of hydrocolloids, which is valued at $4.4 billion. Europe represents 30% of the market (Kraan 2012). The main polysaccharides are alginates, agars and carrageenan. More recently, microalgae, bacteria and cyanobacteria have been considered an interesting source of polysaccharides. Mudflat benthic bacteria and diatoms are potentially an important source of bioactive molecules for the pharmaceutical industry, including anti-cancer molecules, antivirals, or functional foods such as the polyunsaturated fatty acids of microalgae (eicosapentaenoic acid: EPA, docosahexaenoic acid: DHA), carotenoids, astaxanthin, beta-carotene, and lutein.

4.1.4 Climate Regulation

Estimates of the annual benthic net production rate obtained through *in situ* measurements of carbon dioxide fluxes at the benthic community level, have been proposed for diverse tidal sedimentary systems including mudflats (Migné et al. 2004; Spilmont et al. 2005; Hubas and Davoult 2006; Spilmont et al. 2006; Davoult et al. 2009). Intertidal muddy sediments are characterized by large fluctuations in environmental parameters in response to the superimposition of diurnal and tidal cycles, which induces a variability of both production and respiration processes over a number of time scales (day, tide, season, year). These systems are generally considered heterotrophic (i.e. net CO_2 degassing; Borges 2005; Migné et al. 2009). Ecosystem engineers, and especially microphytobenthos, play a key role in regulating CO_2 fluxes in these ecosystems. Generally speaking, carbon is fixed by microphytobenthos and transferred very quickly to heterotrophic bacteria and higher trophic levels (Middelburg et al. 2000), but there is currently a large gap in knowledge about the relationships between microbial diversity and C fluxes.

4.1.5 Eutrophication Control

Microphytobenthic biofilms drive and modulate fluxes of carbon (C) and nitrogen (N) across the sediment-water interface, thus playing a pivotal role in the coastal filter function, affecting coastal eutrophication and water quality (Hochard et al. 2010).

4.1.6 Cultural Services: Recreation, Aesthetics, Educational, etc.

As pointed out by Rees et al. (2010), the mudflat recreational industry (e.g. fishing, see Chap. 13 and seabird watching, see Chap. 12) depends directly or indirectly on the presence of natural marine resources. In their study, the marine leisure and recreation industry was valued using both monetary and non-monetary methods (see also Chap. 13). In addition, they showed that the leisure and recreation industry are dependent on biodiversity.

As can be seen from Table 10.1 and from the numerous examples developed here, the links between ecosystem engineers and services are numerous (Fig. 10.6); this is to be expected from the crucial roles of ecosystem engineers in creating and maintaining habitat in stressful systems such as mudflats. Due to the particular population dynamics of ecosystem engineers (see Sect. 3.2), driven by numerous interactions and feedbacks, and to the numerous anthropogenic influences on coasts and mudflats, the management of populations of ecosystem engineers is both a

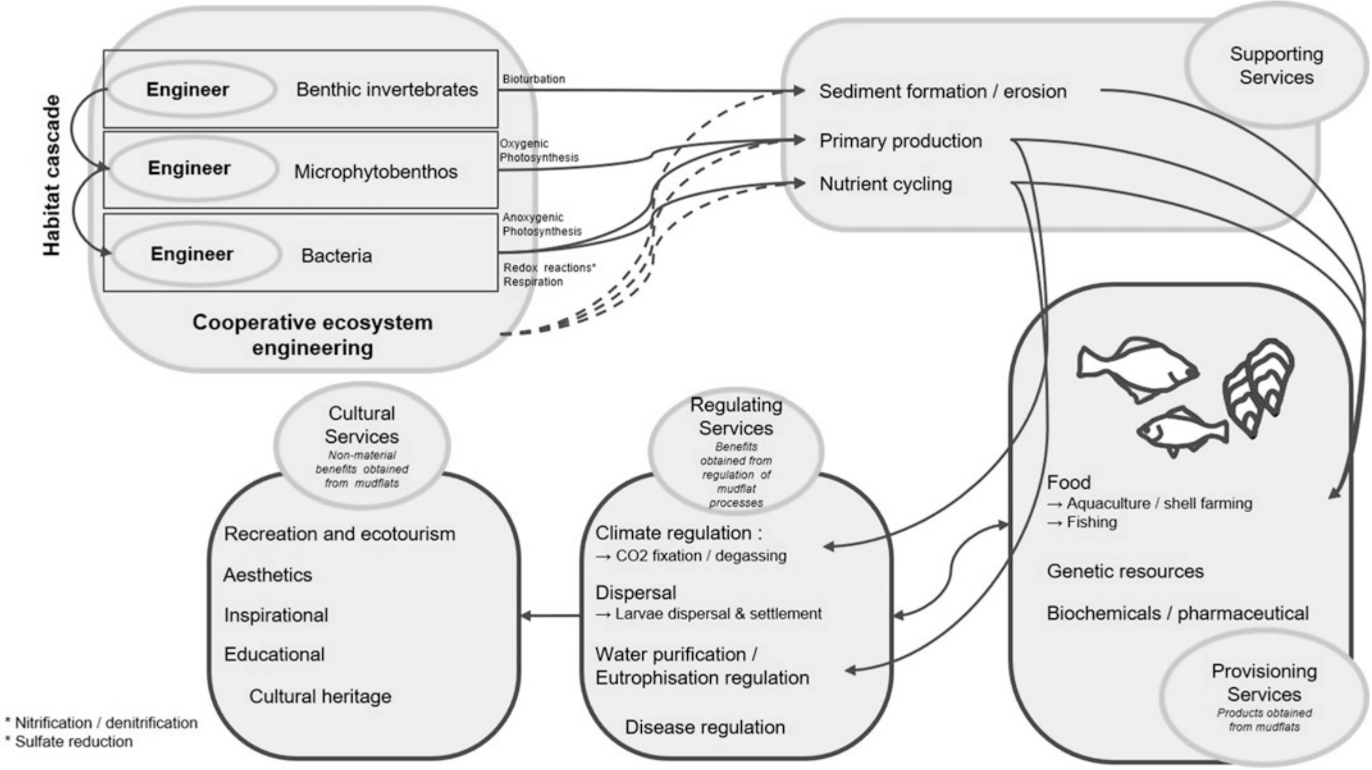

Fig. 10.6 Ecosystem engineers and ecosystem services on the mudflat. See text for details.

challenge and a necessity, if we are to continue to enjoy the services provided by these systems.

4.2 Estimation of Service Value and Implications for Mudflat Management

Decision making, in terms of environmental conservation, becomes political, an often-uncomfortable truth for conservation scientists and ecologists (Borja et al. 2017). The best available scientific knowledge should feed into political decision-making, but the economy is also a powerful force in shaping policy. As described above, one mechanism for realising/emphasising the importance of coastal habitats is to formalise the valuation of the ecosystem services provided. This supports economic valuations becoming more holistic, incorporating both direct and indirect benefits. A detailed review of the methodology is beyond the scope of this chapter (see Hanley and Barbier 2009), but it is important for the next generation of ecological scientists to understand the decision-making processes to help make the best-case possible for management decisions.

Direct economic benefits are relatively straightforward to assess, such as local fisheries and the benefits in terms of direct financial return (see Chap. 13). Others are more complex, and include aspects such as the aesthetic and health benefits of regular outdoor excursions, the denaturing of xenobiotic compounds or the turnover of nutrients. These services are hard to value because there is often no “market” that supports the “trade”; the economic valuation then relies on much more abstract methods such as determining the “willingness to pay” of the relevant human population for particular outcome. A recent example by Pakalniete et al. (2017) considered the willingness of Latvian citizens to “pay” for improving the ecological status of habitats around the Baltic coast. Using highly-structured questionnaires, and a discrete choice (DC) methodology, based on a proposed increased in taxation as the suggested funding mechanism, the sample group was supportive of coastal habitat protection. A similar approach can be applied to less glamorous systems such as mudflats. However, this type of valuation may also have limitations. The level of knowledge of the individual making the assessment may affect the outcome, and charismatic habitats, such as rainforests, may attract higher valuation than less-charismatic systems such as mudflats, despite delivering similar services. Therefore, while methods such as DC are not foolproof, and are widely discussed, they are nevertheless an important step toward promoting the value that society places on ecosystem services. The more information that can be provided about systems such as mudflats, the more likely that evidence in support of good management approaches can be sustained into the future.

5 Conclusion

Mudflats and other coastal systems are largely impacted by human populations, which build on and modify the coastline, release nutrients and pollutants into coastal waters, introduce new species that can become invasive, and collect mudflat organisms for consumption. Because of the crucial roles of ecosystem engineers in controlling diversity and ecosystem functions in mudflats, understanding how mudflat engineers influence and interact with their environment is necessary in order to guide good management practices that will ensure the provision of ecosystem services by mudflats in the future.

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References

Agasse A, Boyen C, Durand P, Chaussade M (2015) Polysaccharides marins pour les santés végétale, animale et humaine. In: Paper presented at the Colloque Polymerix 2015, Rennes (France)

Altieri AH, Silliman BR, Bertness MD (2007) Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. Am Nat 169:195–206

Alvarez MF, Addino M, Iribarne O, Botto F (2015) Combined engineering effects of clams and crabs on infaunal assemblages and food availability in intertidal systems. Mar Ecol Prog Ser 540:57–71

Alves RMS, Vanaverbeke J, Bouma TJ, Guarini JM, Vincx M, Van Colen C (2017) Effects of temporal fluctuation in population processes of intertidal *Lanice conchilega* (Pallas, 1766) aggregations on its ecosystem engineering. Estuar Coast Shelf Sci 188:88–98

Andersen TJ, Jensen KT, Lund-Hansen L, Mouritsen KN, Pejrup M (2002) Enhanced erodibility of fine-grained marine sediments by *Hydrobia ulvae*. J Sea Res 48:51–58

Bateman DC, Bishop MJ (2017) The environmental context and traits of habitat-forming bivalves influence the magnitude of their ecosystem engineering. Mar Ecol Prog Ser 563:95–110

Beaumont NJ, Austen MC, Mangi SC, Townsend M (2008) Economic valuation for the conservation of marine biodiversity. Mar Pollut Bull 56:386–396

Bell SS (1985) Habitat complexity of polychaete tube-caps: influence of architecture on dynamics of a meioepibenthic assemblage. J Mar Res 43:647–671

Berke SK (2010) Functional groups of ecosystem engineers: a proposed classification with comments on current issues. Integr Comp Biol 50:147–157

Bertness MD (1984) Habitat and community modification by an introduced herbivorous snail. Ecology 65:370–381

Bertness MD, Leonard GH (1997) The role of positive interactions in communities: lessons from intertidal habitats. Ecology 78:1976–1989

Black KS, Tolhurst TJ, Paterson DM, Hagerthey SE (2002) Working with natural cohesive sediments. J Hydraul Eng 128:2–8

Boldina I, Beninger PG (2014) Fine-scale spatial distribution of the common lugworm *Arenicola marina*, and effects of intertidal clam fishing. Estuar Coast Shelf Sci 143:32–40

Boogert NJ, Paterson DM, Laland KN (2006) The implications of niche construction and ecosystem engineering for conservation biology. Bioscience 56:570–578

Borges AV (2005) Do we have enough pieces of the jigsaw to integrate CO_2 fluxes in the coastal ocean? Estuaries 28:3–27

Borja A, Elliot M, Uyarra MC, Carstensen J, Mea M (2017) Editorial: Bridging the gap between policy and science in assessing the health status of marine ecosystems. Front Mar Sci 4:32

Bouma TJ, Olenin S, Reise K, Ysebaert T (2009) Ecosystem engineering and biodiversity in coastal sediments: posing hypotheses. Helgol Mar Res 63:95–106

Boyer KE, Fong P (2005) Co-occurrence of habitat-modifying invertebrates: effects on structural and functional properties of a created salt marsh. Oecologia 143:619–628

Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. Trends Ecol Evol 18:119–125

Caliman A, Carneiro LS, Bozelli RL, Farjalla VF, Esteves FA (2011) Bioturbating space enhances the effects of non-additive interactions among benthic ecosystem engineers on cross-habitat nutrient regeneration. Oikos 120:1639–1648

Catling DC, Claire MW (2005) How Earth’s atmosphere evolved to an oxic state: a status report. Earth Planet Sci Lett 237:1–20

Chennu A, Volkenborn N, de Beer D, Wethey DS, Woodin SA, Polerecky L (2015) Effects of bioadvection by *Arenicola marina* on microphytobenthos in permeable sediments. PLoS One 10:e0134236

Costanza R, d’Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, van den Belt M (1997) The value of the world’s ecosystem services and natural capital. Nature 387:253–260

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the roles of ecosystem engineers. Oikos 97:153–166

Cruz Sueiro M, Bortolus A, Schwindt E (2011) Habitat complexity and community composition: relationships between different ecosystem engineers and the associated macroinvertebrate assemblages. Helgol Mar Res 65:467–477

Daborn GR, Amos CL, Brylinsky M, Christian H, Drapeau G, Faas RW, Grant J, Long B, Paterson DM, Perillo GME, Piccolo MC (1993) An ecological cascade effect: migratory birds affect stability of intertidal sediments. Limnol Oceanogr 38:225–231

Dade WB, Davis JD, Nichols PD, Nowell ARM, Thistle D, Trexler MB, White DC (1990) Effects of bacterial exopolymer adhesion on the entrainment of sand. Geomicrobiol J 8:1–16

Darwin CMA (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London

Davoult D, Migné A, Créach A, Gévaert F, Hubas C, Spilmont N, Boucher G (2009) Spatio-temporal variability of intertidal benthic primary production and respiration in the western part of the Mont Saint-Michel Bay (Western English Channel, France). Hydrobiologia 620:163–172

Defew EC, Tolhurst TJ, Paterson DM, Hagerthey SE (2003) Can the stability of intertidal sediments be predicted from proxy parameters? An *in situ* investigation. In: Raffaelli D, Solan M, Paterson DM, Buck AL, Pomfret JR (eds) The estuaries and coasts of north-east Scotland. Coastal Zone Topics, 5. Estuarine and Coastal Sciences Association, Aberdeen, pp 61–70

Dodd M, Papineau D, Grenne T, Slack JF, Rittner M, Pirajino F, O'Neil J, Little CTS (2017) Evidence for early life in Earth’s oldest hydrothermal vent precipitates. Nature 543:60–64

Eckman JE, Duggins DO, Siddon CE (2003) Current and wave dynamics in the shallow subtidal: implications to the ecology of understory and surface-canopy kelps. Mar Ecol Prog Ser 265: 45–56

Eklöf JS, Van der Heide T, Donadi S, van der Zee EM, O’Hara R, Eriksson BK (2011) Habitat-mediated facilitation and counteracting ecosystem engineering interactively influence ecosystem responses to disturbance. PLoS One 6:e23229

Eklöf JS, Donadi S, van der Heide T, van der Zee EM, Eriksson BK (2015) Effects of antagonistic ecosystem engineers on macrofauna communities in a patchy, intertidal mudflat landscape. J Sea Res 97:56–65

Extended Evolutionnary Synthesis (2016) http://extendedevolutionarysynthesis.com/about-the-ees/. Accessed 17 Jan 2017

Fonseca MS, Fisher JS, Zieman JC, Thayer GW (1982) Influence of the seagrass, *Zostera marina* L., on current flow. Estuar Coast Shelf Sci 15:351–358

Forster S, Graf G (1995) Impact of irrigation on oxygen flux into the sediment: intermittent pumping by *Callianasse subterranea* and "piston-pumping" by *Lanice conchilega*. Mar Biol 123:335–346

Forster RM, Créach V, Sabbe K, Vyverman W, Stal LJ (2006) Biodiversity-ecosystem function relationship in microphytobenthic diatoms of the Westerchelde estuary. Mar Ecol Prog Ser 311: 191–201

Friedrichs M, Graf G, Springer B (2000) Skimming flow induced over a simulated polychaete tube lawn at low population densities. Mar Ecol Prog Ser 192:219–228

Friedrichs M, Leipe T, Peine F, Graf G (2009) Impact of macrozoobenthic structures on near-bed sediment fluxes. J Mar Syst 75:336–347

Ganthy F, Sottolichio A, Verney R (2013) Seasonal modification of tidal flat sediment dynamics by seagrass meadows of *Zostera noltii* (Bassin d'Arcachon, France). J Mar Syst 109-110: S233–S240

Gerbersdorf SU, Bittner R, Lubarsky HV, Manz W, Paterson DM (2009) Microbial assemblages as ecosystem engineers of sediment stability. J Soils Sediments 9:640–652

Gribben PE, Byers JE, Clements M, McKenzie LA, Steinberg PD, Wright JT (2009) Behavioural interactions between ecosystem engineers control community species richness. Ecol Lett 12: 1127–1136

Hagerthey SE, Defew EC, Paterson DM (2002) Influence of *Corophium volutator* and *Hydrobia ulvae* on intertidal benthic diatom assemblages under different nutrient and temperature regimes. Mar Ecol Prog Ser 245:47–59

Hall N (2007) Advanced sequencing technologies and their wider impact in microbiology. J Exp Biol 210:1518–1525

Hanley N, Barbier E (2009) Pricing nature: cost-benefit analysis and environmental policy. Edward Elgar, Cheltenham

Hastings A, Byers JE, Crooks JA, Cuddington K, Jones CG, Lambrinos JG, Talley TS, Wilson WG (2007) Ecosystem engineering in space and time. Ecol Lett 10:153–164

Hedrick PW, Ginevan ME, Ewing EP (1976) Genetic polymorphism in heterogeneous environments. Annu Rev Ecol Evol Syst 7:1–32

Heinz Centre for Science Economics and the Environment (2000) Evaluation of erosion hazards. Report for Federal Emergency Management Agency, Washington, DC

Hochard S, Pinazo C, Grenz C, Burton Evans JL, Pringault O (2010) Impact of microphytobenthos on the sediment biogeochemical cycles: a modelling approach. Ecol Model 221:1687–1701

Hubas C, Davoult D (2006) Does seasonal proliferation of *Enteromorpha sp.* affect the annual benthic metabolism of a small macrotidal estuary? (Roscoff Aber Bay, France). Estuar Coast Shelf Sci 70:287–296

Jesus B, Brotas V, Marani M, Paterson DM (2005) Spatial dynamics of microphytobenthos determined by PAM fluorescence. Estuar Coast Shelf Sci 65:30–42

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957

Kanou K, Sano M, Kohno H (2004) Food habits of fishes on unvegetated tidal mudflats in Tokyo Bay, central Japan. Fish Sci 70:978–987

Kéfi S, Berlow EL, Wieters EA, Navarrete SA, Petchey OL, Wood SA, Boit A, Joppa LN, Lafferty KD, Williams RJ, Martinez ND, Menge BA, Blanchette CA, Iles AC, Brose U (2012) More than a meal... integrating non-feeding interactions into food webs. Ecol Lett 15:291–300

Kraan S (2012) Algal polysaccharides, novel applications and outlook In: Chang C-F (ed) Carbohydrates – comprehensive studies on glycobiology and glycotechnology. INTECH, Croatia

Krumbein WE, Paterson DM, GAE Z (2003) Fossil and recent biofilms. A natural history of life on Earth. Kluwer, Dordrecht

Laland K, Uller T, Feldman M, Sterelny K, Müller GB, Moczek A, Jablonka E, Odling-Smee J, Wray GA, Hoekstra HE, Futuyama DJ, Lenski RE, Mackay TFC, Schulter D, Strassmann JE (2014) Does evolutionary therory need a rethink? Nature 514:161–164

Lawton JH, Jones CG (1995) Linking species and ecosystems: organisms as ecosystem engineers. In: Jones CG, Lawton JH (eds) Linking species and ecosystems. Chapman & Hall, London, pp 141–150

Lee SY, Fong CW, Wu RSS (2001) The effects of seagrass (*Zostera japonica*) canopy structure on associated fauna: a study using artificial seagrass units and sampling of natural beds. J Exp Mar Biol Ecol 259:23–50

Lejart M, Hily C (2011) Differential response of benthic macrofauna to the formation of novel oyster reefs (*Crassostrea gigas*, Thunberg) on soft and rocky substrate in the intertidal of the Bay of Brest, France. J Sea Res 65:84–93

Lubarsky HV, Hubas C, Chocholek M, Larson F, Manz W, Paterson DM, Gerbersdorf SU (2010) The stabilisation potential of individual and mixed assemblages of natural bacteria and microalgae. PLoS One 5:e13794

Luckenbach MW (1986) Sediment stability around animal tubes: the roles of hydrodynamic processes and biotic activity. Limnol Oceanogr 31:779–787

MacIntyre HL, Geider RJ, Miller DC (1996) Microphytobenthos: the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats.1. Distribution, abundance and primary production. Estuaries 19:186–201

Malarkey J, Baas JH, Hoppe JA, Aspden RJ, Parsons DR, Peakall J, Paterson DM, Schindler RJ, Ye L, Lichtman ID, Bass SJ, Davies AG, Manning AJ, Thorne PD (2015) The pervasive role of biological cohesion in bedform development. Nat Commun 6:6257

Manzenrieder H (1983) Retardation of initial erosion under biological effects in sandy tidal flats. Tech University Braunschweig, Brunswick

Markov B, Nedkov S (2016) Mapping of erosion regulation ecosystem services. In: Bandrova T, Konecny M (eds) 6th International conference on cartography and GIS. Albena, Bulgaria, pp 97–108

Meadows PS, Meadows A (1991) The geotechnical and geochemical implications of bioturbation in marine sedimentary ecosystems. In: Meadows PS, Meadows A (eds) The environmental impact of burrowing animals and animal burrows. Oxford Science Publications, Oxford, pp 157–181

Meadows PS, Tait J, Hussain SA (1990) Effects of estuarine infauna on sediment stability and particle sedimentation. Hydrobiologia 190:263–266

Meadows PS, Meadows A, Murray JMH (2012) Biological modifiers of marine benthic seascapes: their role as ecosystem engineers. Geomorphology 157:31–48

Melville AJ, Connolly RM (2005) Food webs supporting fish over subtropical mudflats are based on transported organic matter not in situ microalgae. Mar Biol 148:363–371

Middelburg JJ, Barranguet C, Boschker HTS, Herman PMJ, Moens T, Heip CHR (2000) The fate of intertidal microphytobenthos carbon: an in situ ^{13}C-labeling study. Limnol Oceanogr 45:1224–1234

Migné A, Spilmont N, Davoult D (2004) In situ measurements of benthic production during emersion: seasonal variations and annual production in the Bay of Somme (eastern English Channel, France). Cont Shelf Res 24:1437–1449

Migné A, Spilmont N, Boucher G, Denis L, Hubas C, Janquin MA, Rauch M, Davoult D (2009) Annual budget of benthic production in Mont Saint-Michel Bay considering cloudiness, microphytobenthos migration, and variability of respiration rates with tidal conditions. Cont Shelf Res 29:2280–2285

Millenium Ecosystem Assessment (2003) Ecosystems and human well-being: a framework for assessment. The Millenium Ecosystem Assessment Series. Island Press, Washington, DC

Miller DC, Geider RJ, MacIntyre HL (1996) Microphytobenthos: the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats. 2. Role in sediment stability and shallow-water food webs. Estuaries 19:202–212

Murray JMH, Meadows A, Meadows PS (2002) Biogeomorphological implications of microscale interactions between sediment geotechnics and marine benthos: a review. Geomorphology 47: 15–30

Odling-Smee FJ, Laland KN, Feldman MW (2003) Niche construction: the neglected process in evolution. Princeton Univerity Press, Princeton, NJ

Pakalniete K, Aigars J, Czajkowski M, Strake S, Zawojska E, Hanley N (2017) Understanding the distribution of economic benefits from improving coastal and marine ecosystems. Sci Total Environ 584-585:29–40

Passarelli C, Hubas C, Nicolas Segui A, Grange J, Meziane T (2012a) Surface adhesion of microphytobenthic biofilms is enhanced under *Hediste diversicolor* (O. F. Müller) trophic pressure. J Exp Mar Biol Ecol 438:52–60

Passarelli C, Olivier F, Paterson DM, Hubas C (2012b) Impacts of biogenic structures on benthic assemblages: microbes, meiofauna, macrofauna and related ecosystem functions. Mar Ecol Prog Ser 465:85–97

Passarelli C, Olivier F, Paterson DM, Meziane T, Hubas C (2014) Organisms as cooperative ecosystem engineers in intertidal flats. J Sea Res 92:92–101

Paterson DM (1989) Short-term changes in the erodibility of intertidal cohesive sediments related to the migratory behavior of epipelic diatoms. Limnol Oceanogr 34:223–234

Paterson DM, Black KS (1999) Water flow, sediment dynamics and benthic biology. Adv Ecol Res 29:155–193

Paterson DM, Aspden RJ, Visscher PT, Consalvey M, Andres MS, Decho AW, Stolz J, Reid RP (2008) Light-dependant biostabilisation of sediments by stromatolite assemblages. PLoS One 3: e3176

Paterson DM, Fortune I, Aspden RJ, Black KS (2017) Intertidal mudflats: form and function. In: Perillo G, Wolanski E, Cahoon D, Brinson M (eds) Coastal wetlands: an integrated ecosystem approach. Elsevier Academic, Amsterdam

Powers SP, Rouhani S, Baker MC, Roman H, Grabowski JH, Scyphers SB, Willis JM, Hester MW (2017) Ecosystem services are lost when faciliation between two ecosystem engineers is compromised by oil. Mar Ecol Prog Ser 576:189–202

Project UMS (1997) http://www.ukmarinesac.org.uk/communities/intersand-mud/ism5_4.htm. Accessed 21 July 2017

Rabaut M (2009) *Lanice conchilega*, fisheries and marine conservation: towards an ecosystem approach to marine management. Ghent University, Ghent

Rees SE, Rodwell LD, Attrill MJ, Austen MC, Mangi SC (2010) The value of marine biodiversity to the leisure and recreation industry and its application to marine spatial planning. Mar Policy 34:868–875

Reise K (2002) Sediment mediated species interactions in coastal waters. J Sea Res 48:127–141

Rigolet C, Dubois SF, Thiébaut E (2014) Benthic control freaks: effects of the tubiculous amphipod *Haploops nirae* on the specific diversity and functional structure of benthic communities. J Sea Res 85:413–427

Sanders D, Jones CG, Thébault E, Bouma TJ, van der Heide T, van Belzen J, Barot S (2014) Integrating ecosystem engineering and food webs. Oikos 123:513–524

Sgrò CM, Hoffmann AA (2004) Genetic correlations, tradeoffs and environmental variation. Heredity 93:241–248

Shields A (1936) Anwendung der Aehnlichkeitsmechanik und der Turbulenzforschung auf die Geschiebebewegung. Technical University Berlin, Berlin

Spilmont N, Migné A, Lefebvre A, Artigas LF, Rauch M, Davoult D (2005) Temporal variability of intertidal benthic metabolism under emersed conditions in an exposed sandy beach (Wimereux, eastern English Channel, France). J Sea Res 53:161–167

Spilmont N, Davoult D, Migné A (2006) Benthic primary production during emersion: in situ measurements and potential primary production in the Seine Estuary (English Channel, France). Mar Pollut Bull 53:49–55

Stal LJ (2010) Microphytobenthos as a biogeomorphological force in intertidal sediment stabilization. Ecol Eng 36:236–245

Summerhayes SA, Bishop MJ, Leigh A, Kelaher BP (2009) Effects of oyster death and shell disarticulation on associated communities of epibiota. J Exp Mar Biol Ecol 379:60–67

Thomsen MS, Wernberg T, Altieri A, Tuya F, Gulbransen D, McGlathery KJ, Holmer M, Silliman BR (2010) Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integr Comp Biol 50:158–175

Tolhurst TJ, Consalvey M, Paterson DM (2008) Changes in cohesive sediment particles associated with the growth of a diatom biofilm. Hydrobiologia 596:225–239

Van Colen C, Thrush SF, Parkes S, Harris R, Woodin SA, Wethey DS, Pilditch CA, Hewitt JE, Lohrer AM, Vincx M (2015) Bottom-up and top-down mechanisms indirectly mediate interactions between benthic biotic ecosystem components. J Sea Res 98:42–48

Van De Koppel J, Herman PMJ, Thoolen P, Heip CHR (2001) Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. Ecology 82:3449–3461

van der Heide T, van Nes EH, Geerling GW, Smolders AJP, Bouma TJ, van Katwijk MM (2007) Positive feedbacks in seagrass ecosystems: implications for success in conservation and restoration. Ecosystems 10:1311–1322

Volkenborn N, Reise K (2006) Lugworm exclusion experiment: responses by deposit feeding worms to biogenic habitat transformations. J Exp Mar Biol Ecol 330:169–179

Volkenborn N, Reise K (2007) Effects of *Arenicola marina* on polychaete functional diversity revealed by large-scale experimental lugworm exclusion. J Sea Res 57:78–88

Volkenborn N, Hedtkamp SIC, van Beusekom JEE, Reise K (2007) Effects of bioturbation and bioirrigation by lugworms (*Arenicola marina*) on physical and chemical sediment properties and implications for intertidal habitat succession. Estuar Coast Shelf Sci 74:331–343

Volkenborn N, Robertson DM, Reise K (2009) Sediment destabilizing and stabilizing bio-engineers on tidal flats: cascading effects of experimental exclusion. Helgol Mar Res 63:27–35

Web of Science (2017) webofknowledge.com. Accessed 21 July 2017

Wethey DS, Woodin SA, Hilbish TJ, Jones SJ, Lima FP, Brannock PM (2011) Response of intertidal populations to climate: effects of extreme events versus long term change. J Exp Mar Biol Ecol 400:132–144

Whitman WB, Coleman DC, Wiebe WJ (1998) Prokaryotes: the unseen majority. PNAS 95: 6578–6583

Wilson JB, Agnew DQ (1992) Positive-feedback switches in plant communities. Adv Ecol Res 23: 263–336

Woodin SA (1978) Refuges, disturbance, and community structure: a marine soft-bottom example. Ecology 59:274–284

Woodin SA, Jackson JBC (1979) Interphyletic competition among marine benthos. Am Zool 19: 1029–1043

Zühlke R (2001) Polychaete tubes create ephemeral community patterns: *Lanice conchilega* (Pallas, 1766) associations studied over six years. J Sea Res 46:261–272

Zühlke R, Blome D, van Bernem KH, Dittmann S (1998) Effects of the tube-building polychaete *Lanice conchilega* (Pallas) on benthic macrofauna and nematodes in an intertidal sandflat. Senckenberg Marit 29:131–138

Chapter 11
Biological Invasions of Mudflats

Jennifer Ruesink

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Abstract Thousands of marine species have been moved around the globe by human activities, at increasing rates over the past century. Many of these species (here termed "alien") have taken up residence on mudflats. How are mudflats changing as a consequence of this biological reshuffling? The preceding chapters document mudflats as productive environments with strong species interactions, which both shape and are shaped by the physical environment. The same pattern appears when alien species are added to the system. Attributes of the physical environment play strong roles in determining the success of different alien species on mudflats, while many high-impact alien species create biogenic structure and/or

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modify sediment stability. Above-ground habitat complexity from alien vegetation or reefs can facilitate both alien and native species, but it can also interfere with infauna and birds that depend on an unimpeded sediment interface or particular grain size. Most mudflat aliens, however, simply add to the diversity and linkages of native communities. The biological changes from invasions are occurring within a context of other global changes, all likely to interact because alien species can be promoted by anthropogenic hard structure and warming temperatures.

1 Introduction

1.1 Chapter Overview

The story of biological invasions of mudflats bears much in common with the ecological understanding of biological invasions more generally. Fundamental questions include how new species arrive, from where, what intrinsic and extrinsic factors influence their probability of establishment and dynamics of spread, and how the recipient ecosystem is changed. Frequently, the answers to these questions bear on management interventions. For example, what practices could be encouraged to slow global homogenization, so that not every place on the planet contains the same suite of common species (Arrival stage)? Does a species have weak links in its life cycle where interventions could reduce population growth or density (Increase and spread stage)? When many aliens are present, which ones have the greatest ecological or economic consequences for management prioritization? Alternatively, there remains interest in finding species elsewhere to serve functional roles that are not presently being met, e.g. following degradation of conditions for native species (Impact stage). Although these topics are of general concern in invasion biology, mudflats are particularly interesting from a perspective of biological invasions because:

- Many mudflats are situated in wave-protected embayments close to ports where propagule pressure figures prominently in establishment of new species. At the same time infaunal meio- and macro-fauna require specialized identification, leading to challenges in simply documenting the pace of change.
- Ecosystem transformation, akin to a state shift, can be caused by biological invasions. Mudflats appear particularly susceptible to such transformation due to their geomorphological position at the dynamic land-water interface and due to single ecosystem engineers that add above-ground structure, stabilize or destabilize sediments. After all, mudflats are flat, but species that add extra structural complexity can live on them.
- Context-dependence emerges in two ways on mudflats: first, because infaunal and epifaunal communities depend on different habitat attributes, which could result in one community being enhanced at the expense of the other (context-

dependence by functional group); and second, because reef-forming species may have different effects when they aggregate on mudflats than when they colonize rocky habitats (context-dependence by habitat).
- Although food web disruptions are documented following biological invasions of other habitats, trophic and competitive effects of alien species on mudflats tend to be weak or play out at population- rather than community- or ecosystem-levels.

This chapter builds the evidence for each of these ecological concepts, with a larger goal of determining how the genesis of novel ecosystems through invasion threatens (or not) the historic functional roles of mudflats. For the purposes of evaluating these concepts, some examples are included that stretch the definition of mudflat to deeper and/or sandier sediments. At the same time, many other forces of global change also contribute to novel ecosystems in low-energy intertidal areas, including warming, sea level rise, and the hardening of shorelines from anthropogenic structures. These changes are on the physical end of a spectrum of human impacts, in contrast to biological invasions, which directly determine the members of the biological community.

1.2 What Is a Biological Invasion, Anyway?

Biological invasions have occurred on mudflats throughout the world. The term "invasion" has a negative connotation, indicating that something both does not belong and is disruptive. Yet invasion biology as a discipline treats these topics as hypotheses, not accusations, asking questions about origin and impact. It is important to recognize the existence of social values associated with species of different original range and different functional roles, and also to recognize that these social values are mutable (Box 11.1). Because of social differences in how species are valued, clear terminology aids the science of invasion biology. "Status" of a species is attributed by humans, whereas "traits" are measured (Costello et al. 2015). Invasion "status" thus emerges in part from societal values and anthropocentric, subjective judgments and is subject to change over time (Davis and Thompson 2000). Given such caveats, terminological care is needed to address this chapter's topic of species occupying mudflats where they were not historically present. When a species has been moved outside its native range through human agency, and it has survived and reproduced, it is typically termed: introduced, alien, non-indigenous, non-native, exotic, or naturalized (stage III in the scheme of Colautti and MacIsaac 2004). The choice in this chapter is to use "alien."

Box 11.1 Battling an Alien to Save a Mudflat

Spartina alterniflora in Willapa Bay, Washington, USA (Photo Jennifer Ruesink).

In 2004, despite a decade of control efforts, cordgrass (*Spartina alterniflora*) affected about 30% of the intertidal area of Willapa Bay, Washington, and was continuing to expand through seedling germination and coalescence of patches undergoing clonal growth (Buhle et al. 2012). At the time, I was collaborating with a sabbatical visitor from Korea to document the dynamics of a different alien plant on those mudflats, and most of our interaction with *S. alterniflora* was simply to force our way through dense, head-high stands en route to the lower elevations where we did our field work. My colleague returned to the US from Korea in summer 2017 for a short reconnaissance trip, on a fact-finding mission to understand how Korea should respond to their own incipient invasion. *S. alterniflora* had recently appeared in three places along the Korean coast, probably through dispersal from the extensive invasion in China. Only one population had been possible to dig up and remove. He had heard that the vast acreage of *S. alterniflora* was essentially gone from Willapa Bay. How had the social, practical, and ecological challenges been resolved to achieve that goal?

We heard the story from a variety of perspectives—coordinators of early control efforts, on-ground soldiers in the search-and-destroy mission, discoverer

(continued)

Box 11.1 (continued)

of an effective herbicide that led to 99% reduction from 2004–2007, and even a fellow out collecting burrowing shrimp for bait, which wouldn't have been possible if the invasion had proceeded to that portion of the tidal flat. All used similar language that pitted humans against this transformational plant in a battle to save the mudflats, primarily for shorebirds and for shellfish aquaculture. However, numerous lawsuits occurred in parallel with—and sometimes halting—control, based on other social values against direct application of herbicides in an aquatic environment.

Conflict stemmed from different perceptions about problems from chemical and biological pollution. Delays were also attributed to the mudflat habitat itself, where, as one coordinator noted, "We didn't even know how to walk on it when we started." Finally, although the immediate control after 2004 was rapid through herbicide application at agricultural scales (helicopter and tracked vehicle), *S. alterniflora* has not been eradicated from Willapa Bay and requires on-going investment every year to find scattered shoots hidden in native marsh and dissected sloughs.

Leading ecologists consider all alien species to have ecological impacts, simply by virtue of adding a species to a locale (Ricciardi et al. 2013). However, an increase or decrease in a response variable does not necessarily equate to a positive or negative effect on the ecosystem, human health, or finance. Indeed, alien species—even those at the top of the "Worst" lists—are increasingly recognized for their systemic influences that simultaneously bolster and impair ecosystem services valued by humans (Katsanevakis et al. 2014). The terms "invasive" and "invader" frequently are limited to high-impact populations that change systems in ways counter to societal values (but see Richardson et al. 2000), or are both widespread and ecologically dominant (Colautti and MacIsaac 2004). Because such high-impact species have disproportionate interest from ecologists and the general public, they form the focus of the present chapter on biological invasions of mudflats.

At what point has an alien species been present so long in a system that it becomes part of the accepted milieu? This point could be reached ecologically, through accommodations—changes in abundance or traits—in the species of the recipient environment. Or it could be part of a new social baseline with which human society is comfortable. A species' status as alien is permanent because the criterion depends on its transportation to that place by or with humans. (Alien status can be missed if establishment occurred prior to systematic biological surveys at a site, and later identified by population genetic patterns, e.g. Einfeldt et al. 2014). However, a species' status as invasive may be more flexible, as its impacts change over time, and also as people pass new judgments on the importance of those impacts.

2 Patterns of Alien Species on Mudflats

2.1 Invasibility of Mudflats

Although earlier chapters in this book certainly show otherwise, a naïve observer might look at a featureless flat expanse of mudflat and consider it a blank slate, just waiting to be colonized by something that could change it into a living seascape. Or on the other hand, perhaps its conditions are too harsh to support any life. These two perspectives tend towards opposite ends of a spectrum of invasibility, that is, whether alien species are frequent or infrequent members of mudflat communities. Here it pays to examine some data. The question about invasibility of mudflats can be considered in two ways: first, as how many marine alien species can use mudflat habitat relative to those that cannot; and second, as the alien fraction on mudflats relative to other marine habitat types.

Among high-impact marine invaders in Europe, 13% use mudflats (11 of 87 taxa; Fig. 11.1a). In contrast, mudflats are the habitat of a much higher fraction of taxa established in marine waters of North America (63%; 90 of 142; Fig. 11.1b). This difference is probably not strictly biogeographic, but rather reflects that the European list ranks by impact and the North American list does not. As a consequence, small-bodied infaunal species that prevail among amphipods, copepods, and worms augment the fraction of total aliens on mudflats, but not the high-impact species. In some cases, simply identifying mudflat aliens is a challenge, given a hidden infaunal position, small body size, and superficially-similar morphologies. For example, polychaete experts from Japan collected worms from eastern Pacific mudflats in order to study the unusual life history strategy of *Hediste (Nereis) limnicola*, only to find that these worms actually displayed the distinct reproductive structures of *H. diversicolor*, a familiar Japanese species (Nishizawa et al. 2014). Subsequent molecular evaluation showed that *H. diversicolor* was well established in U.S. estuaries spanning more than 1000 km, likely from multiple source populations (Japanese and U.S. haplotypes intermingled at branch tips in the cladogram) and with on-going genetic exchange within the alien range (little population genetic structure; Tosuji and Furota 2016). This cryptic invasion evidently escaped notice for many years due to the morphological similarity of the native and alien species.

When infaunal species are difficult to distinguish, this raises challenges for both enumerating alien species and determining their effects. A separate challenge emerges for other species, especially those above the sediment surface, whose use of mudflats is conditional on patches of vegetation or hard structure. Such species add as much as one-quarter to one-third of total aliens to mudflat habitats (Fig. 11.1). Similarly, among high-impact macroalgal invaders worldwide, few attach directly to soft sediments and therefore would primarily occur in mudflat habitats with interspersed hard structure (Davidson et al. 2015).

While many marine aliens appear on mudflats, and some have high impacts, a different type of study is necessary to assess representation of aliens relative to native species. Substantial evidence exists for a high fraction of aliens within estuaries in

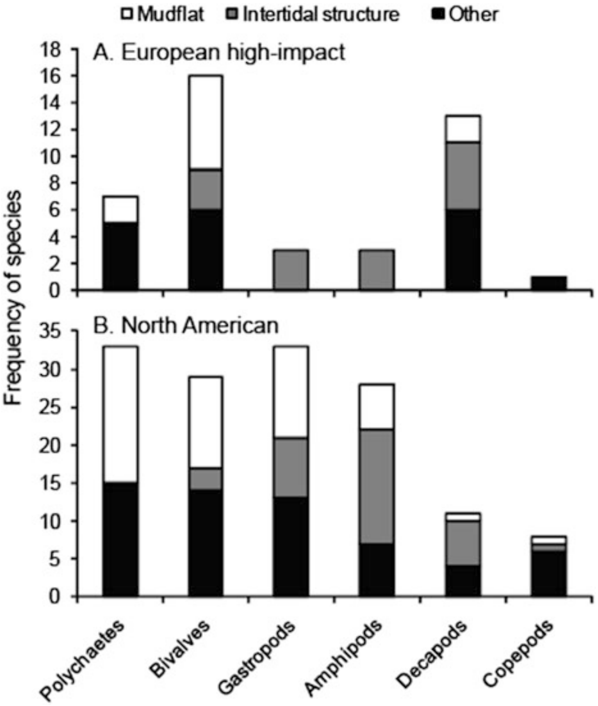

Fig. 11.1 Compilation of alien marine species occupying different habitat types. (**a**) Subset (43) of 87 high-impact aliens in Europe. In addition to the 43 taxa displayed in the figure, several other animal taxa contained no species documented in mudflat habitat: ascidians (7 species), bryozoans (3), cnidarians (8), ctenophores (3) and fish (11). High impact was determined from experiments, correlations, or expert judgment, out of 110 species screened (Katsanevakis et al. 2014). (**b**) Marine and estuarine species established in North America (Fofonoff et al. 2017). Taxa not known to be established (only found once) were omitted from consideration here. "Other" habitat refers to rock, sand, subtidal, pelagic, and shallow marsh habitats, as well as fouling organisms if they do not occur in biogenic habitats (vegetation or reefs) that can form on mudflats.

comparison to other marine habitats (Priesler et al. 2009). European estuaries contain proportionally more alien species (1:5 alien:native) than open coasts (1:20) or marine waters (1:40; Reise et al. 2006). The possible explanations for invasibility of estuaries include propagule pressure, because many human activities occur in these wave-protected embayments. For example, the number of ship-vectored species increases with shipping traffic across regions of Europe (Gollasch 2006). Additionally, estuaries may be more invasible due to environmental filters including habitat match and interactions with resident species, or from low native diversity (Reise et al. 2006). However, estuaries consist of a variety of habitats in addition to mudflats (i.e. pelagic, anthropogenic hard structure). Within a northeastern Pacific estuary, aliens represented 52% of species on hard substrate, but only 21% of species on soft sediment; the difference was even more striking for sessile taxa (Wasson et al. 2005). This indicates that some aliens capitalize on a critical habitat match of hard substrate, such as docks, floats, and armoring, in their invasion of estuaries. Generally, these hard structures placed in marine environments by people, termed "ocean sprawl", disproportionately promote alien species (Firth et al. 2016).

2.2 Traits Underlying Mudflat Transformation

For some time, mudflats have been recognized as a habitat where species that modify abiotic conditions play stronger ecological roles than through traditional food-web linkages (Reise 2002). Mudflats are flat and muddy. Logically, this sets the stage for organisms to reshape mudflats by adding structure or by changing properties of the sediment. Throughout other chapters in this book, native species received consideration as ecosystem engineers that nevertheless maintained a superficial sense of mudflat, e.g. infauna and biofilms that change grain size or stability. However, as noted in the typology of Reise (2002), mudflats also undergo transitions to other biogenic habitats consisting of emergent structure such as reefs, seagrass, or salt marsh. These transitions are addressed in the present chapter when due to alien species, even though they arguably include a state that is no longer a mudflat.

Mudflats share features with other land-water interfaces that make them susceptible to major geomorphological change by alien species (Fei et al. 2014). Mudflats, along with unstable dunes and braided river systems, are inherently dynamic places where physical factors frequently reshape landforms. When organisms are in place that modify the consequence of these physical factors, landscape metamorphosis can occur; that is, a state shift in the dominant processes. The transition of mudflat to salt marsh by alien *Spartina alterniflora* provides one such example (An et al. 2007). Oyster reefs also change community structure and functioning of their environment (Ruesink et al. 2005). Reciprocally, the burrowing activities of an alien isopod in high marsh can remove sufficient sediment to transition these habitats to mudflat (Talley et al. 2001).

Figure 11.2 summarizes five different transitions that mudflats may undergo due to functionally-distinct aliens, having different traits. These transitions are aligned with several other schemes previously presented in the literature (Reise 2002; Fei et al. 2014). Near the top of the figure are transitions in which alien species produce or accumulate material. Near the middle of the figure are transitions to alien species that remove sediment due to the structure or activities of organisms, e.g. through scour around widely-spaced structure or through burrowing or deposit-feeding organisms in mudflats. Novel food web interactions are depicted near the bottom of Fig. 11.2. Each of the five transitions is reviewed in Sects. 3.1, 3.2, 3.3, 3.4 and 3.5 of this chapter.

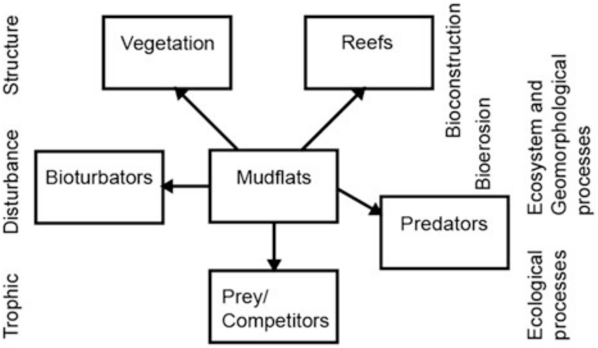

Fig. 11.2 Conceptual outline of processes potentially changed by alien species on mudflats. Arrows represent state changes caused by invaders of different types, including those that change physical structure, sediment disturbance, or trophic connections (left-hand terminology). Trophic changes occur when aliens add new prey resources or are predators. Predators can also be a source of disturbance of mudflat habitats, along with alien species that are bioturbators and therefore influence sediment stability and chemistry. Typically, organisms involved in bioturbation will increase bioerosion, and reciprocally, those involved in bioconstruction will increase bioprotection (Fei et al. 2014).

2.3 General Scheme for Understanding Impact

Three major factors have been advanced to explain variation in impact across invasions (Ricciardi et al. 2013). First, impact may increase with how well adapted an alien species is to the abiotic environment, because a better match is likely to increase both the local abundance and the geographic range, two key parameters in calculating invasion impact (Parker et al. 1999). In the case of mudflats, examples of matching between organism traits and abiotic environment could include grain size or salinity, well known to result in different infaunal communities (Wieser 1959; Hewitt et al. 2005). Second, impact may increase with the number of individuals introduced, in part reflecting a positive relationship between alien abundance and propagule pressure (Lockwood et al. 2005), but also because multiple introductions might come from different source populations and therefore reshuffle genetic traits in ways that enable the success of an alien species. Here, an example might be the invasion of Chinese mudflats by *S. alterniflora* (cordgrass), which can be traced to source populations that differ in water temperature, tidal regime, and salinity tolerance (An et al. 2007). The third general factor underlying impact is whether an alien species plays a novel ecological role or occupies a previously unoccupied niche (Ricciardi et al. 2013). Accordingly, alien species would be expected to have high impacts on mudflats for the same reasons that native species can shape this habitat—as ecosystem engineers that modify above-ground structural complexity or the stability and grain size of sediments; and as top-down predators foraging on infaunal species (Wilson 1990; Reise 2002). Alien species that simply replace roles of existing species might have competitive effects on that species but would be unlikely to transform the system as a whole;

that is, high-impact invasions of mudflats modify the whole community or ecosystem, while similar native species could exhibit population-level responses but dampen emergent change.

Experiments in marine systems have overall confirmed that impacts increase with alien abundance and can be linked to functionally-distinct traits. Across 88 field experiments, manipulations of alien density led to linear increases in a variety of ecological responses, and manipulations of different alien species showed "unique" effects (Thomsen et al. 2011). However, in contrast to species-specific effects, few tests have been set up to examine the impacts of the same alien across different contexts (abiotic conditions or resident biota; Thomsen et al. 2011). Such a gap raises the profile of comparisons of reef-forming species on rocks vs. self-recruiting within a mudflat habitat.

Although novel traits contribute to invasion impact, these impacts may fall disproportionately on particular trophic levels or functional groups. Across field experiments in marine systems, the presence of a sessile alien species weakly reduced the diversity of other sessile species, but strongly increased the diversity of mobile species (Thomsen et al. 2014). Few of the studies in this review came from soft sediments, but the principle can be logically extended to invasions of mudflats. The arrival of novel structure-formers would be expected to increase diversity and abundance of epifauna, given distinct functional positions. However, functional types differ in their mobility within sediments, and large community-level impacts on infauna might arise from alien species that markedly changed sediment stability. Although sediment stabilization is generally considered facilitative and destabilization inhibitory (Reise 2002), stabilization achieved through emergent reefs or vegetation might act through space competition and negatively affect infaunal diversity.

This conceptual overview has highlighted that mudflats may be particularly susceptible to ecosystem transformation by alien species because of the spatial position in a dynamic land-water margin, and additionally suggests how impacts could follow from functional traits:

- *Facilitation*: Alien vegetation that adds above-ground structure to mudflats should augment epifaunal biodiversity but reduce infaunal taxa. Vegetation could participate in a habitat cascade (indirect effect in which one species facilitates another structure-forming species, which is used as habitat by other species) if it requires attachment to biogenic hard surfaces such as shell or tubes in mudflats.
- *Context-dependence and non-linearity*: Reef-forming species should have larger effects on community structure in mudflats relative to rocky environments, providing examples of context-dependence of invasions that depend on surrounding abiotic conditions. Within mudflats, small amounts of hard structure could protect infauna from predation, but this facilitation could disappear at high reef density as the abiotic conditions in the sediment are altered; thus reef-forming species are expected to have nonlinear impacts in mudflats.
- *Food web resilience*: Whole-community impacts of alien species that recapitulate existing roles are less likely than for those with novel traits on mudflats, therefore

impacts through trophic interactions or resource competition may be weak. Weak trophic interactions from alien species could also emerge if alien predators are not suited to mudflats but rather associate with structure, or if alien prey are kept in check through biotic resistance by generalist native predators. Key non-consumptive effects in mudflats, such as burrowing depth of bivalves, also decouple predators and prey.

Some empirical evidence supports each of these connections, interwoven into the five types of mudflat invaders reviewed in Sects. 3.1, 3.2, 3.3, 3.4 and 3.5 (Fig. 11.2), yet many opportunities remain for future ecological research, especially under combined homogenization of biota and physical placement of hard structures through ocean sprawl.

3 Impacts to Mudflats from Aliens with Different Functional Traits

3.1 Vegetation

Invasion of mudflats by vegetation alters above-ground structural complexity and tends to stabilize sediment through bioconstruction (Fig. 11.2). Because flowering plants can take root in soft sediments, a clear mechanism exists for a mudflat to transition to a salt marsh or seagrass bed, if a novel plant species arrives with the capacity to use a zone containing no locally-adapted plant. Some mudflats have an "empty niche" for intertidal vegetation. For example, *S. alterniflora* (cordgrass) is typically a low marsh species, adapted to saltwater inundation every day. However, Pacific Ocean coastlines (Washington State, USA, and China) do not naturally have a plant that survives under low marsh conditions; rather, salt marshes exist primarily above mean higher high water. As such, *S. alterniflora* arrived in a region where no other rooted plants existed in conditions that suited it, and it was able to occupy tens of thousands of hectares (An et al. 2007; Strong and Ayres 2013). In a case reversing the relative alien and native intertidal zones, alien dwarf eelgrass (*Zostera japonica*) from the western Pacific Ocean occupies mudflat above native eelgrass in the eastern Pacific (Ruesink et al. 2010). *Z. japonica* is damaged by desiccation, but has a flexible morphology that remains in contact with the sediment and therefore moist at low tide (Shafer et al. 2007), while its distribution down-slope is limited by competition from the larger, native congener (Hannam and Wyllie-Echeverria 2015).

Because the establishment of vegetation is sensitive to existing sediment stability, bioturbators may prevent a transformation from mudflat to vegetated habitat, as by *H. diversicolor* (annelid worm) precluding alien *Spartina anglica* (cordgrass; Emmerson 2000) and *Neotrypaea californica* (burrowing shrimp) interfering with alien *Z. japonica* (Dumbauld and Wyllie-Echeverria 2003). Such resistance to invasion acts through trophic group amensalism (Woodin 1976), in which the adult organisms present at a site are positively self-reinforcing and prevent the settlement of different organisms.

3.1.1 Comparison of Epifaunal and Infaunal Responses to Alien Vegetation on Mudflats

Alien vegetation often increases epifaunal diversity and abundance, as a consequence of above-ground surface area and resources, but can have opposite effects on infauna. This differential response of above- and below-ground organisms has been identified following invasion of *Caulerpa taxifolia* (macroalga), typically studied in shallow subtidal soft-sediment environments. Relative to uninvaded areas, *C. taxifolia* contains more individuals and species within its structure, but fewer within the sediment where the macroalga competes for space and/or makes conditions more stressful (McKinnon et al. 2009; Gribben et al. 2013). Detrital material from *C. taxifolia* can be transported away from invaded areas, and when it is deposited on intertidal mudflats, acts to reduce infaunal diversity and abundance (Taylor et al. 2010). The brown alga *Sargassum muticum* has been studied as an alien species in rocky shallow subtidal environments (Engelen et al. 2015), on oyster reefs within soft sediment (Lang and Buschbaum 2010), and in intertidal seagrass beds, where it can attach to shell or clam siphons (White and Orr 2011). In all systems, epifauna respond positively to *S. muticum*, but it can displace other space occupants. Among macrophytes with more obvious intertidal mudflat distributions, alien *Spartina* spp. (cordgrass) tends to have negative effects on infauna overall, while shifting the infaunal community composition from suspension-feeders and grazers, to deposit-feeders and detritivores (Levin et al. 2006; Neira et al. 2007). In contrast, distinct above- and below-ground effects are less apparent for dwarf eelgrass (*Z. japonica*). Its associated community has so far been sampled with sediment cores, which show elevated faunal diversity and abundance relative to unvegetated mudflats (Posey 1988; Ferraro and Cole 2012). Nevertheless, *Z. japonica* can reduce productivity of a suspension-feeding clam, concordant with reduced water flow (Tsai et al. 2010).

3.1.2 Habitat Cascades Involving Alien Vegetation on Mudflats

Given the ability to facilitate species by providing habitat, alien vegetation may also serve as an intermediate species in a habitat cascade. Habitat cascades involve two facilitative interactions, in which an initiator species provides a surface for attachment of an intermediate (transmitter) species, which then creates space and resources for additional (receiver) species (Thomsen et al. 2010). On mudflats in particular, small amounts of hard structure provided by clam siphons, tubes, shell, or gravel may enable establishment of macroalgae, whereas soft sediments provide little anchorage for holdfasts. Macroalgae then provide structure and/or resources that increase epifaunal abundance and diversity. The case of the widespread alien macroalga

Gracilaria vermiculophylla, which inspired the concept of habitat cascades, is presented in Box 11.2.

Box 11.2 Alien Alga on Mudflats

Gracilaria vermiculophylla in Hood Canal, Washington, USA (Photo credit: Jennifer Ruesink).

Gracilaria vermiculophylla, a red alga with many alien populations on mudflats worldwide, inspired the development of the concept of habitat cascades (Thomsen et al. 2010). Although *G. vermiculophylla* can attach to any small hard surface on mudflats, and even persist as drifting material, its role in the habitat cascade emerges when the initiator species, a tubeworm inhabiting mudflats of eastern North America, actively decorates its tube. Diversity and abundance of epifauna are weakly augmented by tubes alone, but strongly increased with *G. vermiculophylla* (Thomsen et al. 2010). Indeed, even relatively low cover of *G. vermiculophylla* can dramatically increase the abundance and richness of epifaunal and nekton species compared to surrounding mudflat (Ramus et al. 2017).

By combining fragments of *G. vermiculophylla* from different genets, manipulations of genotypic diversity are possible. Diversity confers higher primary productivity in the mid-intertidal (but not lower intertidal) zones, but the facilitative effect of *G. vermiculophylla* on epifauna was consistent regardless of

(continued)

Box 11.2 (continued)

genotypic diversity (Gerstenmaier et al. 2016). Experiments have also been set up to compare *G. vermiculophylla* and structural mimics, testing whether epifauna respond solely to structure or require the living alga. The latter appears to be important, as structural mimics of *G. vermiculophylla* do not generate an identical epifaunal community to the alga itself (Byers et al. 2012). However, at least one amphipod simply uses *G. vermiculophylla* as habitat, without consuming it directly (Wright et al. 2014). Within the three-part habitat cascade, the tubeworm also consumes some of the epifauna, which makes the interaction between the tubeworm and G. *vermiculophylla* mutualistic—the red alga receives a place for anchorage and growth, and the tubeworm acquires additional prey (Kollars et al. 2016).

3.2 Reefs

Alien species explored in this section fall in the category of those that form hard external structures, especially protruding above the sediment and/or persisting at the sediment surface after the death of the living organism. Charles Elton (1958) provided an early warning about such species in his landmark book on biological invasions, through his identification of Pacific oysters (*Crassostrea gigas*) as a globally-transported species, able to reach high density and dominate space, while also vectoring additional aliens. Conceptually, the framework for impacts of such alien species is well-developed (Fig. 11.3). Any species that increases the structural complexity of a habitat is likely to augment the diversity and abundance of other species, whereas species that decrease structural complexity will accordingly reduce diversity and abundance (Crooks 2002). When reefs form in soft sediments, the change is not just quantitative (increased surface area), but also qualitative (hard added to soft). This qualitative change in habitat type promotes different types of associated species relative to mudflat, not just overall higher abundance and diversity from surface area considerations (Fig. 11.3). In keeping with the facilitative interactions described earlier for habitat cascades, hard structure created by alien species often increases richness and abundance of associated organisms, both sessile and mobile (Heiman and Micheli 2010). However, when other alien species are better able to use such habitat than are native species, invasional meltdown occurs, in which the establishment of one alien species increases subsequent invasibility (Simberloff and von Holle 1999).

Not all reefs consist of molluscs, and not all molluscs build reefs. However, the role of molluscs as shell-forming ecosystem engineers in soft sediments is well known. Sousa et al. (2009) summarized 24 examples of alien marine molluscs, spanning a range of habitats, but disproportionately noted in mudflats, due to seven infaunal clam species and 10 mussel and oyster species able to build up on soft sediments through settlement on or near adults. Molluscs that have shells above

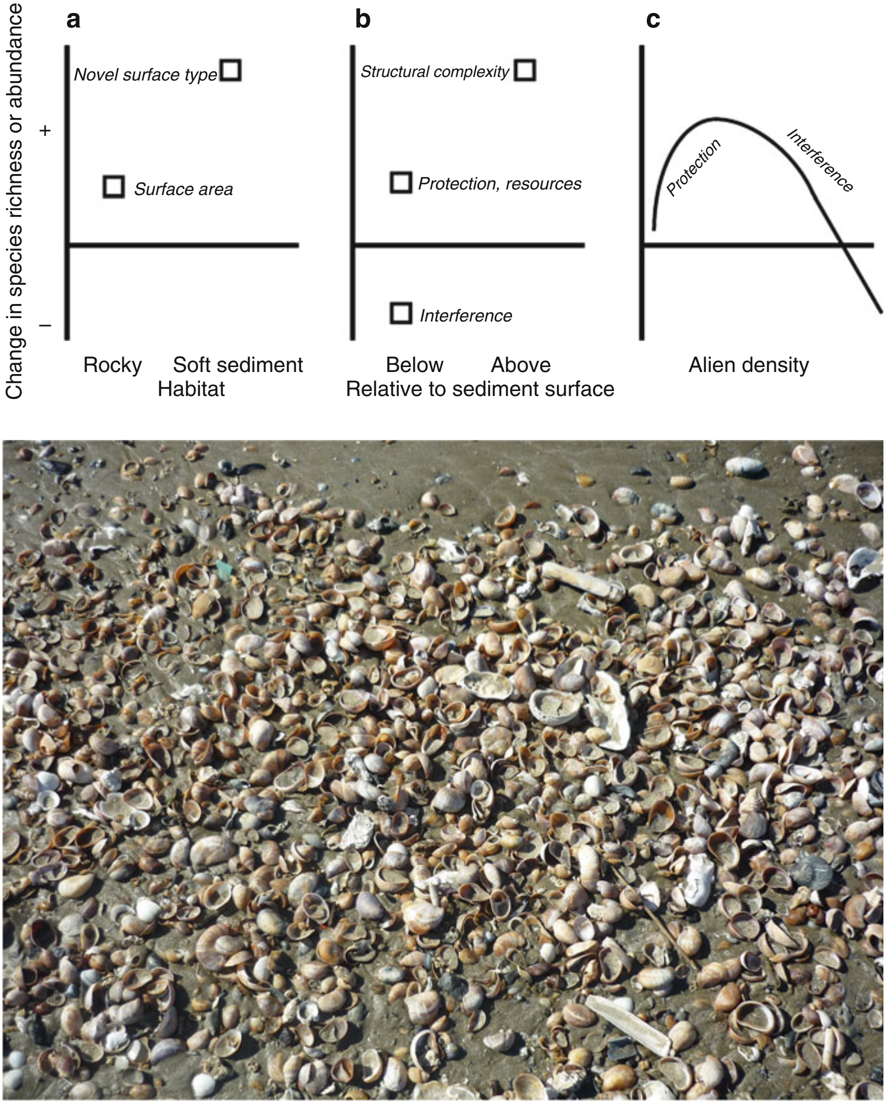

Fig. 11.3 Alien species that form biogenic structure may have context-dependent effects on mudflat communities. In (**a**), structure-forming aliens on mudflats could increase richness and abundance due to both surface area and a novel (hard) surface type. In (**b**), structure-forming aliens on mudflats could benefit above-ground more than below-ground communities. In (**c**), mudflat communities could be protected from surface-feeding predators when structure-forming aliens occur at low density, but could be impaired by a high-density layer impeding connections to the sediment surface. Photograph shows *Crepidula fornicata* shells washed up on the supratidal fringe from the adjacent mudflat, La Bernerie, France (Photo PG Beninger).

the sediment may contribute both complexity and surface area, thus augmenting habitat for other species (Gutierrez et al. 2003; Sousa et al. 2009). In addition to the surface area of reefs, biodeposits from reef-forming organisms increase the resource base for deposit-feeders. Careful experimental designs involving both live organisms and structural mimics are critical to resolving the relative importance of energy and structure in responses to reefs (Novais et al. 2015).

3.2.1 Context-Dependence by Invaded Habitat

Reef-forming species often have the capacity to settle on conspecifics, thereby building up on soft sediments, or on other hard surfaces. Accordingly, a major ecological lesson from studies of reef-forming species is in regard to their context-dependence—do they have similar impacts when in soft sediments vs. hard substrates, or in comparison to native shellfish beds (Fig. 11.3)? Generally, reefs formed on soft sediments change the ecosystem more than on rock, which is documented in Box 11.3 for Pacific oysters and in Box 11.4 for the tube-building serpulid polychaete *Ficopomatus enigmaticus*. However, relative to native mussels, reefs of alien Pacific oysters have similar facilitation of epifauna, as well as infauna in adjacent sediments (Box 11.3, Kochmann et al. 2008; Green and Crowe 2014).

Box 11.3 Pacific Oyster Reefs

Pacific Oyster Reefs in Willapa Bay, Washington, USA (Photo credit: Jennifer Ruesink).

For the Pacific oyster (*Crassostrea gigas*), novel functions are more dramatic in soft- than hard-substrate environments, and where native reef-formers are absent (Padilla 2010; Troost 2010). In a comparative study of communities associated with oysters on rocks and on mudflats, diversity and abundance of associated fauna were higher with oysters in both substrate types (Lejart and Hily 2011). However, the modification of the associated community was greater on mudflats, where 41% of oyster-associated species were not generally found in that habitat, than on rocks, where only 16% were atypical of the habitat. The results are consistent with oysters adding structural complexity (and some fine biodeposits) on rocks, and adding both novel substrate and structural complexity on mudflats. Additionally, the overall increase in abundance and diversity in response to oysters on mudflats, even amongst infauna, coupled with little evidence in this study of physicochemical modification (Lejart and Hily 2011), indicates that habitat complexity (promoting diversity) outweighed competitive exclusion.

Other studies of context-dependence of Pacific oysters have compared their effects when added to mudflats or added to native mussel beds (which also occur on mudflats in European study regions). Kochmann et al. (2008) created

(continued)

Box 11.3 (continued)

large (4 m diameter) rings of bivalves on mudflats in the northern Wadden Sea, and analyzed the organisms in the sedimentary centers of these rings, with treatments involving oysters alone, native blue mussels alone, a combined mussel-oyster treatment, and no addition. Treatments in which oysters were combined with native mussels were similar to mussels alone, whereas treatments in which oysters were added to mudflat had strong facilitative effects on epifaunal abundances and on many infauna as well. Here, all the bivalve treatments increased organic content and reduced particle size relative to mudflat. Green and Crowe (2014) manipulated oysters across a range of cover on mudflats and on mussels in Ireland. Effects on diversity and abundance (combined epifauna and infauna) increased with oyster cover on mudflats but was similar regardless of oyster cover on mussels (declining at the highest oyster cover in mussels), thus suggesting that oysters were functionally similar to native mussel beds on mudflats. Accordingly, community structure converged with mussel beds as oysters were added at higher cover (Green and Crowe 2014). However, ammonium concentration in sediment, as well as flux from sediment, was greatest at intermediate cover of oysters added to either mussel beds or directly to mudflats (Green et al. 2013).

Context-dependent effects of Pacific oysters have been documented even at within-patch scales. When native blue mussels are positioned at the top of oyster reefs, they experience detrimental effects from both predation and competition from barnacles that live on their shells. However, within the oyster reef matrix, predation rates decline (Eschweiler and Christensen 2011), and mussel shells host fewer barnacles (Buschbaum et al. 2016).

Part of the context-dependence of Pacific oysters also reflects different human values. People may appreciate the ecosystem functions related to production (commercially-valuable in aquaculture) and regulation (biofilter that could improve water quality), but not the habitat transformation of mudflats to sharp, emergent reefs (Herbert et al. 2016).

Box 11.4 Tubeworm Reefs

Ficopomatus enigmaticus Reefs in Elkhorn Slough, California, USA. Photo credit: Kimberly Heiman.

Ficopomatus enigmaticus, a widespread reef-forming tubeworm, illustrates the transformative role of alien species creating hard structure on mudflats. These tubeworm reefs often harbor higher abundance and diversity of invertebrates than in surrounding unstructured habitat (McQuaid and Griffiths 2014; Heiman and Micheli 2010), although in a U.S. Pacific coast estuary, much of this community was alien, and few organisms withstood conditions under the reefs (Heiman and Micheli 2010). In comparison to native oyster beds, *F. enigmaticus* had a similar community of native species, but substantially more aliens (Heiman et al. 2008). In Argentina, reefs of *F. enigmaticus* within soft sediment promote red algae but not green algae, which are instead found on pieces of shell (Cielo-Bazterrica et al. 2012). The reef effect on green algae is probably indirect, via augmented herbivore density on reefs. Similarly, these grazing crabs exert top-down control on the benthic primary production near reefs, which would otherwise be enhanced by organic matter from worm biodeposits (Bruschetti et al. 2011). However, much of the reef effect on nearby sediment can be attributed to structural addition above the sediment, rather than the biological activity of *F. enigmaticus* (Schwindt et al. 2004).

Although properly an example of alien macrophyte, *Sargassum muticum* supports the principle that the same species has different effects across contexts that depend on the novelty of the role it plays. *S. muticum* on rocky shores shared an epifaunal community with other native macroalgae, but when surrounded by sand, it enhanced epifaunal diversity in a manner that differed from a native macroalga in that habitat (Buschbaum et al. 2006).

3.2.2 Nonlinearities in Shell Effects

For infauna, shell material could serve as a structural impediment to epibenthic predators, so an initially positive relationship might be expected between infaunal abundance and alien shell-formers. Yet the complete occupation of mudflats by reef-formers can exclude infauna due to transformation of sediment stability, grain size, or chemistry, or through direct space competition (Heiman and Micheli 2010; Fig. 11.3). These links set up opportunities for non-linear effects in which low cover of reef-building organisms enhances typical mudflat species, but these are reduced or excluded as reefs reach 100% cover. Several examples of such nonlinearities in shell effects have been documented. The exclusion of native seagrass from soft sediments by alien oysters occurs at a threshold shell cover around 20% (Wagner et al. 2012). Pacific oysters generated a unimodal relationship between the diversity of associated species and oyster cover when fouling mussel beds in soft sediments (Box 11.3, Green and Crowe 2014). Large shells, which wash in from deep offshore populations of a gastropod alien to Australia, enhance infaunal abundance at moderate but not high shell cover, possibly by modifying the ability of alien crabs (*Carcinus maenas*) to consume native clams (Nicastro et al. 2009). Despite these examples, the evidence of nonlinearities in shell effects is less compelling than the conceptual framework might suggest. Indeed, impacts of alien marine species increase linearly with density in experiments that involve treatments beyond simple presence/absence (Thomsen et al. 2011). A particular focus on gradients of shell and infaunal response will be needed to clarify the prevalence of nonlinearities.

3.3 Bioturbators

While vegetation and reefs tend to stabilize sediments, some alien species have an opposite influence through traits of higher mobility or deeper activity relative to native infaunal species (Fig. 11.2). When the Atlantic bamboo worm (*Clymenella torquata*) reaches high density on Pacific mudflats, the sediment becomes “spongy” and may displace on-bottom aquaculture (Mach et al. 2012). A strong rationale underlies an expectation for alien bioturbators to influence fundamental sediment properties, such as organic content and aerobic depth, and accordingly infaunal community structure, but empirical studies of ecosystem-level effects appear sparse, relative to vegetation and reefs. For example, among the alien molluscs reviewed by Sousa et al. (2009), none of the seven clam species, which could exert part of their influence through bioturbation, showed empirical evidence of impact. Since that review, bioturbation potential (calculated from abundance and species' traits) was evaluated at three sites across Europe where Manila clams (*Tapes* [synonyms *Venerupis* and *Ruditapes*] *philippinarum*) are established. Alien clams were among the top contributors in the community, but generally not as influential as native species. Further, environmental factors such as macroalgal mats influenced whether the calculated bioturbation potential linked well to observed mixing depth (Queiros et al. 2011). Thus, two issues—existing traits in the native community, and context dependence in the link from community structure to ecosystem function—could decouple an alien bioturbator from any change in mudflat functioning.

Analyses may also use the identity, turnover, or dispersion of the traits themselves as descriptors of ecosystem change. Subtidal soft sediments in the Baltic Sea were invaded by the polychaete *Marenzelleria* spp. since the 1980s. These worms have modified the functional traits represented by infaunal communities at some sites due to their deeper burrowing depths (Hewitt et al. 2016). Native species, especially longer-lived species with hard shells, have traits that are now less prevalent in infaunal communities (Weigel et al. 2015). Trait dispersion (range of functionally-distinct types) has generally increased, but also shifted due to replacement of functional traits in the native assemblage by those of a distinct and abundant invader (Weigel et al. 2015).

Among alien bioturbators are some taxa whose activities can remove vegetation, and lead to an expansion of mudflats along a vegetated border. Alien green crabs (*C. maenas*) were particularly abundant in Casco Bay, Maine, USA during a rapid decline in eelgrass, and prevented reestablishment of transplants (Neckles 2015). Green crabs are not primarily herbivorous but can uproot shoots while foraging for benthic prey. Alien isopods (*Sphaeroma quoianum*) invaded estuaries of the north-eastern Pacific Ocean about a century ago, where they have become much more abundant in marsh banks than in their native range (Davidson et al. 2008). Their burrowing activities can lead to marsh erosion and loss of vegetation, and consequently a transition to mudflat (Talley et al. 2001).

Bioturbation may be reduced by alien parasites of native bioturbators. This link has been drawn from infection to population decline, but has not yet been linked to a change in sediment properties. Following the appearance of a castrating parasite (bopyrid isopod *Orthione griffenis*), native burrowing shrimp declined in several estuaries of the U.S. Pacific coast (Griffen 2009; Chapman et al. 2012). A similar precipitous decline occurred for one species in a diverse crab community (*Eurypanopeus depressus*), which is preferentially infected by the alien rhizocephalan barnacle, *Loxothylacus panopei* (Eash-Loucks et al. 2014).

A clear example of species-level effects on sediment properties comes with a twist, which is that the amphipod (*Corophium volutator*) was not known to be alien before recent genetic analyses (Einfeldt and Addison 2015). On a tideflat in the Bay of Fundy, *C. volutator* decreases sediment stability through grazing benthic diatoms that would otherwise glue sediment together (Daborn et al. 1993). The evidence for the ecological role of amphipods comes from the observed increase in sediment stability during shorebird migration, which reduced both the density of amphipods and their activity at the sediment surface at low tide (Daborn et al. 1993).

3.4 Trophic Interactions

In a predator-prey interaction on a mudflat, an alien species may constitute the predator (usually crabs or gastropods) or prey (usually bivalves or worms). Given that soft-sediment community structure can respond strongly to top-down effects of mobile consumers (Wilson 1990; Reise 2002), alien predators would be predicted to constitute a high-impact functional group. While this prediction may be generally accurate for alien marine predators, it was surprisingly difficult to find evidence for their top-down effects on mudflats. Primarily this lack of evidence stems from predators being tested in structurally-complex habitats such as shell, boulders, or vegetation, and so results cannot necessarily be extrapolated to mudflats in the absence of such structure. Alien *Rhithropanopeus harrisii* has colonized complex structure but not mudflats in the Baltic Sea (Turoboyski 1973; Nurkse et al. 2015). Similarly, alien *Hemigrapsus takanoi* occupy structured habitats in the Wadden Sea, where they appear to displace native crabs (van den Brink et al. 2012; Landschoff et al. 2013).

Green crabs, which occupy a variety of substrate types in both their native and widely-introduced range, provide some of the best examples of strong pairwise effects reducing abundance of native species where it has invaded, as well as controlling alien species where it is native (Box 11.5). Although green crabs are generally found to consume easily-accessed prey on the small end of a body size spectrum, another crab species (*Charybdis* spp.) removes large-bodied prey from subtidal soft sediments in New Zealand (Townsend et al. 2015). The arrival of the alien gastropod *Euspira fortunei* in Japan was followed by declines in native clams on mudflats (Sato et al. 2012), whereas the alien gastropod *Rapana venosa* in the Adriatic Sea prefers alien over native bivalves (Munari and Mistri 2011). Thus the community-level consequence of alien predators on mudflats will depend on species-specific preferences for prey of different sizes or taxa.

Box 11.5 Alien predator on mudflats

Carcinus maenas in Washington State, USA (Photo credit: P. Sean McDonald).

Green crabs (*Carcinus maenas*) are alien predators in eastern and western North America, Australia, South Africa, and eastern South America, and they also interact with several alien prey species in their native range in Europe. *C. maenas* or hybrids with *C. aestuarii* are present in Japan. *C. maenas* occupies a wide variety of intertidal and subtidal habitats in Europe and eastern North America, but has a restricted habitat range in western North America and Australia (intertidal soft sediments) and South Africa (rocky embayments). Recruits typically occur in structured habitats, and post-moult adults may be restricted physiologically to subtidal zones, but at intermediate ontogenetic stages, individuals forage with the tides across soft sediment environments including mudflats. Green crabs are dietary generalists, documented to consume more than 150 plant and animal prey (Cohen et al. 1995). From feeding trials involving shelled prey, crabs disproportionately consume items that are smaller than their own body size and with relatively thin shells (Mascaro and Seed 2000a, b; Miron et al. 2005). Alien *C. maenas* reduces the density of infaunal bivalves intertidally (Grosholz et al. 2000), and evidence exists of subtidal impacts on some species (Ross et al. 2004, 2006). However, some clams increase their burial depth in response to green crabs, thus avoiding consumption (Whitlow et al. 2003; Whitlow 2010).

Where it is alien in western North America, *C. maenas* displaces native juvenile crabs from shelter (McDonald et al. 2001), but where it is native in Europe, *C. maenas* is displaced from shelter by alien crabs (van den Brink et al. 2012; Landschoff et al. 2013). Thus, regardless of whether *C. maenas* is alien or native, physical structure fosters alien crabs.

(continued)

Box 11.5 (continued)

Two recent studies of *C. maenas* in its native range provide examples of trophic links with alien species beyond pair-wise interactions. Alien oysters (*C. gigas*) provide a refuge for small mussels, which would otherwise be consumed by *C. maenas* (Waser et al. 2015). Here, the alien oyster alters the direct interaction between two native species. In the second example, either crabs or trophic amensalism served to reduce density of an alien clam, but these effects were not additive. Alien surf clams (*Ensis directus*) experienced strong top-down control from native predators (including *C. maenas*) in the Dutch Wadden Sea, such that the inhibition of these clams by sediment-stabilizing species was only evident under predator exclusion treatments (Van der Heide et al. 2014). These examples both show that trophic interactions on mudflats are intertwined with physical aspects of sediment stability and structural complexity (Reise 2002).

3.4.1 Biotic Resistance

When native predators limit the density of alien prey, this constitutes a form of biotic resistance (Papacostas et al. 2017). Alternatively, if negative interactions are more prevalent in the native than alien range, a species may become an abundant invader due to enemy release. Reports from the literature strongly support biotic resistance by predators on mudflats (Table 11.1). Cases in which an alien initially “booms,” but subsequently is kept at low density by predation, may imply a time lag in which predators learn or adapt to use a novel resource (Palacios et al. 2000). When predators are examined individually, they can exhibit large intraspecific variation in feeding preferences, providing a potential mechanism for top-down impact to change over time. For example, predation on alien crabs (*Petrolisthes armatus*) is presently expected to be weak, given that only 14% of native crab individuals specialized on this diet item in feeding trials (Pintor and Byers 2015).

In addition to top-down control from predators, biotic resistance could derive from native parasites that infect a novel alien host species. Mudflats provide a habitat for several of the alien marine invertebrates whose parasites are best known, including green crabs, Pacific oysters, and mudsnails (Goedknegt et al. 2016). However, the number of pathways by which alien species benefit from parasites exceeds the one pathway for biotic resistance, which is to acquire a new parasite at the site of introduction. Alien hosts may escape their own parasites, fail to serve as a suitable host for specialist parasites in the new range, or carry generalist parasites that harm native species (Goedknegt et al. 2016).

Biotic resistance has been demonstrated experimentally through improved survival of alien prey in predator-exclusion treatments (Table 11.1). Additional studies capitalize on natural variation in predator density. For instance, the southern limit of alien *C. maenas* on the U.S. Atlantic coast abuts the range of native blue crabs. Mortality of tethered *C. maenas* was much more rapid when they were moved to

Table 11.1 Predator-prey interactions involving alien bivalves consumed by native predators on mudflats

Predator taxon	Bivalve prey	Study location	Impacts	References
Metacarcinus (previously *Cancer) productus* (crab)	*Tapes philippinarum*, *Nuttallia obscurata*, *Mya arenaria* (alien); also *Protothaca staminea* (native)	North American Pacific coast	Clam mortality declines with larger grain size, thicker shells, and deeper burial	Smith et al. (1999), Byers (2002, 2005), Dudas et al. (2005) and Ruesink et al. (2014)
Carcinus maenas (crab), *Crangon crangon* (shrimp)	*Ensis directus*	Dutch Wadden Sea	Top-down effects	Van der Heide et al. (2014)
Panuliris interruptus (lobster), *Pteropurpurus festiva* (gastropod)	*Arcuatula senhousia*	California, USA	Top-down effects primarily at outer, not inner, bay; weaker effects at higher mussel density	Kushner and Hovel (2006) and Cheng and Hovel (2010)

areas with blue crabs than in the present range (DeRivera et al. 2005). The nearly complete exclusion of mussels *Arcuatula* (previously *Musculista*) *senhousia* from the ocean end of Mission Bay, California, was determined experimentally to be due to predation from native lobsters and snails, which did not occur up-estuary (Cheng and Hovel 2010). Such transplant studies, carried out along environmental gradients such as tidal elevation and salinity, suggest a role of predation by native species in determining alien range, in addition to local density.

3.4.2 Bird Response to Alien Species on Mudflats

Mudflats have high ecological value to birds, especially as foraging habitats for migratory waterbirds (Chap. 12). The extent to which alien species could provide a bottom-up enhancement of higher trophic levels such as birds has not been well characterized, but would depend on its being an abundant, accessible, high-quality resource. It appears, for example, that shorebirds forage sufficiently on alien amphipods to reduced their density at a migration stopover in the Bay of Fundy (Daborn et al. 1993). However, most research examining bird response to aliens on mudflats focuses on interactions mediated through vegetation or reefs (Table 11.2). Since these structurally-complex habitats often contain denser invertebrates, they can provide resources to birds able to forage in that structure. However, shorebirds generally are reduced or excluded following these habitat transformations. Alien invertebrate consumers could also reduce resources used by birds on mudflats. In an

Table 11.2 Response of birds to alien species on mudflats

Alien taxon	Study location	Bird response	References
Carcinus maenas (crab)	US west coast, N Am east coast	Depends on whether birds consume green crabs, or the prey of green crabs	Estelle and Grosholz (2012) and Wong and Dowd (2014) (model)
Spartina alterniflora (cordgrass)	US west coast, China	Salt marsh nester improved	Casazza et al. (2016)
		Shorebirds reduced use for foraging or high-tide roosting	Ge et al. (2009) and Patten and O'Casey (2007)
Ficopomatus enigmaticus (reef-forming polychaete)	Argentina	Suitable for roosting, enhanced prey density	Bruschetti et al. (2009)
Crassostrea gigas (reef-forming oyster)	Wadden Sea	Oystercatcher and curlew feeding improved in unconsolidated reef	Markert et al. (2013)
Zostera japonica (seagrass)	British Columbia, Canada	Waterfowl diets include large fractions of alien eelgrass	Baldwin and Lovvorn (1994)

experimental study on dunlin (*Calidris alpina*), captured individuals were caged on mudflats that had previously been manipulated through the presence/absence of alien green crabs. The presence of *C. maenas* in Bodega Harbor reduced the prey available to shorebirds in these field experiments (Estelle and Grosholz 2012).

The diversity of bird responses to alien species on mudflats can complicate management. The removal of *S. alterniflora* from San Francisco Bay (western U.S.) was recently halted when it was discovered that an endangered bird (clapper rail) was using alien cordgrass as nesting habitat. In contrast, shorebirds were likely to benefit from the transformation back to mudflat (Casazza et al. 2016).

3.4.3 Non-Consumptive Effects

Predators influence their prey not simply through mortality, but also because prey may respond to the risk of predation by modifying structural, chemical, or behavioral traits. On mudflats, behavioral responses related to vertical distribution enable prey to change their risk of being consumed, especially by predators foraging from the surface. For instance, native clams (*Mya arenaria*) bury deeper when alien green crabs (*C. maenas*) are present, which reduces mortality from crabs (Whitlow 2010). Alien mussels (*A. senhousia*) behaviorally reduce their predation risk by responding to chemical cues from native predators (Castorani and Hovel 2016).

The strength of trophic interactions following establishment of alien species depends on the ability of species with no recent shared evolutionary history, to recognize each other as potential predator or prey. Further, even if a new species can be detected, a native species may not mount an appropriate behavioral response, i.e. to be able to catch and consume prey or to avoid a predator. These principles apply whether the combination involves alien predator and native prey, or vice versa. A key test of these ideas would be whether alien prey have less appropriate induced defenses than native prey, and what information is used to detect predation risk. Among seven mudflat-associated snail species, aliens used general risk cues (damage to conspecifics), but natives used specific cues from a threatening predator, in mounting avoidance behavior (Grason 2017). Overall, these results support the logical idea that coevolutionary history matters for the type of information used in trophic interactions. Successful aliens may disproportionately use general, rather than species-specific, information to gauge risk in their environment.

3.5 Competition from Soft-Sediment Invaders: Mixed Evidence

Competition is generally considered weak on mudflats due to the three-dimensional structure (when we include the sediment, and relative to space competition on rocky shores), regular delivery of phytoplankton or detrital resources, and predation limiting species densities (Wilson 1990). In contrast, trophic group amensalism can result in different dominant taxa on mudflats, mediated through substrate stability or adults preventing settlement of heterospecifics (Woodin 1976). Several taxa of alien molluscs have been tested for their capacity to compete with natives, and results span the range from no effect, to competition eliminating native species (Table 11.3). In some cases, the species interact not just through resource competition but because they share a predator or parasite (Bidegain and Antonio Juanes 2013; Castorani and Hovel 2015), or the alien includes eggs or juveniles of the native species in its diet (Race 1982). The slipper limpet *Crepidula fornicata* reaches high densities in its invaded range in western Europe, but experimental tests of competition with other suspension-feeders have shown little impact, and instead the alien species could benefit other bivalves by preventing harmful algal blooms, intervening with predators, and serving as a sink for parasites (Thieltges et al. 2006). If competition from alien species often seems unimportant on mudflats, this aligns with its lower position in a hierarchy of interactions among native species, as well as with a general perspective that marine aliens tend to increase local diversity, rather than causing extirpations (Reise et al. 2006).

Table 11.3 Tests of competition from alien species on mudflats

Alien taxon	Responding taxon	Study location	Impacts	References
Ilyannassa obsoleta (gastropod)	*Cerithidia californica* (gastropod)	California, USA	Native absent from mudflats invaded by alien, restricted to marsh (O)	Race (1982)
Batillaria attramentaria (gastropod)	*Cerithidia californica* (gastropod)	California, USA	Resource competition (E); population growth higher for alien than native (M)	Byers (2000) and Byers and Goldwasser (2001)
Tapes philippinarum (clam)	*Ruditapes decussatus* (clam)	Spain	No effects on growth or survival, but predators affected high-density treatment (E)	Bidegain and Antonio Juanes (2013)
Tapes philippinarum (clam)	Other infauna	British Columbia, Canada	Negative correlation (O)	Bendell (2014)
Arcuatula senhousia (mussel)	Native infaunal bivalves	California, USA	Reduced abundance and growth, also apparent competition from attracting shared predators	Castorani and Hovel (2015)
Arcuatula senhousia (mussel)	*Tapes decussatus* (native clam), *T. philippinarum* (alien)	Italy	No effects on growth or survival (E)	Mistri (2004)
Crepidula fornicata (gastropod)	*Crassostrea gigas* (alien oyster)	France	Seasonal trophic overlap (O); no effects on growth or survival (E)	de Montaudouin et al. (1999) and Decottignes et al. (2007)
Cyclope neritea (gastropod)	*Nassarius reticulatus* (gastropod)	France	Different substrate preferences; shared carrion resource probably not limiting (O)	Bachelet et al. (2004)
Marenzelleria viridis (polychaete)	Polychaetes and other fauna	Odense fjord, Denmark	In 25-year time series, *Hediste diversicolor* was less common, and *Arenicola marina* more common after invasion (O)	Delefosse et al. (2012)

O observational, *E* field experiment, *M* model. Responding taxon is native unless specifically noted as alien

4 Novel Ecosystems: Interactions of Biological Invasions, Other Global Changes, and Evolutionary Change

In this chapter, alien species have been examined piecemeal by functional type for their effects on mudflats. Yet the rate of introduction of alien species to coastal environments is a global deluge (Ruiz et al. 2000), opening up the possibility for either cumulative or non-additive effects of bioinvasions. At the same time, mudflats are undergoing two other global changes anticipated to foster invasions—hardened anthropogenic habitats (ocean sprawl, particular to erosive and developed coasts) and climate warming (as a general global change). As both the complement and traits of species change, mudflats are becoming novel ecosystems, consisting of combinations of species in spatial arrangements not previously in existence.

4.1 Ocean Sprawl and Climate Change Fostering Invasions

The greatest change that occurs to mudflats is their wholesale conversion through diking or filling to provide terrestrial space for the expansion of human activities. Reclamation is estimated to have reduced tidal flats in the Yellow Sea, Asia, by 65% over a half century (Murray et al. 2014). In China specifically, 200,000 ha of salt marsh have been reclaimed for terrestrial use (An et al. 2007), and lower mudflats have disappeared from the invasion of cordgrass (*S. alterniflora*; 40,000–112,000 ha), which was intentionally planted until the mid-1980s, for its engineering capacity to form habitat and protect shorelines (An et al. 2007; Strong and Ayres 2013). Mudflats frequently occur under wave-protected conditions in natural harbors, and as people build shipping channels, docks, and buildings, mudflats disappear. About 20% of the world's coastline consists of soft sediment, and 10% of the coastline of Europe and the US has been artificially hardened (Firth et al. 2016). This loss of mudflats from reclamation and hardening could be compounded by sea level rise, as the present intertidal zone drops below the rising water, which often is prevented from flooding new area because of built features that wall off the water. In some areas, however, sea level rise could initially lead to the expansion of mudflats as marshes are flooded.

Ocean sprawl forms novel marine habitat, unless accompanied by filling that moves space out of the ocean altogether. With some exceptions, diversity and composition are depauperate on artificial relative to natural hard substrates, and artificial surfaces are disproportionately colonized by alien species (Firth et al. 2016). Such hard structures also replace soft sediments and their ecological communities, while additionally creating a new border with soft sediment, which can be influenced through modified water motion, foraging by predators associated with structure, and organic materials produced by fouling organisms that accumulate in soft sediments nearby (Heery et al. 2017).

Ocean sprawl generates an unmistakable shift in mudflat communities due to hard substrate, which likely also fosters invasion. In contrast, the role of climate warming in invasion is more speculative. Some evidence exists for marine aliens to benefit relative to native species as water warms (Stachowicz et al. 2002; Sorte et al. 2010, 2013). This pattern could emerge if the life histories of alien species tend toward r-selected, where a thermal increase accelerates reproductive processes. Or the pattern could reflect generalist species with wide thermal tolerances that tend to be transported. Several mudflat invaders, whose poleward expansion was previously thought to be constrained by low temperatures, have become established or reached higher density in concert with warming. These species include cordgrass (*S. anglica*) in the Wadden Sea and eastern North Sea (Loebl et al. 2006; Nehring and Hesse 2008) and a barnacle (*Austromineus modestus*) that uses shell and reefs as substrate within intertidal soft-sediment habitats in the eastern North Sea (Witte et al. 2010). Pacific oysters may benefit both from warmer summers, due to water temperatures necessary for larval development, and warmer winters (Diederich et al. 2005; Dutertre et al. 2010; Herbert et al. 2016; Valdez and Ruesink 2017). Warming could also increase the per capita effects of poikilothermic species; for instance, alien bioturbators burrow faster at projected higher temperature (Davidson et al. 2013).

4.2 Evolution After Invasion

Climate warming is not the sole explanation for alien species to exceed their distribution based on prior abiotic limiting factors. A second possibility depends on adaptation to novel conditions. Few tests of evolution after invasion have been carried out for mudflat species, although rapid contemporary evolution has been documented for native and alien species in other habitats (Westley 2011). Pacific oysters (*C. gigas*) now spawn at northern latitudes where temperature constraints were expected to prevent establishment (Wrange et al. 2010). Although warmer summers provide a partial explanation, capacity for larval development under cooler temperatures may also contribute. Pacific oysters also show evidence of rapid adaptation to local strains of a pathogen, based on their capacity to survive experimental infection by their local pathogen strain while suffering mortality from a strain from another part of their introduced range. Larvae derived from crosses of the two oyster populations were resistant to all pathogen strains, which implies that mixing propagules from different sources could result in more successful invasion (Wendling and Wegner 2015). Cordgrass (*S. alterniflora*) was introduced to China from several parts of its native range, where populations had different thermal and salinity tolerances (although these ecotypes have not been determined to have a genetic basis; An et al. 2007). Mixing propagules from different source populations has the potential to provide genetic variability from which highly-adapted lineages emerge, which could contribute to exceptional growth and expansion fates of *S. alterniflora* in China (An et al. 2007; Strong and Ayres 2013). An open challenge is to understand how contemporary evolution shapes species traits and interactions in novel ecosystems.

4.3 Cumulative Role of Alien Species

As alien species accumulate, they have the potential to interact with the recipient system in new ways. More species might have cumulative impacts, but it is also possible that some aliens mitigate the effects of others. For instance, two alien species in a trophic cascade could protect native prey. As a possible example, an alien seaslug (*Philine orientalis*) consumes crabs including alien *C. maenas*, which is, in turn a predator of native clams. *P. orientalis* reduced feeding by crabs in laboratory studies (but not under relative abundances typical in the field; Newsom and Williams 2014). In contrast, positive interactions among alien species could augment impact, such as by alien hornsnails (*Batillaria attramentaria*) that promote cover of a habitat engineer (alien eelgrass *Z. japonica*; Wonham et al. 2005).

The functioning of mudflats for nutrient cycling, energy transfer, and sediment dynamics appears quite resilient to most alien species, except those that form emergent structure through vegetation or reefs (Fig. 11.2). Mudflats of the future will still contain worms, bivalves, crustaceans, and other taxa whose traits suit them to life in a particular physicochemical environment governed by grain size. Open questions remain about the consequences of different scales of heterogeneity of structure on and around mudflats. Research is needed to support rational engineering of coastal structures and living shoreline design to protect against erosion, but also in regard to potential non-linearities associated with mosaics of alien species forming biogenic habitat on mudflats, and methods to prevent wholesale conversion. As Reise (2002) stated so elegantly, the interface of biology as driver of and response to the physical environment "provides sediment ecology with a salient subject which can be studied particularly well in marine coastal sediment communities." When such ecological processes are associated with alien species, they raise the importance of mudflats for testing general concepts in invasion biology, but also highlight the critical role of coastal planning and management to achieve on-going resilience.

References

An SQ, Gu BH, Zhou CF, Wang ZS, Deng ZF, Zhi YB, Li HL, Chen L, Yu DH, Liu YH (2007) *Spartina* invasion in China: implications for invasive species management and future research. Weed Res 47:183–191

Bachelet G, Simon-Bouhet B, Desclaux C, Garcia-Meunier P, Mairesse G, de Mountaudouin X, Raigne H, Randriambao K, Sauriau P, Viard F (2004) Invasions of the eastern Bay of Biscay by the nassariid gastropod *Cyclope neritea*: origin and effects on resident fauna. Mar Ecol Prog Ser 276:147–159

Baldwin JR, Lovvorn JR (1994) Habitats and tidal accessibility of the marine foods of dabbling ducks and Brant in Boundary Bay, British Columbia. Mar Biol 120:627–638

Bendell LI (2014) Evidence for declines in the native *Leukoma staminea* as a result of the intentional introduction of the non-native *Venerupis philippinarum* in coastal British Columbia, Canada. Estuar Coasts 37:369–380

Bidegain G, Antonio Juanes J (2013) Does expansion of the introduced manila clam *Ruditapes philippinarum* cause competitive displacement of the European native clam *Ruditapes decussatus*? J Exp Mar Biol Ecol 445:44–52

Bruschetti M, Bazterrica C, Luppi T, Iribarne O (2009) An invasive intertidal reef-forming polychaete affect habitat use and feeding behavior of migratory and locals birds in a SW Atlantic coastal lagoon. J Exp Mar Biol Ecol 375:76–83

Bruschetti M, Bazterrica C, Fanjul E, Luppi T, Iribarne O (2011) Effect of biodeposition of an invasive polychaete on organic matter content and productivity of the sediment in a coastal lagoon. J Sea Res 66:20–28

Buhle ER, Feist BE, Hilborn R (2012) Population dynamics and control of invasive *Spartina alterniflora*: inference and forecasting under uncertainty. Ecol Appl 22:880–893

Buschbaum C, Chapman AS, Saier B (2006) How an introduced seaweed can affect epibiota diversity in different coastal systems. Mar Biol 148:743–754

Buschbaum C, Cornelius A, Goedknegt MA (2016) Deeply hidden inside introduced biogenic structures—Pacific oyster reefs reduce detrimental barnacle overgrowth on native blue mussels. J Sea Res 117:20–26

Byers JE (2000) Competition between two estuarine snails: implications for invasions of exotic species. Ecology 81:1225–1239

Byers JE (2002) Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. Oecologia 130:146–156

Byers JE (2005) Marine reserves enhance abundance but not competitive impacts of a harvested nonindigenous species. Ecology 86:487–500

Byers JE, Goldwasser L (2001) Exposing the mechanism and timing of impact of nonindigenous species on native species. Ecology 82:1330–1343

Byers JE, Gribben PE, Yeager C, Sotka EE (2012) Impacts of an abundant introduced ecosystem engineer within mudflats of the southeastern US coast. Biol Invasions 14:2587–2600

Casazza ML, Overton CT, Bui TVD, Hull JM, Albertson JD, Bloom VK, Bobzien S, McBroom J, Latta M, Olofson P, Rohmer TM, Schwarzbach S, Strong DR, Grijalva E, Wood JK, Skalos SM, Takekawa J (2016) Endangered species management and ecosystem restoration: finding the common ground. Ecol Soc 21:19

Castorani MCN, Hovel KA (2015) Invasive prey indirectly increase predation on their native competitors. Ecology 96:1911–1922

Castorani MCN, Hovel KA (2016) Native predator chemical cues induce anti-predation behaviors in an invasive marine bivalve. Biol Invasions 18:169–181

Chapman JW, Dumbauld BR, Itano G, Markham JC (2012) An introduced Asian parasite threatens northeastern Pacific estuarine ecosystems. Biol Invasions 14:1221–1236

Cheng BS, Hovel KA (2010) Biotic resistance to invasion along an estuarine gradient. Oecologia 164:1049–1059

Cielo-Bazterrica M, Botto F, Iribarne O (2012) Effects of an invasive reef-building polychaete on the biomass and composition of estuarine macroalgal assemblages. Biol Invasions 14:765–777

Cohen AN, Carlton JT, Fountain MC (1995) Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. Mar Biol 122:225–237

Colautti RI, MacIsaac HJ (2004) A neutral terminology to define ‘invasive’ species. Divers Distrib 10:135–141

Costello MJ, Claus S, Dekeyzer S, Vandepitte L, Tuama EO, Lear D, Tyler-Walters H (2015) Biological and ecological traits of marine species. PeerJ 3:e1201. https://doi.org/10.7717/peerj.1201

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166

Daborn GR, Amos CL, Brylinsky M, Christian H, Drapeau G (1993) An ecological cascade effect: migratory birds affect stability of intertidal sediments. Limnol Oceanogr 38:225–231

Davidson TM, Hewitt CL, Campbell M (2008) Distribution, density, and habitat use among native and introduced populations of the Australasian burrowing isopod *Sphaeroma quoianum*. Biol Invasions 10:399–410

Davidson TM, de Rivera CE, Canton JT (2013) Small increases in temperature exacerbate the erosive effects of a non-native burrowing crustacean. J Exp Mar Biol Ecol 446:115–121

Davidson AD, Campbell ML, Hewitt CL, Schaffelke B (2015) Assessing the impacts of nonindigenous marine macroalgae: an update of current knowledge. Bot Mar 58:55–79

Davis MA, Thompson K (2000) Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature scheme for invasion ecology. Bull Ecol Soc Am 81:226–230

de Montaudouin X, Audemard C, Labourg PJ (1999) Does the slipper limpet (*Crepidula fornicata*, L.) impair oyster growth and zoobenthos biodiversity? A revisited hypothesis. J Exp Mar Biol Ecol 235:105–124

Decottignes P, Beninger PG, Rincé Y, Riera P (2007) Trophic interactions between two introduced suspension-feeders, *Crepidula fornicata* and *Crassostrea gigas*, are influenced by seasonal effects and qualitative selection capacity. J Exp Mar Biol Ecol 342:231–241

Delefosse M, Banta GT, Canal-Vergés P, Penha-Lopes G, Quintana CO, Valdemarsen T, Kristensen E (2012) Macrobenthic community response to the *Marenzelleria viridis* (Polychaeta) invasion of a Danish estuary. Mar Ecol Prog Ser 461:83–94

Derivera CE, Ruiz GM, Hines AH, Jivoff P (2005) Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. Ecology 86:3364–3376

Diederich S, Nehls G, van Beusekom JEE, Reise K (2005) Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: invasion accelerated by warm summers? Helgol Mar Res 59:97–106

Dudas SE, McGaw IJ, Dower JF (2005) Selective crab predation on native and introduced bivalves in British Columbia. J Exp Mar Biol Ecol 325:8–17

Dumbauld BR, Wyllie-Echeverria S (2003) The influence of burrowing thalassinid shrimps on the distribution of intertidal seagrasses in Willapa Bay, Washington, USA. Aquat Bot 77:27–42

Dutertre M, Beninger PG, Barillé L, Papin M, Haure J (2010) Rising water temperatures, reproduction and recruitment of an invasive oyster, *Crassostrea gigas*, on the French Atlantic coast. Mar Environ Res 69:1–9

Eash-Loucks WE, Kimball ME, Petrinec MK (2014) Long-term changes in an estuarine mud crab community: evaluating the impact of non-native species. J Crustac Biol 34:731–738

Einfeldt AL, Addison JA (2015) Anthropocene invasion of an ecosystem engineer: resolving the history of *Corophium volutator* (Amphipoda: Corophiidae) in the North Atlantic. Biol J Linn Soc 115:288–304

Einfeldt AL, Doucet JR, Addison JA (2014) Phylogeography and cryptic introduction of the ragworm *Hediste diversicolor* (Annelida, Nereididae) in the Northwest Atlantic. Invertebr Biol 133:232–241

Elton CS (1958) The ecology of invasions by animals and plants. University of Chicago Press, Chicago, 181 pp

Emmerson M (2000) Remedial habitat creation: does *Nereis diversicolor* play a confounding role in the colonisation and establishment of the pioneering saltmarsh plant, *Spartina anglica*? Helgol Mar Res 54:110–116

Engelen AH, Serebryakova A, Ang P, Britton-Simmons K, Mineur F, Pedersen MF, Arenas F, Fernandez C, Steen H, Svenson R, Pavia H, Toth G, Viard F, Santos R (2015) Circumglobal invasion by the brown seaweed *Sargassum muticum*. Oceanogr Mar Biol Annu Rev 53:81–126

Eschweiler N, Christensen HT (2011) Trade-off between increased survival and reduced growth for blue mussels living on Pacific oyster reefs. J Exp Mar Biol Ecol 403:90–95

Estelle V, Grosholz ED (2012) Experimental test of the effects of a non-native invasive species on a wintering shorebird. Conserv Biol 26:472–481

Fei S, Phillips J, Shouse M (2014) Biogeomorphic impacts of invasive species. Annu Rev Ecol Evol Syst 45:69–87

Ferraro SP, Cole FA (2012) Ecological periodic tables for benthic macrofaunal usage of estuarine habitats: insights from a case study in Tillamook Bay, Oregon, USA. Estuar Coast Shelf Sci 102–103:70–83

Firth LB, Knights AM, Bridger D, Evans AJ, Mieszkowska N, Moore PJ, O'Connor NE, Sheehan EV, Thompson RC, Hawkins SJ (2016) Ocean sprawl: challenges and opportunities for biodiversity management in a changing world. Oceanogr Mar Biol Annu Rev 54:193–269

Fofonoff PW, Ruiz GM, Steves B, Simkanin C, Carlton JT (2017) National Exotic Marine and Estuarine Species Information System. http://invasions.si.edu/nemesis/. Accessed 1 Jun 2017

Ge ZM, Zhou X, Wang TH, Wang KY, Pei E, Yuan X (2009) Effects of vegetative cover changes on the carrying capacity of migratory shorebirds in a newly formed wetland, Yangtze River estuary, China. Zool Stud 48:769–779

Gerstenmaier CE, Krueger-Hadfield SA, Sotka EE (2016) Genotypic diversity in a non-native ecosystem engineer has variable impacts on productivity. Mar Ecol Prog Ser 556:79–89

Goedknegt MA, Feis ME, Wegner KM, Luttikhuizen PC, Buschbaum C, Camphuysen CJ, van der Meer J, Thieltges DW (2016) Parasites and marine invasions: ecological and evolutionary perspectives. J Sea Res 113:11–27

Gollasch S (2006) Overview on introduced aquatic species in European navigational and adjacent waters. Helgol Mar Res 60:84–89

Grason EW (2017) Does cohistory constrain information use? Evidence for generalized risk assessment in nonnative prey. Am Nat 189:213–226

Green DS, Crowe TP (2014) Context- and density-dependent effects of introduced oysters on biodiversity. Biol Invasions 16:1145–1163

Green DS, Rocha C, Crowe TP (2013) Effects of non-indigenous oysters on ecosystem processes vary with abundance and context. Ecosystems 16:881–893

Gribben PE, Byers JE, Wright JT, Glasby TM (2013) Positive versus negative effects of an invasive ecosystem engineer on different components of a marine ecosystem. Oikos 122:816–824

Griffen BD (2009) Effects of a newly invasive parasite on the burrowing mud shrimp, a widespread ecosystem engineer. Mar Ecol Prog Ser 391:73–83

Grosholz ED, Ruiz GM, Dean CA, Shirley KA, Maron JL, Connors PG (2000) The impacts of a nonindigenous marine predator in a California bay. Ecology 81:1206–1224

Gutierrez JL, Jones CG, Strayer DL, Iribarne OO (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101:79–90

Hannam MP, Wyllie-Echeverria S (2015) Microtopography promotes coexistence of an invasive seagrass and its native congener. Biol Invasions 17:381–395

Heery EC, Bishop MJ, Critchley LP, Bugnot AB, Airoldi L, Mayer-Pinto M, Sheehan EV, Coleman RA, Loke LHL, Johnston EL, Komyakova V, Morris RL, Strain EMA, Naylor LA, Dafforn KA (2017) Identifying the consequences of ocean sprawl for sedimentary habitats. J Exp Mar Biol Ecol 492:31–48

Heiman KW, Micheli F (2010) Non-native ecosystem engineer alters estuarine communities. Integr Comp Biol 50:226–236

Heiman KW, Vidargas N, Micheli F (2008) Non-native habitat as home for non-native species: comparison of communities associated with invasive tubeworm and native oyster reefs. Aquat Biol 2:47–56

Herbert RJH, Humphreys J, Davies CJ, Roberts C, Fletcher S, Crowe TP (2016) Ecological impacts of non-native Pacific oysters (*Crassostrea gigas*) and management measures for protected areas in Europe. Biodivers Conserv 25:2835–2865

Hewitt JE, Anderson MJ, Thrush SF (2005) Assessing and monitoring ecological community health in marine systems. Ecol Appl 15:942–953

Hewitt JE, Norkko J, Kauppi L, Villnäs A, Norkko A (2016) Species and functional trait turnover in response to broad-scale change and an invasive species. Ecosphere 7:e01289

Katsanevakis S, Wallentinus I, Zenetos A, Leppäkoski E, Çinar ME, Oztürk B, Grabowski M, Golani D, Cardoso AC (2014) Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. Aquat Invasions 9:391–423

Kochmann J, Buschbaum C, Volkenborn N, Reise K (2008) Shift from native mussels to alien oysters: differential effects of ecosystem engineers. J Exp Mar Biol Ecol 364:1–10

Kollars NM, Byers JE, Sotka EE (2016) Invasive decor: an association between a native decorator worm and a non-native seaweed can be mutualistic. Mar Ecol Prog Ser 545:135–145

Kushner RB, Hovel KA (2006) Effects of native predators and eelgrass habitat structure on the introduced Asian mussel *Musculista senhousia* (Benson in cantor) in southern California. J Exp Mar Biol Ecol 332:166–177

Landschoff J, Lackschewitz D, Kesy K, Reise K (2013) Globalization pressure and habitat change: Pacific rocky shore crabs invade armored shorelines in the Atlantic Wadden Sea. Aquat Invasions 8:77–87

Lang AC, Buschbaum C (2010) Facilitative effects of introduced Pacific oysters on native macroalgae are limited by a secondary invader, the seaweed *Sargassum muticum*. J Sea Res 63:119–128

Lejart M, Hily C (2011) Differential response of benthic macrofauna to the formation of novel oyster reefs (*Crassostrea gigas*, Thunberg) on soft and rocky substrate in the intertidal of the bay of Brest, France. J Sea Res 65:84–93

Levin LA, Neira C, Grosholz ED (2006) Invasive cordgrass modifies wetland trophic function. Ecology 87:419–432

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends Ecol Evol 20:223–228

Loebl M, van Beusekom JEE, Reise K (2006) Is spread of the neophyte *Spartina anglica* recently enhanced by increasing temperatures? Aquat Ecol 40:315–324

Mach ME, Levings CD, McDonald PS, Chan KMA (2012) An Atlantic infaunal engineer is established in the Northeast Pacific: *Clymenella torquata* (Polychaeta: Maldanidae) on the British Columbia and Washington coasts. Biol Invasions 14:503–507

Markert A, Esser W, Frank D, Wehrmann A, Exo KM (2013) Habitat change by the formation of alien *Crassostrea*-reefs in the Wadden Sea and its role as feeding sites for waterbirds. Estuar Coast Shelf Sci 131:41–51

Mascaro M, Seed R (2000a) Foraging behavior of *Carcinus maenas* (L.): comparisons of size-selective predation on four species of bivalve prey. J Shellfish Res 19:283–291

Mascaro M, Seed R (2000b) Foraging behavior of *Carcinus maenas* (L.): species-selective predation among four bivalve prey. J Shellfish Res 19:293–300

McDonald PS, Jensen GC, Armstrong DA (2001) The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. J Exp Mar Biol Ecol 258:39–54

McKinnon JG, Gribben PE, Davis AR, Jolley DF, Wright JT (2009) Differences in soft-sediment macrobenthic assemblages invaded by *Caulerpa taxifolia* compared to uninvaded habitats. Mar Ecol Prog Ser 380:59–71

McQuaid KA, Griffiths CL (2014) Alien reef-building polychaete drives long-term changes in invertebrate biomass and diversity in a small, urban estuary. Estuar Coast Shelf Sci 138:101–106

Miron G, Audet D, Landry T, Moriyasu M (2005) Predation potential of the invasive green crab (*Carcinus maenas*) and other common predators on commercial bivalve species found on Prince Edward Island. J Shellfish Res 24:579–586

Mistri M (2004) Effect of *Musculista senhousia* mats on clam mortality and growth: much ado about nothing? Aquaculture 421:207–218

Munari C, Mistri M (2011) Short-term hypoxia modulates *Rapana venosa* (Muricidae) prey preference in Adriatic lagoons. J Exp Mar Biol Ecol 407(2):166–170

Murray NJ, Clemens RS, Phinn SR, Possingham HP, Fuller RA (2014) Tracking the rapid loss of tidal wetlands in the Yellow Sea. Front Ecol Environ 12:267–272

Neckles HA (2015) Loss of eelgrass in Casco bay, Maine, linked to green crab disturbance. Northeast Nat 22:478–500

Nehring S, Hess KJ (2008) Invasive alien plants in marine protected areas: the *Spartina anglica* affair in the European Wadden Sea. Biol Invasions 10:937–950

Neira C, Levin LA, Grosholz ED, Mendoza G (2007) Influence of invasive *Spartina* growth stages on associated macrofaunal communities. Biol Invasions 9:975–993

Newsom AJ, Williams SL (2014) Predation and functional responses of *Carcinus maenas* and *Cancer magister* in the presence of the introduced Cephalaspidean *Philine orientalis*. Estuar Coasts 37:1284–1294

Nicastro A, Bishop MJ, Kelaher BP, Benedetti-Cechi L (2009) Export of non-native gastropod shells to a coastal lagoon: alteration of habitat structure has negligible effects on infauna. J Exp Mar Biol Ecol 374(1):31–36

Nishizawa R, Sato M, Furota T, Tosuji H (2014) Cryptic invasion of Northeast Pacific estuaries by the Asian polychaete, *Hediste diadroma* (Nereididae). Mar Biol 161:187–194

Novais A, Souza AT, Ilarri M, Pascoal C, Sousa R (2015) Facilitation in the low intertidal: effects of an invasive species on the structure of an estuarine macrozoobenthic assemblage. Mar Ecol Prog Ser 522:157–167

Nurkse K, Kotta J, Orav-Kotta H, Parnoja M, Kuprijanov I (2015) Laboratory analysis of the habitat occupancy of the crab *Rhithropanopeus harrisii* (Gould) in an invaded ecosystem: the North-Eastern Baltic Sea. Estuar Coast Shelf Sci 154:152–157

Padilla DK (2010) Context-dependent impacts of a non-native ecosystem engineer, the Pacific oyster *Crassostrea gigas*. Integr Comp Biol 50:213–225

Palacios R, Armstrong DA, Orensanz J (2000) Fate and legacy of an invasion: extinct and extant populations of the soft-shell clam (*Mya arenaria*) in Grays Harbor (Washington). Aquat Conserv Mar Freshw Ecosyst 10:279–303

Papacostas KJ, Rielly-Carroll EW, Georgian SE, Long DJ, Princiotta SD, Quattrini AM, Reuter KE, Freestone AL (2017) Biological mechanisms of marine invasions. Mar Ecol Prog Ser 565:251–268

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3–19

Patten K, O'Casey C (2007) Use of Willapa Bay, Washington, by shorebirds and waterfowl after *Spartina* control efforts. J Field Ornithol 78:395–400

Pintor LM, Byers JE (2015) Individual variation in predator behavior and demographics affects consumption of non-native prey. Behav Ecol 26:797–804

Posey M (1988) Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. Ecology 69:974–983

Priesler RK, Wasson K, Wolff WJ, Tyrell MC (2009) Invasions of estuaries vs the adjacent open coast: a global perspective. In: Rilov G, Crooks JA (eds) Biological invasions in marine ecosystems, Ecological studies, vol 204. Springer, Berlin, pp 587–617

Queiros A, Hiddink JG, Johnson G, Cabral HN, Kaiser MJ (2011) Context dependence of marine ecosystem engineer invasion impacts on benthic ecosystem functioning. Biol Invasions 13:1059–1075

Race MS (1982) Competitive displacement and predation between introduced and native mud snails. Oecologia 54:337–347

Ramus AP, Silliman BR, Thomsen MS, Long ZT (2017) An invasive foundation species enhances multifunctionality in a coastal ecosystem. Proc Natl Acad Sci 114:8580–8585

Reise K (2002) Sediment mediated species interactions in coastal waters. J Sea Res 48:127–141

Reise K, Olenin S, Thieltges DW (2006) Are aliens threatening European aquatic coastal ecosystems? Helgol Mar Res 60:77–83

Ricciardi A, Hoopes MF, Marchetti M, Lockwood JL (2013) Progress toward understanding the ecological impacts of non-native species. Ecol Monogr 83:263–282

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definition. Divers Distrib 6:93–107

Ross DJ, Johnson CR, Hewitt CL, Ruiz GM (2004) Interaction and impacts of two introduced species on a soft-sediment marine assemblage in SE Tasmania. Mar Biol 144:747–756

Ross DJ, Johnson CR, Hewitt CL (2006) Abundance of the introduced seastar, *Asterias amurensis*, and spatial variability in soft sediment assemblages in SE Tasmania: clear correlations but complex interpretation. Estuar Coast Shelf Sci 67:695–707

Ruesink JL, Lenihan HS, Trimble AC, Heiman KW, Micheli F, Byers JE, Kay MC (2005) Introduction of non-native oysters: ecosystem effects and restoration implications. Annu Rev Ecol Evol Syst 36:643–689

Ruesink JL, Hong JS, Wisehart L, Hacker SD, Dumbauld BR, Hessing-Lewis M, Trimble AC (2010) Congener comparison of native (*Zostera marina*) and introduced (*Z. japonica*) eelgrass at multiple scales within a Pacific northwest estuary. Biol Invasions 12:1773–1790

Ruesink JL, Freshley N, Herrold S, Trimble AC, Patten K (2014) Influence of substratum on non-native clam recruitment in Willapa Bay, Washington, USA. J Exp Mar Biol Ecol 459:23–30

Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. Annu Rev Ecol Syst 31:481–531

Sato S, Chiba T, Hasegawa H (2012) Long-term fluctuations in mollusk populations before and after the appearance of the alien predator *Euspira fortunei* on the Tona coast, Miyagi prefecture, northern Japan. Fish Sci 78:589–595

Schwindt E, Iribarne OO, Isla FI (2004) Physical effects of an invading reef-building polychaete on an Argentinean estuarine environment. Estuar Coast Shelf Sci 59:109–120

Shafer DJ, Sherman TD, Wyllie-Echeverria S (2007) Do desiccation tolerances control the vertical distribution of intertidal seagrasses? Aquat Bot 87:161–166

Simberloff D, von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biol Invasions 1:21–32

Smith TE, Ydenberg RC, Elner RW (1999) Foraging behaviour of an excavating predator, the red rock crab (*Cancer productus* Randall) on soft-shell clam (*Mya arenaria* L.). J Exp Mar Biol Ecol 238:185–197

Sorte CJB, Williams SL, Zerebecki RA (2010) Ocean warming increases threat of invasive species in a marine fouling community. Ecology 91:2198–2204

Sorte CJB, Ibañez I, Blumenthal DM, Molinari NA, Miller LP, Grosholz ED, Diez JM, D'Antonio CM, Olden JD, Jones SJ, Dukes JS (2013) Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. Ecol Lett 16:261–270

Sousa R, Guttierrez JL, Aldridge DC (2009) Non-indigenous invasive bivalves as ecosystem engineers. Biol Invasions 11:2367–2385

Stachowicz JJ, Terwin JR, Whitlatch RB, Osman RW (2002) Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. Proc Natl Acad Sci USA 99:15497–15500

Strong DR, Ayres DR (2013) Ecological and evolutionary misadventures of *Spartina*. Annu Rev Ecol Evol Syst 44:389–410

Talley T, Crooks J, Levin L (2001) Habitat utilization and alteration by the invasive burrowing isopod, *Sphaeroma quoyanum*, in California salt marshes. Mar Biol 138:561–573

Taylor SL, Bishop MJ, Kelaher BP, Glasby TM (2010) Impacts of detritus from the invasive alga *Caulerpa taxifolia* on a soft sediment community. Mar Ecol Prog Ser 420:73–81

Thieltges DW, Strasser M, Reise K (2006) How bad are invaders in coastal waters? The case of the American slipper limpet *Crepidula fornicata* in western Europe. Biol Invasions 8:1673–1680

Thomsen MS, Wernberg T, Altieri A, Tuya F, Gulbransen D, McGlathery KJ, Holmer M, Silliman BR (2010) Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integr Comp Biol 50:158–175

Thomsen MS, Wernberg T, Olden JD, Griffin JN, Silliman BR (2011) A framework to study the context-dependent impacts of marine invasions. J Exp Mar Biol Ecol 400:322–327

Thomsen MS, Byers JE, Schiel DR, Bruno JF, Olden JD, Wernberg T, Silliman BR (2014) Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. Mar Ecol Prog Ser 495:39–47

Tosuji H, Furota T (2016) Molecular evidence for the expansion of the Asian cryptic invader *Hediste diadroma* (Nereididae: Annelida) into the Northeast Pacific habitats of the native *H. limnicola*. Zool Sci 33:162–169

Townsend M, Lohrer AM, Rodil IF, Chiaroni LD (2015) The targeting of large-sized benthic macrofauna by an invasive portunid predator: evidence from a caging study. Biol Invasions 17:231–244

Troost K (2010) Causes and effects of a highly successful marine invasion: case-study of the introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries. J Sea Res 64:145–165

Tsai C, Yang S, Trimble AC, Ruesink JL (2010) Interactions between two introduced species: *Zostera japonica* (dwarf eelgrass) facilitates itself and reduces condition of *Ruditapes philippinarum* (manila clam) on intertidal flats. Mar Biol 157:1929–1936

Turoboyski K (1973) Biology and ecology of the crab *Rhithropanopeus harrisii ssp. tridentatus*. Mar Biol 23:303–313

Valdez SR, Ruesink JL (2017) Scales of recruitment variability in warming waters: comparing native and introduced oysters in Hood Canal, Washington, USA. Mar Ecol 38(3):e12435

van den Brink AM, Wijnhoven S, McLay CL (2012) Competition and niche segregation following the arrival of *Hemigrapsus takanoi* in the formerly *Carcinus maenas* dominated Dutch delta. J Sea Res 73:126–136

van der Heide T, Tielens E, van der Zee EM, Weerman EJ, Holthuijsen S, Eriksson BK, Piersma T, van de Koppel J, Olff H (2014) Predation and habitat modification synergistically interact to control bivalve recruitment on intertidal mudflats. Biol Conserv 172:163–169

Wagner E, Dumbauld B, Hacker S, Trimble AC, Wisehart LM, Ruesink JL (2012) Density-dependent effects of an introduced oyster (*Crassostrea gigas*) on a native intertidal seagrass (*Zostera marina*). Mar Ecol Prog Ser 468:149–160

Waser AM, Splinter W, van der Meer J (2015) Indirect effects of invasive species affecting the population structure of an ecosystem engineer. Ecosphere 6(7):art109

Wasson K, Fenn K, Pearse JS (2005) Habitat differences in marine invasions of Central California. Biol Invasions 7:935–948

Weigel B, Blenckner T, Bonsdorff E (2015) Maintained functional diversity in benthic communities in spite of diverging functional identities. Oikos 125:1421–1433

Wendling CC, Wegner KM (2015) Adaptation to enemy shifts: rapid resistance evolution to local *Vibrio* spp. in invasive Pacific oysters. Proc R Soc B 282:20142244

Westley PAH (2011) What invasive species reveal about the rate and form of contemporary phenotypic change in nature. Am Nat 177:496–509

White LF, Orr LC (2011) Native clams facilitate invasive species in an eelgrass bed. Mar Ecol Prog Ser 424:87–95

Whitlow WL (2010) Changes in survivorship, behavior, and morphology in native soft-shell clams induced by invasive green crab predators. Mar Ecol 31:418–430

Whitlow WL, Rice NA, Sweeney C (2003) Native species vulnerability to introduced predators: testing an inducible defense and a refuge from predation. Biol Invasions 5:23–31

Wieser W (1959) The effect of grain size on the distribution of small invertebrates inhabiting the beaches of Puget Sound. Limnol Oceanogr 4:181–194

Wilson WH (1990) Competition and predation in marine soft-sediment communities. Annu Rev Ecol Syst 21:221–241

Witte S, Buschbaum C, van Beusekom JEE, Reise K (2010) Does climatic warming explain why an introduced barnacle finally takes over after a lag of more than 50 years? Biol Invasions 12:3579–3589

Wong MC, Dowd M (2014) Role of invasive green crabs in the food web of an intertidal sand flat determined from field observations and a dynamic simulation model. Estuar Coasts 37:1004–1016

Wonham MJ, O'Connor M, Harley CDG (2005) Positive effects of a dominant invader on introduced and native mudflat species. Mar Ecol Prog Ser 289:109–116

Woodin SA (1976) Adult-larval interactions in dense infaunal assemblages: patterns of abundance. J Mar Res 34:25–41

Wrange AL, Valero J, Harkestad LS, Strand O, Lindegarth S, Christensen HT, Dolmer P, Kristensen PS, Mortensen S (2010) Massive settlements of the Pacific oyster, *Crassostrea gigas*, in Scandinavia. Biol Invasions 12:1145–1152

Wright JT, Byers JE, Devore JL, Sotka EE (2014) Engineering or food? Mechanisms of facilitation by a habitat-forming invasive seaweed. Ecology 95:2699–2706

Chapter 12
Shorebirds as Integrators and Indicators of Mudflat Ecology

Kimberley J. Mathot, Theunis Piersma, and Robert W. Elner

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Abstract Shorebirds are major, but thus far under-acknowledged, players in mudflat food webs and associated physio-chemical processes. Mud is a critical habitat

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type for shorebirds, offering a multi-dimensional matrix of feeding opportunities through space and time. Shorebirds have evolved a spectrum of foraging modes with associated morphologies, and sensory and physiological adaptations which exploit these foraging opportunities. Although shorebirds are mud specialists and sentinels of mudflat ecosystem functioning, they have not yet been well integrated into the "mud club". In this chapter, we highlight the key roles shorebirds play in food webs, and in physical and chemical processes within mudflat ecosystems. We illustrate how shorebird distribution and behaviour provides a mirror of mudflat ecology because their foraging behaviour reflects the underlying ecological conditions, including temporal and spatial patterns in food/community structure in and across mud. In particular, shorebirds may be important indicators of essential fatty acid production by diatoms in epibenthic biofilm fields covering muddy intertidal flats, especially in estuaries. We conclude by highlighting the major challenges facing shorebirds today and call for a paradigm shift in shorebird conservation, based on recreating and restoring intertidal mud ecosystems.

1 Introduction

In this chapter, we will discuss the role of shorebirds, or waders (order Charadriifomes) in mudflat ecology. Exposed intertidal mudflats provide critical habitat for shorebirds for roosting, and more particularly, for foraging. Spectacular numbers of shorebirds congregate on mudflats at different stages in their annual cycles, with many mudflats and estuaries supporting >100,000 shorebirds annually (Fig. 12.1).

Mudflats are important feeding areas to shorebirds for various reasons. Mudflats tend to be productive, offering a wide diversity and high abundance of potential food. In addition, mudflats remain accessible in winter, even after interior wetlands at similar latitudes have become inaccessible, both due to the lower freezing point of sea water, and the relatively warmer ambient temperatures in coastal compared to inland areas (Warnock et al. 2002).

As has been repeatedly demonstrated in this book, while mudflats appear deceptively simple, uniform and barren from the shore, the realities of mud are physically, chemically and biologically complex. The biotic communities of mudflats populate a three-dimensional mosaic subjected to alternating periods of exposure and inundation by tides in addition to seasonal cycles (Whitlatch 1977; Martini and Wanless 2014). Tides limit shorebird distributions by making areas of mudflat inaccessible during flood and ebb tides every lunar day (24 h 50 min), and also shape shorebird distributions through their effects on the distribution of food (see Chaps. 5, 6 and 8). In this chapter, we will discuss the central role of shorebirds in mudflat ecosystems, including their role as primary consumers of intertidal epibenthic biofilms (Kuwae et al. 2008, 2012).

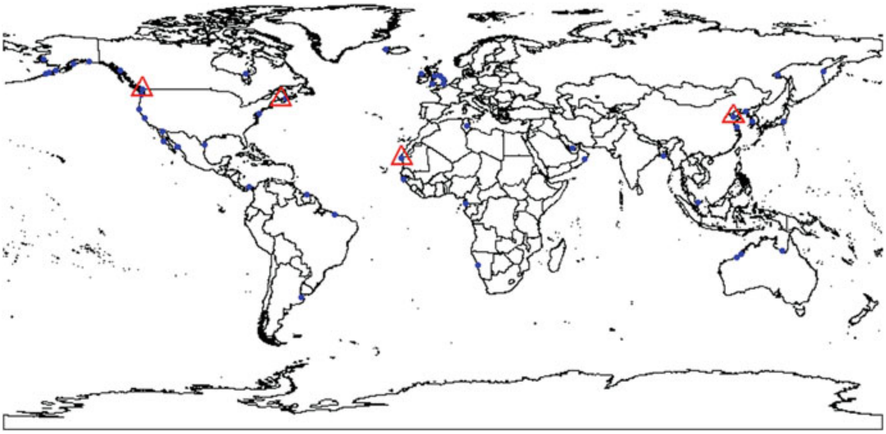

Fig. 12.1 Mudflats that annually host >100,000 shorebirds illustrated with solid blue circles. Data taken from summary Table in Butler et al. (2001). The four study areas highlighted as case studies are indicated with red open triangles. Map created in R v3.3.3 (R Development Core Team 2017) using the 'rworldxtra' library.

2 Shorebird Foraging Modes and Diets

Shorebirds that forage on intertidal mudflats face the challenges of locating and extracting food at sufficient rates, without ingesting excessive amounts of sediment within a tidal cycle. Several broad categories of foraging mode have been described, with individual species usually exhibiting more than one mode, depending on habitat, season and prey availability (van de Kam et al. 2004; Colwell 2010). Epifaunal prey visible on the surface are captured by *pecking* (Zweers and Gerritsen 1997), while prey suspended in shallow water are taken up the bill via *surface tension transport* (Rubega 1997) or *bill sweeping* (Moreira 1995; Barbosa and Moreno 1999). Shorebirds can capture buried prey by *probing* their bills into the sediment (Zweers and Gerritsen 1997). These modes each target a range of invertebrate taxa and sometimes the rhizomes of marine plants such as seagrasses (Robin et al. 2013). The fifth, most recently discovered foraging mode, *biofilm grazing*, targets an entirely distinct food source at the base of the food chain that was previously thought accessible only to invertebrates and fish (Kuwae et al. 2008, 2012).

2.1 Functional Morphology, Digestion and Physiology

For shorebirds, life on mudflats is associated with a suite of morphological and physiological adaptations. Shorebirds are characterized by having relatively long, slender legs compared to other birds (Johnsgard 1981; Barbosa and Moreno 1999), which allow them to wade while foraging without wetting their body feathers. In general, shorebird feet exhibit a similar arrangement of toes, with three forward facing digits and one backward facing digit, and many species exhibit partial or complete webbing between the toes (Johnsgard 1981). Both of these foot characteristics facilitate walking on mudflat surfaces but do not appear to be associated with particular foraging modes (Barbosa and Moreno 1999).

Other aspects of morphology (e.g., body size, eye size and placement, bill and tongue structure) and physiology (e.g., digestive organ size, enzyme activities) show clear associations with the specific foraging modes described in the previous section (Table 12.1). Shorebirds specialized in visual hunting of surface or shallowly buried prey (e.g., Charadriidae, see Fig. 12.2) tend to have short bills, and large, frontally positioned eyes with high visual acuity and a broad binocular field (Martin 2007). In comparison, shorebirds that forage on buried prey (e.g., Scolopacidae) cannot locate prey by sight. Their eyes are set higher in the skull, resulting in a narrow binocular field and maximizes their ability to detect approaching predators (Martin and Piersma 2009). Also, their bills are longer, more robust (Martin and Piersma 2009), and contain receptors (Herbst and Grandry corpuscules) that can detect changes in pressure, and are used to locate invertebrates within the sediment (Gerritsen and Meiboom 1986). Some probing foragers specialize on ‘soft’ food items, such as lugworms, while others may specialize on ‘hard’ food items, such as molluscs (van de Kam et al. 2004; Colwell 2010). Red knots, *Calidris canutus*, are particularly specialized in locating small hard objects in wet soft sediments by sensing the deviations from a spherical pressure field built up around a probing bill (Piersma et al. 1998; de Fouw et al. 2016). Molluscivoran shorebirds that swallow their prey whole, such as red knots, possess large, muscular digestive organs (e.g., the gizzard, a muscular stomach), effective in both crushing shells and processing large volumes of indigestible materials (Piersma et al. 1993; Battley and Piersma 2005b).

In contrast to the morphological adaptations for shorebirds foraging on invertebrates, epibenthic biofilm feeding depends primarily on tongue microstructure rather than bill macrostructure. Intertidal epibenthic biofilm is a thin, matrix-enclosed community of microphytobenthos (MPB), bacteria, and organic detritus bound together and adhered to the sediment surface by copious amounts of extracellular polymeric substances (EPS) (Stal 2003; Underwood and Paterson 2003, and see Chaps. 2, 3, 4, 5, 8 and 10). Diatoms within the biofilm afford easily digestible energy as well as a rich source of omega-3 fatty acids, particularly in their blooming phase (Duerksen et al. 2014; Stonik and Stonik 2015). Keratinized lateral spines coated in mucus along the edges and at the tip of the shorebird tongue are used to rapidly dab biofilm off the sediment surface, while backwardly-directed maxillary denticles on the tongue prevent biofilm boli from slipping forward out of the bill (Elner et al. 2005). Biofilm feeding appears most prevalent in “peeps” (Kuwae et al. 2008; Beninger et al. 2011; Quinn and Hamilton 2012; Jiménez et al. 2015), the smallest of the shorebirds, and in stints (Lourenço et al. 2017), but all shorebirds, including plovers, appear functionally able, and likely, to graze biofilm (Kuwae et al. 2012). Because biofilm is an easily digested food source (Duerksen et al. 2014; Stonik and Stonik 2015), large digestive organs are not a prerequisite (Kuwae et al. 2012). However, biofilm feeders likely require specific enzymes to process

Table 12.1 Overview of morphological and physiological adaptations associated with principle foraging modes, associated food types and representative shorebird species

Foraging mode	Body size	Search mode	Morphological adaptations	Physiological requirements	Diet	Representative shorebirds
Biofilm grazing	Small	Visual or gustatory	Short bill, spines on tongue	Enzymes for processing omega-3 fatty acids	Biofilm, diatoms, meiofaunal prey suspended in biofilm matrix	Peeps and stints
Pecking		Visual	Large, proximally placed eyes short bill		Epifaunal invertebrates, wide range of sizes	Plovers
Probing	Medium to large	Tactile	Long, robust bill with sensory pits	Large digestive organs	Infaunal invertebrates, large size	Medium to large sized sandpipers (red knots, curlews, whimbrels, etc)
STT		Visual	Needle shaped bill			Phalaropes, avocets

Where there are not specific adaptations required for effective use of a foraging mode, the cell is left blank. Surface tension transport (STT) requires little specialized morphological adaptation, and is therefore likely used opportunistically by a variety of shorebirds

Fig. 12.2 Ringed plovers (here capturing a polychaete) exhibit the typical morphology of visual foargers; large, frontally located eyes and short bills. Photo by Jan van de Kam.

Fig. 12.3 An avocet with prey enveloped in a water droplet at the tip of the bill. Photo by Jan van de Kam.

the omega-3 fatty acids that comprise a major component of diatomaceous biofilms (Duerksen et al. 2014; Stonik and Stonik 2015).

Although there has not been a detailed cataloguing of shorebird species that use surface tension transport to move small prey items up the bill, this foraging mode is commonly used in phalaropes and avocets (Rubega and Obst 1993; Rubega 1997) (see Fig. 12.3). Surface tension transport requires only the ability to modulate gape size, and a needle-shaped bill. The needle-shaped bill results in an increase in contact area and reduction in the free surface area of water drops in a proximal to distal direction along the bill, which facilitates the transport of droplets up the bill (Rubega and Obst 1993; Rubega 1997). As this bill shape is almost universal among shorebirds, surface tension transport is likely also widespread (Rubega 1997), and may represent an opportunistic foraging mode as opposed to a true specialization.

2.2 Flexible Foragers

The morphological and physiological adaptations required by the alternative foraging modes and diets do not constrain shorebirds to any single mode. Seasonal shifts in foraging mode and diet occur as a result of changes in the availability of alternative food types (Beukema et al. 1993) as well as fluxes in the demand for particular nutrients. Red knots (*Calidris canutus islandica*) are an excellent example of such foraging plasticity across their annual cycle. Red knots feed primarily on hard-shelled molluscs during the non-breeding season in the Dutch Wadden Sea in Northwestern Europe and, consequently, have large digestive organs including the gizzard, which process these prey (Battley and Piersma 2005a). However, during the breeding season in the Canadian High Arctic, they feed on superabundant arthropod prey, which are of higher digestive quality. Consequently, their gizzards atrophy, becoming a fraction of their winter gizzard mass (Vézina et al. 2012). On return to the non-breeding grounds in late summer, peaks in the availability of the common shrimp (*Crangon crangon*), a high quality food item, allow red knots to continue pecking for surface prey and to maintain relatively small digestive organs until autumn, when the availability of these prey types decline and knots resume feeding on low digestive quality bivalves (van Gils et al. 2005).

Western sandpipers (*Calidris mauri*) also exhibit a high degree of flexibility in the use of alternative foraging modes and diets (Elner and Seaman 2003). Females, the longer-billed sex, have a higher use of probing compared with males (Mathot and Elner 2004), and also winter in more southerly regions where buried prey are relatively more abundant (Mathot et al. 2007). Yet in both males and females, epibenthic biofilm grazing peaks during northward migration at stopovers such as the Fraser River Delta, British Columbia (Beninger et al. 2011) (see also Sect. 4 in Chap. 8). This peak in biofilm use coincides with a period in the annual cycle of migrant shorebirds when deposition of nutrient stores (both fat and protein) is critical for making long-distance flights between successive stopover sites (Piersma et al. 2005; Guglielmo 2010).

3 Shorebirds as Sentinels

Shorebirds depend on mudflats, and exhibit a suite of morphological and physiological adaptations which aid in efficiently locating and exploiting the foods mudflats have to offer [see above and review in van de Kam et al. (2016)]. Given their evolved relationship with mudflats, what, if anything, can careful observation of habitat use and foraging decisions by shorebirds teach us about mudflats? It turns out, quite a bit.

3.1 Shorebird Distributions

Shorebirds integrate information on multiple fitness-relevant parameters when selecting habitat, including the distribution and abundance of food, predators, and competitors (Piersma and Lindström 2004; Escudero et al. 2012). This occurs on 'contemporary' time scales, yet current shorebird distributions may also reflect competitive processes that have their origin in 'deep time' (Bom et al. 2018). With a solid understanding of their biology, the distribution of shorebirds can provide clues about the positioning of these factors (Piersma and Lindström 2004). For example, global patterns of shorebird distributions may provide a coarse proxy for global patterns of mudflat productivity (Butler et al. 2001). Mudflats require particular combinations of geological, physical and chemical conditions to form (see Chap. 2), and there are some seventy-nine intertidal mudflat areas worldwide with surface areas of over 5000 hectares (Deppe 1999). However, shorebirds are not found in equal densities across all available mudflats. Shorebirds are generally found in areas where species-specific food availability is highest, moderated by additional factors such as their own risk of predation by falcons (Zwarts and Wanink 1993; Ydenberg et al. 2002; van de Kam et al. 2004; Quaintenne et al. 2011; Piersma 2012).

Within sites, the behaviour and distribution of shorebirds also provide clues about local conditions (Folmer et al. 2012; Folmer and Piersma 2012). For example, the use of different zones in the intertidal reveals information about the distribution of food resources in general, and differences in the distributions of shorebirds known to specialize on different types of prey provide clues about differential distributions of prey types (Duijns et al. 2014, 2015; Bijleveld et al. 2016).

As mudflats are tidally-structured environments, shorebirds can only feed when the mudflats become exposed and accessible to foraging. Some shorebirds, such as dunlin (*Calidris alpina*) or redshank (*Tringa totanus*), will begin feeding almost the moment the upper intertidal area begins to be exposed, while other shorebirds, such as oystercatchers (*Haemotopus ostralegus*) and curlew (*Numenius arquata*), tend to wait longer on the falling tide before beginning feeding (van de Kam et al. 2004). Readers with some knowledge about shorebirds will realize that dunlin and redshank are small shorebirds, while curlew and oystercatcher are large, and as detailed above, smaller birds eat smaller prey. The timing of feeding of small shorebirds relative to large shorebirds on the falling tide reflects the spatial distribution of their preferred prey (van de Kam et al. 2004; Piersma et al. 2017), as well as limitations in their ability to access prey at different times based on their morphology (e.g., leg and bill length) and water depth. The larger prey preferred by oystercatchers and curlews occur mainly low in the intertidal zone, while the most important food for small shorebirds such as dunlin and redshank are found higher in the intertidal area.

The movement of shorebirds across the intertidal areas as they become exposed, also integrates information on the distribution of resources. However, food is not the only factor shaping foraging decisions. Shorebirds must also avoid predators. For many shorebirds, the upper intertidal area is the most dangerous during daytime

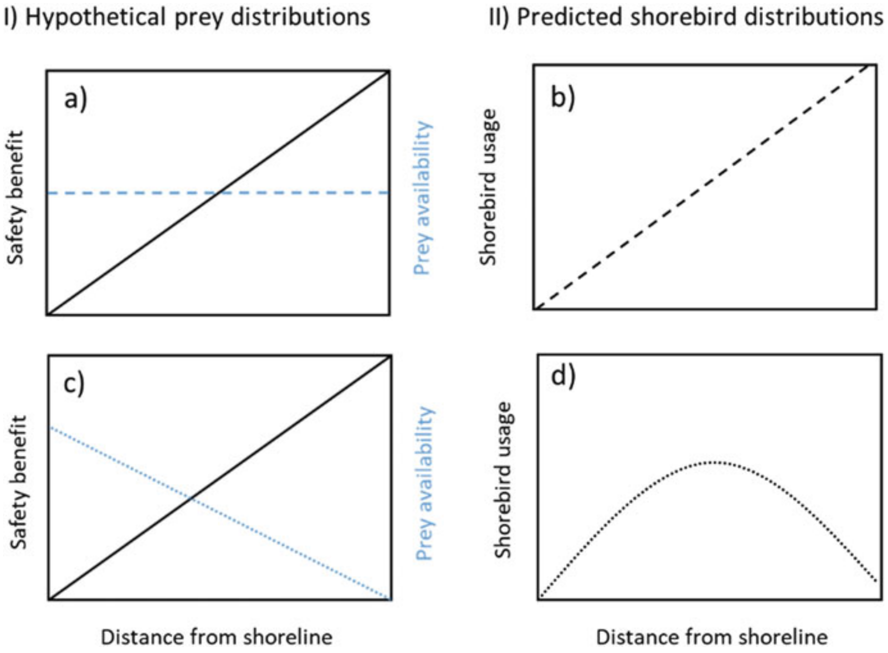

Fig. 12.4 Two hypothetical scenarios of food distribution along the intertidal (**a**, **c**) and the consequences for predicted shorebird distributions (**b**, **d**) if shorebirds are balancing food and safety. The first scenario (**a**), with a homogenous distribution of prey relative to the location in the intertidal predicts shorebird distributions to mirror the safety (**b**), while the second scenario, where prey abundance decreases with increasing distance from the shoreline (**c**), predicts a peak in shorebird use at intermediate distances from the shore (**d**).

foraging, because common shorebird predators, notably peregrine falcons (*Falco peregrinus*), sparrowhawks (*Accipiter nisus*) and merlin (*Falco columbarius*), have the greatest attack success when they are able to fly low over marsh vegetation, concealing their approach (Page and Whitacre 1975; Lazarus and Symonds 1992; Cresswell 1993; Dekker and Ydenberg 2004; Quinn and Cresswell 2004; van den Hout et al. 2014, 2017). If predation danger declines moving down the intertidal zones, we can predict how shorebirds should use the mudflat under different scenarios of resource distribution (Fig. 12.4). If appropriate-sized prey are distributed homogenously across the intertidal, then shorebirds would be expected to follow the tide as it moves out, because they can reduce predation danger without any reduction in food availability. Alternatively, if prey abundance is higher in the upper intertidal, for example because of differences in sediment characteristics or nutrient availability, then shorebirds would face a conflict between following the tide (minimizing predation risk), and remaining in the upper intertidal (maximizing intake rates), and they would be expected to show a peak intensity of mudflat use reflecting a compromise between avoiding predation and gaining energy (Pomeroy 2006; Fuller et al. 2013; but see also Jiménez et al. 2015).

Obtaining an overall estimate of mudflat use is challenging when intertidal areas are so vast as to make it impossible to perform simultaneous shorebird counts across the full intertidal zone. Nevertheless, just as distribution of shorebirds can be used to infer local resource conditions, the density of shorebird droppings can be used to infer the intensity of use of different zones in the intertidal area. Pomeroy (2006) found that shorebird droppings showed a peaked distribution in the mid-intertidal, consistent with the scenario where food abundance declined with distance from the upper intertidal. The invertebrate resource distribution was later confirmed to decline from the upper to lower intertidal, via benthos sampling (see Fig. 1 in Pomeroy 2006).

If the distribution and behaviour of shorebirds within- and across mudflats reflects current ecological conditions, then it follows that long-term changes in their distribution and/or behaviour may reflect long-term changes in ecological conditions. Given our knowledge of the factors driving variation in shorebird numbers, behaviour, morphology, and physiology, shorebirds may also serve as sentinels of changing conditions (Piersma 2003; Piersma and Lindström 2004; Kraan et al. 2009). We illustrate this notion with two examples.

3.2 Shorebirds as Indicators of Local Prey Changes

When shorebirds are highly specialized on particular prey resources at a site, changes in the availability of that resource may be mirrored by changes in the abundance of shorebirds at those sites. For example, the overexploitation of horseshoe crabs by humans resulted in catastrophic declines in the *rufa* subspecies of red knot (*Calidris canutus rufa*), which are highly dependent on lipid-rich horseshoe crab eggs while on stopover in Delaware Bay (USA) to refuel during their northward migration (Myers 1986; Baker et al. 2004; Niles et al. 2009). Similarly, declines in the abundance of shellfish in the UK and The Netherlands caused by local shellfisheries were associated with declines in molluscivore shorebirds (Piersma 2007; Kraan et al. 2009; Atkinson et al. 2010; van Roomen et al. 2012). At the same time, polychaete abundances increased, which was correlated with increases in the abundance of worm-eating waders (van Roomen et al. 2012).

In another example, the initiation of a baitworm harvesting industry in the Bay of Fundy, Canada, resulted in dramatic changes in foraging efficiency in semipalmated sandpipers, via its effects on non-target species in the community (Shepherd and Boates 1999). Areas of sediment that were disturbed by baitworm harvesting had 39% lower densities of *Corophium volutator* compared with undisturbed areas of sediment, and juvenile *C. volutator* were most strongly affected. This translated to a nearly 70% lower rate of capture of *C. volutator* by foraging semipalmated sandpipers, suggesting that the disturbance of sediment during baitworm harvesting may have additionally interfered with the use of visual and tactile cues (Shepherd and Boates 1999). Changes in the abundance and distribution of invertebrates, with concomitant shifts in shorebird abundances have also been documented in response to eutrophication (Alves et al. 2012) and the presence of pollutants (Furness 1993).

3.3 Shorebirds as Integrated Sentinels of Global Change

It is important to recognize that local changes in shorebird abundance or behaviour do not necessarily reflect changes in local conditions. Many shorebirds cover large areas of the globe over the course of their annual migratory cycle, and changing conditions at any one location could have cascading effects throughout their distribution. Perhaps the most striking example of shorebirds as integrated sentinels of global change comes from long-term studies of red knots at a major non-breeding site, the Banc d'Arguin, Mauritania.

The *canutus* subspecies of red knot (*Calidris canutus canutus*) has been studied intensively on the Banc d'Arguin for over 30 years. Red knots feed primarily on molluscs during the non-breeding season, which they consume whole and crush in their muscular gizzards (Battley and Piersma 2005a). On the Banc d'Arguin, the two principal molluscs making up their diet are *Dosinia isocardia* and *Loripes lucinalis* (see also Sect. 5.2). As part of a long-term research program aimed at monitoring the relative consumption of these two prey types, blood samples were collected over a period of 12 years and stable isotope analyses were used to infer diet. Unexpectedly, the analyses revealed that red knots were consuming rhizomes of the seagrass *Zostera noltii* and further that the relative contribution of seagrass to the diet was increasing across years (van Gils et al. 2016). More intriguingly, benthos sampling programs suggested that bivalve prey abundances were stable over the same time period. If local conditions on the Banc d'Arguin weren't driving the shift in diet, what was?

In fact, the changing diet of knots in Mauritania appears to be a cascading consequence of warming Arctic temperatures (van Gils et al. 2016). Red knots breed in the High Arctic. They arrive in early spring and must wait until after snowmelt to initiate their nests. Over the last 30 years, the date of snowmelt has advanced by an average of 0.5 days per year. Knots have simultaneously advanced the timing of their northward migration to the breeding grounds, but at only half the rate of the advancing snow melt (0.25 days per year on average) (van Gils et al. 2016). Consequently, knots are breeding later relative to snow melt dates, which may be contributing to a mismatch between the timing of chick hatching and the timing of invertebrate emergence (i.e., trophic mismatch). Such phenological mismatches have been proposed to result in decreased body size, due to organisms receiving suboptimal nutrition during their periods of most rapid growth. Indeed, knots have also decreased in body size, and more importantly, in bill length, over the last 30 years (van Gils et al. 2016).

The decrease in bill length may explain the diet shifts observed in Mauritania. Seagrass rhizomes are found very near the sediment surface, whereas *Dosinia* and *Loripes* are buried below the surface (Fig. 12.5). Thus, the bivalves are less

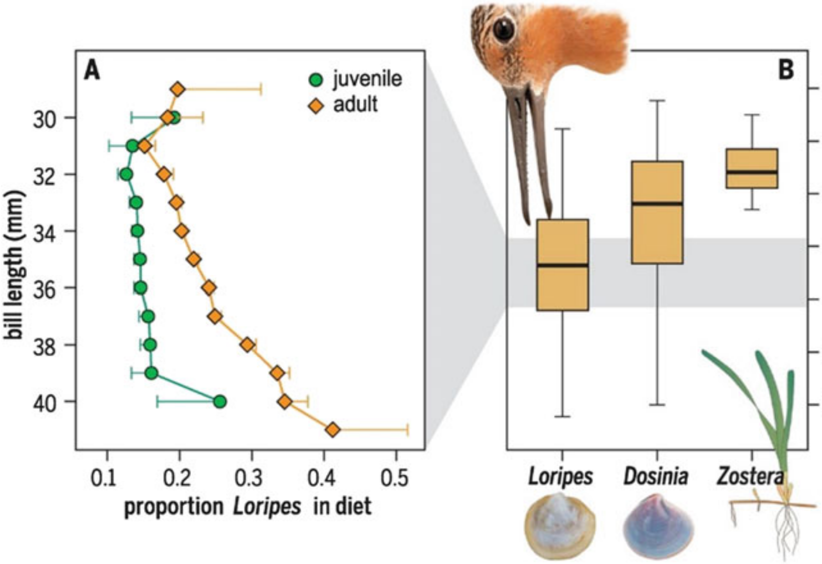

Fig. 12.5 Illustration of how decreasing bill length in red knots is associated with shifts in diets. (**a**) The proportion of *Loripes* in the diet is positively correlated with bill length. (**b**) The most accessible food to short-billed knots is *Zostera* seagrass. Figure reproduced with permission from van Gils et al. (2016).

accessible to shorter-billed birds, which may explain the recent increase in contribution of seagrass rhizomes to the overall diet of red knots in Mauritania.

4 Ecological Impacts of Shorebirds on Mudflats

Although shorebirds are major players in mudflat communities, and can contribute substantially to the understanding of intertidal mudflat ecology, to date, they have more typically been viewed as minor predators of low economic importance, compared to other players such as fish and invertebrates. Most shorebird research has been conducted with a strong ornithological focus, with only narrow connectivity to other intertidal mud-related disciplines in biology, ecology and oceanography. Yet shorebirds occupy a central place in mudflat trophic webs (Piersma 1987; Kuwae et al. 2012), and exert major predatory, physical and chemical impacts on mudflats.

The direct trophic links between shorebirds and primary producers, and between primary consumers and secondary consumers, reveals more complex trophic relationships than previously thought for shorebirds (Kuwae et al. 2012), and has provided new insights into community structure of mudflat ecosystems around the world. For example, direct competition between shorebirds and invertebrates for epibenthic biofilm could explain why small shorebirds are less abundant in the

African-Eurasian flyways, where they face high competition with other biofilm grazers (Bocher et al. 2007; Kuwae et al. 2012). In addition, complex food webs with greater trophic redundancy are generally more resilient, compared with relatively more simple food webs (Hooper et al. 2005). Further work identifying and modelling the links between food web complexity and ecosystem resilience should provide critical information for more effective management of shorebird habitats (Catry et al. 2016).

Does predation by shorebirds reduce prey populations? Observations on foraging rates of shorebirds, combined with shorebird densities, would suggest that they almost certainly must. However, detecting depletion of invertebrate prey by shorebirds is notoriously difficult (Sutherland et al. 2000; van der Meer et al. 2001; Colwell 2010). Estimating invertebrate abundances is itself challenging, given the heterogeneous nature of mudflats (both temporally and spatially), combined with the challenges of accurately identifying and enumerating samples (see Chaps. 5, 6, 8, and 15). In addition, rates of prey removal, though great, may not exceed rates of prey replacement (e.g., via reproduction) (e.g., Kalejta 1993).

Despite the technical complexities of detecting the predatory impacts of shorebirds, numerous studies have documented significant depletion of invertebrate prey by shorebirds, and in some cases, extreme depletion (reviewed in Colwell 2010). For example, shorebirds in the coastal wetlands of South Carolina during northward migration reduced both the density and biomass of invertebrates by approximately 50% (Weber and Haig 1997), and shorebirds at staging areas in Massachusetts during southward migration depleted prey by between 7 and 90%, depending on the year and prey type (Schneider and Harrington 1981).

Not surprisingly, evidence for prey depletion by shorebirds has more commonly been detected during migration, a period where increased energy demand couples with large numbers of shorebirds (sometimes in the hundreds of thousands) passing through a single site over a very punctuated time period. However, moderate levels of depletion of invertebrate prey by shorebirds has also been detected on the non-breeding grounds (e.g., Zwarts and Drent 1981; Zharikov and Skilleter 2003; Bijleveld et al. 2015). One example of extreme depletion of prey during the non-breeding season was that of an estimated depletion of *Hydrobia* and *Nereis* by approximately 90% in the Tees estuary, UK, where the intensity of prey depletion was likely exacerbated by port developments that significantly reduced the foraging areas available to shorebirds (Evans et al. 1979).

In addition to exerting strong effects on invertebrate numbers and biomass, predation by shorebirds has substantial physical and chemical impacts on mudflat ecosystems. Invertebrate grazers on epibenthic biofilm are recognized as important ecosystem engineers, altering the spatial-self organization of mudflats (Weerman et al. 2011, and see Chaps. 5, 6, 8, and 10). With grazing rates on epibenthic biofilm during migration at Roberts Bank in the Fraser River estuary, Canada, estimated at seven times body mass per day for an individual western sandpiper, and flock sizes in the tens to hundreds of thousands of shorebirds over a single tidal cycle, western sandpipers are estimated to be turning over 15 tonnes of sediment per day at this site (Elner et al. 2005; Kuwae et al. 2008). Thus, bioturbation resulting from biofilm grazing by large flocks of shorebirds has the potential to dramatically alter the physical structure of mudflat ecosystems.

Shorebirds can also have substantial chemical impacts on mudflats. For example, defaecation by shorebirds on mudflats can be a source of both organic and inorganic nutrients. Experiments have shown that defaecation by shorebirds can increase growth rates of diatomaceous biofilms by 20% (Jauffrais et al. 2015) and provide a route through which both nutrients and toxins move into and out of intertidal ecosystems (Saint-Béat et al. 2013; St. Clair et al. 2015). Comparisons of trophic webs and ecosystem functioning at the Brouage mudflats in the Marenne-Oleron Bay, France, at two different times of year highlight the critical role of shorebirds in nutrient cycling. Although the overall trophic links were similar both in winter (when shorebirds are present) and summer (when shorebirds are absent), the overall ecosystem functioning was enhanced when shorebirds were present, due to their positive impact on primary productivity via increased nutrient cycling (Saint-Béat et al. 2013).

5 Case Studies

Shorebirds are found in coastal and estuarine environments on every continent except Antarctica. Their distributions can be grouped very broadly into three Flyway systems; the Americas, the Asian-Australasian and the Africa-Eurasia flyways (Boere and Piersma 2012). Here, we present case studies of shorebird research from each of the three major flyway systems that illustrate their central role in mudflat ecosystems and highlight some current conservation concerns.

5.1 Discovering New Trophic Links in Mudflat Food Webs

The intertidal estuarine mudflats, marshes and open soil agricultural field habitats of the Fraser River Delta, in British Columbia, Canada, constitute what some refer to as Canada's most Important Bird Area (IBA) (Butler and Vermeer 1994) and a shorebird stop-over site of global significance (Drever et al. 2014). Roberts Bank, at the southern arm, has been termed the "ecological crucible" of the delta (Sutherland et al. 2013), supporting hundreds of thousands of western sandpipers during a three-week period in April–May, representing most of the global population (Butler et al. 1996; Drever et al. 2014). Despite its multiple conservation designations, the proximity of the Fraser River Delta to the downtown core of the City of Vancouver (30 km north of the delta), urbanization and other anthropogenic pressures have become increasingly intense over the past 40 years. Paradoxically, concerns about port development have resulted in Roberts Bank becoming one of the most intensively studied shorebird stopover sites in the world, which has shed new light on the role of shorebirds in mudflat trophic webs.

Fig. 12.6 Western Sandpiper feeding on epibenthic biofilm during breeding migration stopover on Roberts Bank (British Columbia, Canada). Photo Jason Puddifoot.

Although western sandpipers feed on intertidal mudflats throughout the Fraser River delta, Roberts Bank has the highest usage (Jardine et al. 2015). While invertebrate prey are abundant on Roberts Bank during northward migration (Mathot and Elner 2004), epibenthic biofilm is estimated to account for approximately 50% of the daily energy budget of western sandpipers on northward migration (Kuwae et al. 2008; Beninger et al. 2011; Jardine et al. 2015). Northward migration through the Fraser River Delta coincides with the diatomaceous biofilm blooms, which occur in spring (Admiraal and Peletier 1980; Sawai et al. 2016) (Fig. 12.6), suggesting that shorebirds may be specifically targeting biofilm.

Original studies of sandpiper feeding in the upper Bay of Fundy suggested a simple system with amphipods, *Corophium volutator*, comprising the single major prey (Hicklin and Smith 1979, 1984; Gratto et al. 1984; Barbeau et al. 2009) and shorebird density and foraging behaviour being directly related to *Corophium* availability (Wilson 1990; Wilson and Vogel 1997). A classic "ecological cascade" was then advocated, based on shorebird predation on *C. volutator* grazing on diatoms, and sediment cohesion properties controlled by mucopolysaccharides secreted by diatoms (Daborn et al. 1993). Initially, observations of diatoms in semipalmated sandpiper diet were dismissed as incidental intake resulting from a bill skimming behaviour that was assumed to be directed towards feeding on ostracods (MacDonald et al. 2012), though more recent studies have revealed that diatoms in biofilm are also targeted by sandpipers in the Bay of Fundy (Quinn and Hamilton 2012; Quinn et al. 2017).

While the finding that many shorebirds appear to rely heavily on epibenthic biofilm as a targeted food source adds increasing levels of complexity to system understanding, what is uncertain is whether the evolving picture of shorebird diets represents a more sophisticated knowledge base, or if shorebird diets themselves have altered in response to system changes over the past four decades (e.g., Shepherd et al. 1995). However, the bill and tongue structures associated with biofilm feeding (see Sect. 2.1) suggests that biofilm has long been an important, if unrecognized, component of shorebird diets.

5.2 Shorebirds Alter Mudflat Biogeochemistry and Benthic Communities

The Banc d'Arguin in Mauritania hosts the greatest number and densities of birds along the Africa-Eurasia flyway (Engelmoer et al. 1984; Campredon 2000). With more than two million shorebirds in winter (Altenburg et al. 1982), albeit with a steady decline of some shorebird species since the first counts in 1980 (Oudman et al. 2017), the Banc d'Arguin is by far the most important wintering site for migratory shorebirds using the East-Atlantic flyway in terms of numbers (e.g., Smit and Piersma 1989). The very large shorebird numbers on a rather small area of intertidal mudflats (approximately 500 km^2) results in very high predation pressure (Engelmoer et al. 1984; Wolff et al. 1993).

Although globally, high concentrations of shorebirds often coincide with regions of offshore productivity (Butler et al. 2001), this is not the case for the Banc d'Arguin. The food web of the Banc d'Arguin intertidal is mainly supported by local benthic primary production, a combination of seagrass and microphytobenthos, with much smaller contributions of phytoplankton, macrophytes and epiphytes (Wolff et al. 1993; Carlier et al. 2015; Catry et al. 2016). Seagrass meadows are recognized as one of the most productive of marine communities (Fenchel and Riedl 1970; Fisher and Hand 1984). Since a large portion of the plant material produced is eventually deposited as detritus, the abundance of organic material in the sediment is usually greater than the oxygen available for its degradation. Hemminga and Nieuwenhuize (1991) observed that seagrass leaves at Banc d'Arguin remain trapped in the seagrass beds and decompose *in situ*. Under such anaerobic conditions, decomposition is accomplished by the activity of sulphate-reducing bacteria, which can utilize inorganic compounds other than O_2 as electron acceptors (Fenchel and Riedl 1970). This results in hydrogen sulfide being the major inorganic constituent in the sediments of the Banc d'Arguin (van der Heide et al. 2012; van der Geest et al. 2014).

The hydrogen sulfide, in turn, is metabolized by the (currently) most common bivalve on the intertidal flats of Banc d'Arguin, *Loripes lucinalis* (Wijnsma et al. 1999; Honkoop et al. 2008; see Fig. 12.5). *Loripes* makes use of carbon metabolites produced by endosymbiotic chemoautotrophic bacteria (van der Geest et al. 2014), and carbon dioxide, oxygen and hydrogen sulfide are absorbed by the gill and transported to bacteriocytes harbouring the endocellular sulfur-oxidizing bacteria (Johnson et al. 1994; Le Pennec et al. 1995). The bacteria oxidize the H_2S and use some of the released energy to fix CO_2 in the Calvin cycle. Living close to the surface, *Loripes* is able to exploit sufficient sulfide, while at the same time being able to take up enough oxygen, including the oxygen that diffuses from the roots of seagrasses (Pregnall et al. 1984; van der Heide et al. 2012). The symbiotically-fixed carbon contributes two-thirds of their carbon consumption (Johnson et al. 1994).

In this ecological context, molluscivoran red knots have been shown to affect the biogeochemistry of the intertidal sediments and the functioning of the food web. Because of their dependence on bivalves, red knots reduce competition between the preferred prey species, i.e., the venerid *Dosinia isocardia* (van Gils et al. 2013; Ahmedou Salem et al. 2014; Oudman et al. 2016) and the co-occurring facultative mixotroph *Loripes lucinalis* (van Gils et al. 2012). *Dosinia* is a suspension feeder that only consumes suspended particulate organic matter. In areas where red knots were excluded, *Dosinia* was no longer selectively removed and became dominant over *Loripes*. Thus, without predation on *Dosinia*, stronger competition for suspended particulate organic matter forced *Loripes* to rely on energy produced by endosymbiotic bacteria (van Gils et al. 2012). This reduced sulfide concentrations and led to lower growth rates of *Loripes*. As sulfide is toxic to most organisms, predation by red knots detoxifies the sedimentary environment (van der Heide et al. 2012) and hence facilitates other benthic species.

5.3 Variable Effects of Anthropogenically-Disturbed Environments on Shorebirds

Spanning 20 degrees of latitude, the 18,000 km Yellow Sea coastline, which extends beyond China into the Koreas (Koh and Khim 2014; Wang et al. 2014), at least historically, constituted the largest continuous system of intertidal mudflats in the world (Healy et al. 2002). The Yellow Sea wetlands support 25% of the global total of waterbird species (Ma et al. 2014), but are nonetheless subject to intense anthropogenic disturbance (Fig. 12.7). China's coastal wetlands are heavily exploited for the polychaetes, bivalves, gastropods and crustaceans living in and on these mudflats (Melville et al. 2016; Yang et al. 2016). These benthic resources are impacted in other ways, since most inshore intertidal areas have forms of aquaculture (Li et al. 2011; Yang et al. 2016). Shellfish species of economic importance were introduced at intertidal mudflats where they did not occur previously (Guo 1999; Leung et al. 2008; Li et al. 2011; Tang et al. 2013), and some of these species are now regarded as invasive (Du et al. 2010). Young shellfish are routinely collected at one place and transported to another, and in this way benthic communities both at the mudflats of origin and destination are changed (Wang and Zhang 1995; H.-B. Peng et al. unpublished data).

Perhaps surprisingly, human impacts associated with Chinese mudflats and offshore areas are not always negative for shorebirds (Yang et al. 2016). On the mudflats on the Luannan coast in Bohai Bay, the small bivalve, *Potomocorbula laevis*, the staple food of staging red knots (Yang et al. 2013), appears to be benefiting from anthropogenic disturbances. Competition between settling juveniles and adults has been virtually eliminated by near-complete fishing away of the

Fig. 12.7 Flocks of red knots in Bohai Bay, Yellow Sea, China, an area subject to intense anthropogenic disturbance, including coastal developments (top panel) and fisheries (lower panel). Photos by Jan van de Kam.

population (for shrimp farming) in late summer and autumn, and an absence of predation on spat by epibenthic predators such as shrimps and crabs, due to persistent overfishing in recent decades, has resulted in increased numbers of

Potamocorbula, which now contribute 96% to the total numbers of 17 species. Thus, overfishing of competing marine mesopredators, in this case, might benefit staging shorebirds, at least in the short term.

The great importance of the Chinese mudflats for staging shorebirds, including red knots, during both northward and southward migration, has been established by multiple studies (Gill et al. 2008; Rogers et al. 2010; Battley et al. 2012; Iwamura et al. 2013). There is growing concern that habitat loss (Yang et al. 2011; MacKinnon et al. 2012; Ma et al. 2014; Murray et al. 2014, 2015; Wang et al. 2014; Piersma et al. 2016, 2017), in combination with overfishing, destructive harvesting of clams, and poisoning by pesticides for clearing unwanted organisms from mudflats seeded with spat reared elsewhere (Lin and Yuan 2005; Feng and Ma 2012; MacKinnon et al. 2012; Melville et al. 2016), are now negatively impacting the use by, and indeed the populations of, migrating shorebirds. The coastal wetlands in China are being filled in and reclaimed at accelerating rates, with the extent of the land claims increasing from 24,000 ha/year between 1950 and 2000 to 40,000 ha/year between 2006 and 2010. Over the past two decades, the length of seawall around the Yellow Sea has increased by a factor 3.4, reaching 11,000 km in 2010, prompting major conservation concerns (Ma et al. 2014).

Shorebird species that breed in the High Arctic and rely on the Yellow Sea mudflats to fuel their long-migration have shown the steepest population declines on their southern non-breeding areas (Amano et al. 2010; Wilson et al. 2011; Studds et al. 2017). A demographic study on red knots, great knots (*Calidris tenuirostris*) and bar-tailed godwits (*Limosa lapponica*) showed them to have identical patterns and rates of decline in survival, during the part of the annual cycle encompassing migration through the Yellow Sea area, a ‘coincidence’ that can only be explained by their shared use of the Yellow Sea intertidal mudflats (Piersma et al. 2016). Indeed, without exception, the evidence suggests that coastal shorebirds are currently limited by the shrinking coastal habitats in East Asia.

6 Conservation

As apparent from this and other chapters of this book, a paradigm shift is taking place over the ecological values of mud. Survival and recovery of the world’s shorebird species demands a multidisciplinary scientific approach based on maintaining and restoring the ecological mechanisms supporting the productivity of mud. Conservation actions can no longer be left to ornithologists and habitat managers, however well-intentioned. We need to understand “mud” as a highly complex ecosystem driven by primary producers generating not only energy but also pulses of lipids. Shorebirds are but one indicator of compromised mud systems; commercial fisheries and people who rely on them are also victims, as are tens of thousands of undervalued invertebrate species.

6.1 Mud Is Not a "Wasteland"

Mud, the orphan habitat (Chap. 1), is one that few claim worthwhile for conservation. Generally, mud is regarded as a sticky, foul, pungent wasteland that serves no purpose, and can be developed with impunity. To the casual observer, unvegetated intertidal mud hosts sparse aquatic biodiversity compared to more charismatic habitat types, such as eel-grass and salt marsh (Beck et al. 2001). More perversely, while low productivity systems such as sandy beaches are prized for recreational and economic merits (Cooke et al. 2012), mud is frequently downgraded or altogether ignored in habitat classification schemes (Spurgeon 1999; Barbier et al. 2011). Yet, ironically, mud is not only productive but more ecologically critical to shorebirds than any other coastal habitat component.

As an essential medium to many species, the physical area of mud, and its functional integrity, require protection. In particular, conservation planning needs to incorporate the surrounding physical, chemical and biological processes supporting diatoms in epibenthic biofilm and their periodic production of essential fatty acids (Hixson et al. 2015; Colombo et al. 2016). A mudflat without a functional epibenthic biofilm community has limited value to shorebirds because all shorebirds that feed on mudflats rely on biofilm either as a direct food source (i.e., biofilm grazers; e.g. Kuwae et al. 2008, 2012; Lourenço et al. 2017; Quinn et al. 2017), or indirectly, as a primary food source for their invertebrate prey (Christianen et al. 2017). Thus, even for shorebirds that are not directly grazing biofilm, the epibenthic biofilm community is a critical component of habitat quality. As an example, mechanical dredging in the Dutch Wadden Sea is believed to have negatively impacted benthic diatom communities via sediment disturbance and increased turbidity, with the resultant decrease in benthic diatoms leading to catastrophic declines in *Macoma balthica* populations (Piersma et al. 2001; Compton et al. 2016), a major food source for wintering red knots.

Recognizing the broader conservation imperative of mud has the promise of not only maintaining entire species of migratory shorebirds but by re-creation and remediation of flats, saving others from extinction. Although shorebirds in themselves are important, the broader benefits of restoring mud translate into more sustainable coastal ecosystems and fisheries (Arts et al. 2009).

6.2 Threats to Mud

Intertidal estuarine mud is an irreplaceable habitat for shorebirds, but it is being subjected to global-scale replacement and degradation. The combined forces of global climate change (Struyf et al. 2004), sea level rise (Galbraith et al. 2002), invasive species (Ruiz et al. 1997, Chap. 11), coastal development (Ma et al. 2014), destructive fishing and overfishing (Piersma et al. 2001; Lotze et al. 2006, Chap. 13), and pollution (Kennish 2002), coupled with ignorance in scientific understanding of mud, pose species-level threats to shorebirds worldwide. For example, the major stopover sites along the collapsing Southeastern Asia Flyway have been subject to intensive coastal development (Ma et al. 2014; Piersma et al. 2017), with rates of loss of tidal flat ecosystems ranging between 0.5 and 1.8% per year (Murray and Fuller 2015). Reduced biofilm availability and resource quality to migrating shorebirds could be a contributing cause for these population declines (MacKinnon et al. 2012; Murray and Fuller 2015; Clemens et al. 2016; Piersma et al. 2016; Taylor et al. 2016). Similarly, predicted declines in lipid production at a global level as a consequence of climate change (Hixson and Arts 2016) will only exacerbate the cumulative effects of current factors, either directly reducing mud habitat availability or functioning.

6.3 Restoration and Recovery

We cannot conserve, much less restore, what we do not recognize or understand. Precipitous declines of shorebird populations over the last several decades underscore the need to elucidate supporting ecological mechanisms to better inform conservation strategies. Long distance migratory shorebirds are extreme athletes whose performance relies on an ability to use fatty acids as fuel (Weber 2009; Guglielmo 2010). Some shorebirds may be able to synthesize fatty acids endogenously. For example, the presumed-extinct Eskimo curlew (*Numenius borealis*) is believed to have fed primarily on lipid-poor berries prior to southward migration (Gill et al. 1998), though reports are largely anecdotal. However, most shorebirds are heavily reliant on dietary sources of fatty acids. For example, declines in access to lipid-rich horseshoe crab eggs has proven catastrophic for red knots migrating through Delaware Bay (Haramis et al. 2007). Interestingly, epibenthic biofilm also provides a rich source of polyunsaturated fatty acids (Twining et al. 2016; Quinn et al. 2017), and may therefore be a critical food for shorebirds that rely on dietary intake of fatty acids to fuel long-distance migration.

To date, epibenthic biofilm has not been explicitly considered when assessing general threats to shorebirds (Melville et al. 2016). However, realization of the importance of omega-3 fatty acids produced by phytoplankton, especially diatoms, to aquatic ecosystems is an emerging science, and there is already recognition that not all phytoplankton production is “equal” (Galloway and Winder 2015). The sources of these fatty acids on mudflats need to be identified, understood, restored and protected for effective shorebird conservation. Accordingly, we urge an international conservation initiative on mud. In doing so, conservationists will need to work in teams with engineers, oceanographers, marine chemists, diatomists, ecologists, physiologists and ornithologists, to re-create and/or conserve productive epibenthic biofilm over estuarine intertidal mudflats.

References

Admiraal W, Peletier H (1980) Influence of seasonal variations of temperature and light on the growth rate of cultures and natural populations of intertidal diatoms. Mar Ecol Prog Ser 2:35–43

Ahmedou Salem MV, van der Geest M, Piersma T, Saoud Y, van Gils JA (2014) Seasonal changes in mollusc abundance in a tropical intertidal ecosystem, banc d'Arguin (Mauritania): testing the 'depletion by shorebirds' hypothesis. Estuar Coast Shelf Sci 136:26–34

Altenburg W, Engelmoer M, Mes R, Piersma T (1982) Wintering waders on the banc d'Arguin, Mauritania. Stichting Veth tot steun aan Waddenonderzoek, Leiden, 283 p

Alves JA, Sutherland WJ, Gill JA (2012) Will improving wastewater treatment impact shorebirds? Effects of sewage discharges on estuarine invertebrates and birds. Anim Conserv 15:44–52

Amano T, Székely T, Koyama K, Amano H, Sutherland WJ (2010) A framework for monitoring the status of populations: an example from wader populations in the east Asian–Australasian flyway. Biol Conserv 143:2238–2247

Arts MT, Brett MT, Kains MJ (2009) Lipids in aquatic ecosystems. Springer, New York, 380 p

Atkinson PW, Maclean IMD, Clark NA (2010) Impacts of shellfisheries and nutrient inputs on waterbird communities in the wash, England. J Appl Ecol 47:191–199

Baker AJ, González PM, Piersma T, Niles LJ, Serrano do Nascimento IdL, Atkinson PW, Clark NA, Minton CDT, Peck MK, Aarts G (2004) Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proc R Soc B 271:875–882

Barbeau MA, Grecian LA, Arnold EE, Sheahan DC, Hamilton DJ (2009) Spatial and temporal variation in the population dynamics of the intertidal amphipod *Corophium volutator* in the upper bay of Fundy, Canada. J Crustac Biol 29:491–506

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR (2011) The value of estuarine and coastal ecosystem services. Ecol Monogr 81:169–193

Barbosa A, Moreno E (1999) Evolution of foraging strategies in shorebirds: an ecomorphological approach. Auk 116:712–725

Battley PF, Piersma T (2005a) Adaptive interplay between feeding ecology and features of the digestive tract in birds. In: Starck JM, Wang T (eds) Physiological and ecological adaptations to feeding in vertebrates. Science Publishers, Enfield, pp 201–228

Battley PF, Piersma T (2005b) Body composition and flight ranges of bar-tailed godwits (*Limosa lapponica baueri*) from New Zealand. Auk 122:922–937

Battley PF, Warnock N, Tibbitts TL, Gill RE, Piersma T, Hassell CJ, Douglas DC, Mulcahy DM, Gartrell BD, Schuckard R, Melville DS, Riegen AC (2012) Contrasting extreme long-distance migration patterns in bar-tailed godwits *Limosa lapponica*. J Avian Biol 43:21–32

Beck MW, Heck JKL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: a better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. Bioscience 51:633–641

Beninger PG, Elner RW, Morançais M, Decottignies P (2011) Downward trophic shift during breeding migration in the shorebird *Calidris mauri* (western sandpiper). Mar Ecol Prog Ser 428:259–269

Beukema JJ, Essink K, Michaelis H, Zwarts L (1993) Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds? Neth J Sea Res 31(4):319–330

Bijleveld AI, Twietmeyer S, Piechocki J, van Gils JA, Piersma T (2015) Natural selection by pulsed predation: survival of the thickest. Ecology 96:1943–1956

Bijleveld AI, MacCurdy RB, Chan Y-C, Penning E, Gabrielson RM, Cluderay J, Spaulding EL, Dekinga A, Holthuijsen S, ten Horn J, Brugge M, van Gils JA, Winkler DW, Piersma T (2016)

Understanding spatial distributions: negative density-dependence in prey causes predators to trade-off prey quantity with quality. Proc R Soc B 283:20151557

Bocher P, Piersma T, Dekinga A, Kraan C, Yates MG, Guyot T, Folmer EO, Radenac G (2007) Site- and species-specific distribution patterns of molluscs at five intertidal soft-sediment areas in Northwest Europe during a single winter. Mar Biol 151:577–594

Boere GC, Piersma T (2012) Flyway protection and the predicament of our migrant birds. Ocean Coast Manag 68:157–168

Bom RA, de Fouw J, Klaassen RHG, Piersma T, Lavaleye MSS, Ens BJ, Oudman T, van Gils JA (2018) Food web consequences of an evolutionary arms race: molluscs subject to crab predation on intertidal mudflats in Oman are unavailable to shorebirds. J Biogeogr 45:342–354

Butler RW, Vermeer K (1994) The abundance of distribution of estuarine birds in the strait of Georgia, British Columbia. Can Wildl Serv Occas Paper 83:78 pp

Butler RW, Delgado F, De La Cueva HC, Pulido V, Sandercock BK (1996) Migration routes of the western sandpiper. Wilson Bull 108:662–672

Butler RW, Davidson NC, Morrison RIG (2001) Global-scale shorebird distribution in relation to productivity of near-shore oceans. Waterbirds 24:224–232

Campredon P (2000) Between the Sahara and the Atlantic. Banc d'Arguin National Park. Fondation Internationale du Banc d'Arguin, Arles, 121 p

Carlier A, Chauvaud L, van der Geest M, Le Loc'h F, Le Duff M, Vernet M, Raffray J, Diakhaté D, Labrosse P, Wagué A, Le Goff C, Gohin F, Chapron B, Clavier J (2015) Trophic connectivity between offshore upwelling and the inshore food web of banc d'Arguin (Mauritania): new insights from isotopic analysis. Estuar Coast Shelf Sci 165:149–158

Catry T, Lourenço PM, Lopes RJ, Carneiro C, Alves JA, Costa J, Rguibi-Idrissi H, Bearhop S, Piersma T, Granadeiro JP (2016) Structure and functioning of intertidal food webs along an avian flyway: a comparative approach using stable isotopes. Funct Ecol 30:468–478

Christianen MJA, Middelburg JJ, Holthuijsen SJ, Jouta J, Compton TJ, van der Heide T, Piersma T, Sinninghe Damsté JS, van der Veer HW, Schouten S, Olff H (2017) Benthic primary producers are key to sustain the Wadden Sea food web: stable carbon isotope analysis at landscape scale. Ecology 98:1498–1512

Clemens RS, Rogers DI, Hansen BD, Gosbell K, Minton CDT, Straw P, Bamford M, Woehler EJ, Milton DA, Weston MA, Venables B, Weller D, Hassell C, Rutherford B, Onton K, Herrod A, Studds CE, Choi CY, Dhanjal-Adams KL, Murray NJ, Skilleter GA, Fuller RA (2016) Continental-scale decreases in shorebird populations in Australia. Emu 116:119–135

Colombo SM, Wacker A, Parrish CC, Kainz MJ, Arts MT (2016) A fundamental dichotomy in long-chain polyunsaturated fatty acid abundance between and within marine and terrestrial ecosystems. Environ Rev 25:163–174

Colwell MA (2010) Shorebird ecology, conservation, and management. University of California Press, Berkeley, 344 p

Compton TJ, Bodnar W, Koolhaas A, Dekinga A, Holthuijsen S, ten Horn J, McSweeney N, van Gils JA, Piersma T (2016) Burrowing behavior of a deposit feeding bivalve predicts change in intertidal ecosystem state. Front Ecol Evol 4:19

Cooke BC, Jones AR, Goodwin ID, Bishop MJ (2012) Nourishment practices on Australian sandy beaches: a review. J Environ Manag 113:319–327

Cresswell W (1993) Escape responses by redshanks, *Tringa totanus*, on attack by avian predators. Anim Behav 46:609–611

Daborn GR, Amos CL, Brylinsky M, Christian H, Drapeau G, Faas RW, Grant J, Long B, Paterson DM, Perillo GME, Piccolo MC (1993) An ecological cascade effect: migratory birds affect the stability of intertidal sediments. Limnol Oceanogr 38:225–231

de Fouw J, van der Heide T, Oudman T, Maas LRM, Piersma T, van Gils JA (2016) Structurally complex sea grass obstructs the sixth sense of a specialized avian molluscivore. Anim Behav 115:55–67

Dekker D, Ydenberg R (2004) Raptor predation on wintering dunlins in relation to the tidal cycle. Condor 106:415–419

Deppe F (1999) Intertidal mudflats worldwide. Common Wadden Sea Secretariat (CWSS), Wilhelmshaven, 100 p

Drever MC, Lemon MJF, Butler RW, Millikin RL (2014) Monitoring populations of western sandpipers and Pacific dunlins during northward migration on the Fraser River Delta, British Columbia, 1991–2013. J Field Ornithol 85:10–22

Du H, Sun L, Peng W, Hu J, Bao Z (2010) Sixteen polymorphic microsatellite markers for the mud snail, *Bullacta exarata* (Philippi, 1848). Conserv Genet Resour 2:23–25

Duerksen SW, Thiemann GW, Budge SM, Poulin M, Niemi A, Michel C (2014) Large, omega-3 rich, pelagic diatoms under Arctic Sea ice: sources and implications for food webs. PLoS One 9:18

Duijns S, van Gils JA, Spaans B, ten Horn J, Brugge M, Piersma T (2014) Sex-specific winter distribution in a sexually dimorphic shorebird is explained by resource partitioning. Ecol Evol 4:4009–4018

Duijns S, van Gils JA, Smart J, Piersma T (2015) Phenotype-limited distributions: short-billed birds move away during times that prey bury deeply. R Soc Open Sci 2:150073

Elner RW, Seaman DA (2003) Calidrid conservation: unrequited needs. Wader Study Group Bull 100:30–34

Elner RW, Beninger PG, Jackson DL, Potter TM (2005) Evidence of a new feeding mode in western sandpiper (*Calidris mauri*) and dunlin (*Calidris alpina*) based on bill and tongue morphology and ultrastructure. Mar Biol 146:1223–1234

Engelmoer M, Piersma T, Altenburg W, Mes R (1984) The banc d'Arguin (Mauritania). In: Evans PR, Goss-Custard JD, Hale WG (eds) Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge, pp 293–310

Escudero G, Navedo JG, Piersma T, De Goeij P, Edelaar PIM (2012) Foraging conditions 'at the end of the world' in the context of long-distance migration and population declines in red knots. Austral Ecol 37:355–364

Evans PR, Herdson DM, Knights PJ, Pienkowski MW (1979) Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and shelduck. Oecologia 41:183–206

Fenchel TM, Riedl RJ (1970) The sulfide system: a new biotic community underneath the oxidized layer of marine sand bottoms. Mar Biol 7:255–268

Feng L-H, Ma Y-J (2012) Evolution of tidal flats in China and ecological exploitation of tidal flat resources. Environ Earth Sci 67:1639–1649

Fisher MR, Hand SC (1984) Chemoautotrophic symbionts in the bivalve *Lucina floridana* from seagrass beds. Biol Bull 167:445–459

Folmer EO, Piersma T (2012) The contributions of resource availability and social forces to foraging distributions: a spatial lag modelling approach. Anim Behav 84:1371–1380

Folmer EO, Olff H, Piersma T (2012) The spatial distribution of flocking foragers: disentangling the effects of food availability, interference and conspecific attraction by means of spatial autoregressive modeling. Oikos 121:551–561

Fuller RA, Bearhop S, Metcalfe NB, Piersma T (2013) The effect of group size on vigilance in ruddy turnstones *Arenaria interpres* varies with foraging habitat. Ibis 155:246–257

Furness RW (1993) Birds as monitors of pollutants. In: Furness RW, Greenwood JJD (eds) Birds as monitors of environmental change. Springer, Amsterdam, pp 86–143

Galbraith H, Jones R, Park R, Clough J, Herrod-Julius S, Harrington B, Page G (2002) Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. Waterbirds 25:173–183

Galloway AWE, Winder M (2015) Partitioning the relative importance of phylogeny and environmental conditions on phytoplankton fatty acids. PLoS One 10:23

Gerritsen AFC, Meiboom A (1986) The role of touch in prey density estimation by *Calidris alba*. Neth J Zool 36:530–562

Gill RE Jr, Tibbitts TL, Douglas DC, Handel CM, Malcahy DM, Gottschalck JC, Warnock N, McCaffery BJ, Battley PF, Piersma T (2008) Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? Proc R Soc B 276:447–457

Gill RE, Canevari P, Iverson EH (1998) Eskimo curlew (*Numernius borealisI), version 2.0*. In: Rodewald PG (ed) The birds of North America. Cornell Lab of Ornithology, Ithaca

Gratto GW, Thomas MLH, Gratto CL (1984) Some aspects of the foraging ecology of migrant juvenile sandpipers in the outer bay of Fundy. Can J Zool 62:1889–1892

Guglielmo CG (2010) Move that fatty acid: fuel selection and transport in migratory birds and bats. Integr Comp Biol 50:336–345

Guo Z (1999) Molluscan aquaculture in China. J Shellfish Res 18:19–31

Haramis MG, Link WA, Osenton PC, Carter DB, Weber RG, Clark NA, Teece MA, Mizrahi DS (2007) Stable isotope and pen feeding trial studies confirm the value of horseshoe crab *Limulus polyphemus* eggs to spring migrant shorebirds in Delaware Bay. J Avian Biol 38:367–376

Healy T, Wang YX, Healy J (2002) Muddy costs of the world: processes, deposits, and function. Elsevier Science, Amsterdam, 556 p

Hemminga MA, Nieuwenhuize J (1991) Transport, deposition and in situ decay of seagrasses in a tropical mudflat area (banc d'Arguin, Mauritania). Neth J Sea Res 27:183–190

Hicklin PW, Smith PC (1979) The diets of five species of migrant shorebirds in the bay of Fundy. Proc N S Inst Sci 29:483–488

Hicklin PW, Smith PC (1984) Selection of foraging sites and invertebrate prey by migrant semipalmated sandpipers *Calidris pusilla* (Pallas), in Minas Basin, bay of Fundy. Can J Zool 62:2201–2210

Hixson SM, Arts MT (2016) Climate warming is predicted to reduce omega-3, long-chain, polyunsaturated fatty acid production in phytoplankton. Glob Chang Biol 22:2744–2755

Hixson SM, Sharma B, Kainz MJ, Wacker A, Arts MT (2015) Production, distribution, and abundance of long-chain omega-3 polyunsaturated fatty acids: a fundamental dichotomy between freshwater and terrestrial ecosystems. Environ Rev 23:414–424

Honkoop PJC, Berghuis EM, Holthuijsen S, Lavaleye MSS, Piersma T (2008) Molluscan assemblages of seagrass-covered and bare intertidal flats on the banc d'Arguin, Mauritania, in relation to characteristics of sediment and organic matter. J Sea Res 60:235–243

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35

Iwamura T, Possingham HP, Chadès I, Minton C, Murray NJ, Rogers DI, Treml EA, Fuller RA (2013) Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. Proc R Soc B 280:20130325

Jardine CB, Bond AL, Davidson PJA, Butler RW, Kuwae T (2015) Biofilm consumption and variable diet composition of western sandpipers (*Calidris mauri*) during migratory stopover. PLoS One 10:e0124164

Jauffrais T, Drouet S, Turpin V, Meleder V, Jesus B, Cognie B, Raimbault P, Cosson RP, Decottignies P, Martin-Jezequel V (2015) Growth and biochemical composition of a microphytobenthic diatom (*Entomoneis paludosa*) exposed to shorebird (*Calidris alpina*) droppings. J Exp Mar Biol Ecol 469:83–92

Jiménez A, Elner RW, Favaro C, Rickards K, Ydenberg RC (2015) Intertidal biofilm distribution underpins differential tide-following behavior of two sandpiper species (*Calidris mauri* and *Calidris alpina*) during northward migration. Estuar Coast Shelf Sci 155:8–16

Johnsgard PA (1981) The plovers, sandpipers, and snipes of the world. University of Nebraska Press, Lincoln, 519 p

Johnson MA, Dioris M, Le Pennec M (1994) Endosymbiotic bacterial contribution in the carbon nutrition of *Loripes lucinalis* (Mollusca: Bivalvia). Symbiosis 17:1–3

Kalejta B (1993) Intense predation cannot always be detected experimentally: a case study of shorebird predation on nereid polychaetes in South Africa. Neth J Sea Res 31:385–393

Kennish MJ (2002) Environmental threats and environmental future of estuaries. Environ Conserv 29:78–107

Koh C-H, Khim JS (2014) The Korean tidal flat of the Yellow Sea: physical setting, ecosystem and management. Ocean Coast Manag 102:398–414

Kraan C, van Gils JA, Spaans B, Dekinga A, Bijleveld AI, van Roomen M, Kleefstra R, Piersma T (2009) Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. J Anim Ecol 78:1259–1268

Kuwae T, Beninger PG, Decottignies P, Mathot KJ, Lund DR, Elner RW (2008) Biofilm grazing in a higher vertebrate: the western sandpiper, *Calidris mauri*. Ecology 89:599–606

Kuwae T, Miyoshi E, Hosokawa S, Ichimi K, Hosoya J, Amano T, Moriya T, Kondoh M, Ydenberg RC, Elner RW (2012) Variable and complex food web structures revealed by exploring missing trophic links between birds and biofilm. Ecol Lett 15:347–356

Lazarus J, Symonds M (1992) Contrasting effects of protective and obstructive cover on avian vigilance. Anim Behav 43:519–521

Le Pennec M, Beninger PG, Herry A (1995) Feeding and digestive adaptations of bivalve molluscs to sulphide-rich habitats. Comp Biochem Physiol A 111:183–189

Leung P, Lee CS, O'Bryen PJ (2008) Species and system selection for sustainable aquaculture. Blackwell, United States Aquaculture Society, 528 p

Li X, Li J, Wang Y, Fu L, Fu Y, Li B, Jiao B (2011) Aquaculture industry in China: current state, challenges, and outlook. Rev Fish Sci 19:187–200

Lin KD, Yuan DX (2005) Degradation kinetics and products of triazophos in intertidal sediment. J Environ Sci 17:933–936

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–1809

Lourenço PM, Catry T, Lopes RJ, Piersma T, Granadeiro JP (2017) Invisible trophic links? Quantifying the importance of non-standard food sources for key intertidal avian predators in the eastern Atlantic. Mar Ecol Prog Ser 563:219–232

MacDonald EC, Ginn MG, Hamilton DJ (2012) Variability in foraging behavior and implications for diet breadth among semipalmated sandpipers staging in the Upper Bay of Fundy. Condor 114:135–144

Ma ZJ, Melville DS, Liu JG, Chen Y, Yang HY, Ren WW, Zhang ZW, Piersma T, Li B (2014) Rethinking China's new great wall. Science 346:912–914

MacKinnon J, Verkuil Y, Murray NJ (2012) IUCN situation analysis on east and southeast Asian intertidal habitats, with particular reference to the Yellow Sea (including the Bohai Sea). IUCN, Switzerland, 70 p

Martin GR (2007) Visual fields and their functions in birds. J Ornithol 148:547–562

Martin GR, Piersma T (2009) Vision and touch in relation to foraging and predator detection: insightful contrasts between a plover and a sandpiper. Proc R Soc B 276:437–445

Martini IP, Wanless H (2014) Sedimentary coastal zones from high to low latitudes: similarities and differences (Geological Society of London special publications). The Geological Society, London, 388 p, 600 p

Mathot KJ, Elner RW (2004) Evidence for sexual partitioning of foraging mode in western sandpipers (*Calidris mauri*) during migration. Can J Zool 82:1035–1042

Mathot KJ, Smith BD, Elner RW (2007) Latitudinal clines in food distribution correlate with differential migration in the western sandpiper. Ecology 88:781–791

Melville DS, Chen Y, Ma Z (2016) Shorebirds along the Yellow Sea coast of China face an uncertain future—a review of threats. Emu 116:100–110

Moreira F (1995) The winter feeding ecology of avocets, *Recurvirostra avosetta*, on intertidal areas. I. Feeding strategies. Ibis 137:92–98

Murray NJ, Fuller RA (2015) Protecting stopover habitat for migratory shorebirds in East Asia. J Ornithol 156:S217–S225

Murray NJ, Clemens RS, Phinn SR, Possingham HP, Fuller RA (2014) Tracking the rapid loss of tidal wetlands in the Yellow Sea. Front Ecol Environ 12:267–272

Murray NJ, Ma Z, Fuller RA (2015) Tidal flats of the Yellow Sea: a review of ecosystem status and anthropogenic threats. Aust Ecol 40:472–481

Myers JP (1986) Sex and gluttony on Delaware Bay. Nat Hist 95:68–77

Niles LJ, Bart J, Sitters HP, Dey AD, Clark KE, Atkinson PW, Baker AJ, Bennett KA, Kalasz KS, Clark NA, Clark J, Gillings S, Gates AS, González PM, Hernandez DE, Minton CDT, Morrison RIG, Porter RR, Ross RK, Veitch CR (2009) Effects of horseshoe crab harvest in Delaware Bay on red knots: are harvest restrictions working? Bioscience 59:153–164

Oudman T, Bijleveld AI, Kavelaars MM, Dekinga A, Cluderay J, Piersma T, van Gils JA (2016) Diet preferences as the cause of individual differences rather than the consequence. J Anim Ecol 85:1378–1388

Oudman T, Schekkerman H, Kidee A, Roomen MV, Tentij M, Piersma T (2017) The waterbirds of Parc national du banc d'Arguin: evaluation of all complete winter counts, workshop proceedings and an evaluation. Report of programme towards a rich Wadden Sea. NIOZ, Leeuwarden, 23 p

Page G, Whitacre DF (1975) Raptor predation on wintering shorebirds. Condor 77:73–83

Piersma T (1987) Production by intertidal benthic animals and limits to their predation by shorebirds: a heuristic model. Mar Ecol Prog Ser 38:187–196

Piersma T (2003) Wandernde Kustenvogel im Wattenmeer als Indikatoren globaler Umweltfaktoren. In: Lozan JL, Rachor E, Reise K, Sundermann J, von Westernhagen H (eds) Warnsignale aus Nordsee and Wattenmeer: Eine aktuelle Umweltbilanz. Wissenschaftliche Auswertungen, Hamburg, pp 176–181

Piersma T (2007) Why do molluscivorous shorebirds have such a hard time in the Wadden Sea right now? In: Reineking B, Südbeck P (eds) Seriously declining trends in migratory waterbirds Wadden Sea ecosystem. Common Wadden Sea Secretariat, Wilhemshaven, pp 53–63

Piersma T (2012) What is habitat quality? Dissecting a research portfolio on shorebirds. In: Fuller RJ (ed) Birds and habitat: relationships in a changing landscape. Cambridge University Press, Cambridge, pp 383–407

Piersma T, Lindström Å (2004) Migrating shorebirds as integrative sentinels of global environmental change. Ibis 146:61–69

Piersma T, Koolhaas A, Dekinga A (1993) Interactions between stomach structure and diet choice in shorebirds. Auk 110:552–564

Piersma T, van Aelst R, Kurk K, Berkhoudt H, Maas LRM (1998) A new pressure sensory mechanism for prey detection in birds: the use of principles of seabed dynamics? Proc R Soc B 265:1377–1383

Piersma T, Koolhaas A, Dekinga A, Beukema JJ, Dekker R, Essink K (2001) Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. J Appl Ecol 38:976–990

Piersma T, Rogers DI, González PM, Zwarts L, Niles LJ, De Lima I, Do Nascimento S, Minton CDT, Baker AJ (2005) Fuel storage rates before northward flights in red knots worldwide. In: Greenberg R, Marra PP (eds) Birds of two worlds. Johns Hopkins University Press, Baltimore, pp 262–273

Piersma T, Lok T, Chen Y, Hassell CJ, Yang HY, Boyle A, Slaymaker M, Chan YC, Melville DS, Zhang ZW, Ma Z (2016) Simultaneous declines in summer survival of three shorebird species signals a flyway at risk. J Appl Ecol 53:479–490

Piersma T, Chang Y-C, Mu T, Hassell CJ, Melville DS, Peng H-B, Ma Z, Zhang Z, Wilcove DS (2017) Loss of habitat leads to loss of birds: reflections on the Jiangsu, China, coastal development plans. Wader Study Group Bull 124:93–98

Pomeroy AC (2006) Tradeoffs between food abundance and predation danger in spatial usage of a stopover site by western sandpipers, *Calidris mauri*. Oikos 112:629–637

Pregnall AM, Smith RD, Kursar TA, Alberte RS (1984) Metabolic adaptation of *Zostera marina* (eelgrass) to diurnal periods of root anoxia. Mar Biol 83:141–147

Quaintenne G, van Gils JA, Bocher P, Dekinga A, Piersma T (2011) Scaling up ideals to freedom: are densities of red knots across western Europe consistent with ideal free distribution? Proc R Soc B 278:2728–2736

Quinn JL, Cresswell W (2004) Predator hunting behaviour and prey vulnerability. J Anim Ecol 73:143–154

Quinn JT, Hamilton DJ (2012) Variation in diet of semipalmated sandpipers (*Calidris pusilla*) during stopover in the upper bay of Fundy, Canada. Can J Zool 90:1181–1190

Quinn JT, Hamilton DJ, Hebert CE (2017) Fatty acid composition and concentration of alternative prey of semipalmated sandpipers *Calidris pusilla* in the upper bay of Fundy, Canada. Can J Zool 95:565–573

R Development Core Team (2017) R: a language and environment for statistical computing. 3.3.3 edn. Vienna, Austria. See http://www.R-project.org

Robin F, Piersma T, Meunier F, Bocher P (2013) Expansion into an herbivorous niche by a customary carnivore: black-tailed godwits feeding on rhizomes of *Zostera* at a newly established wintering site. Condor 115:340–347

Rogers DI, Yang H-Y, Hassell CJ, Boyle AN, Rogers KG, Chen B, Zhang Z-W, Piersma T (2010) Red knots (*Calidris canutus piersmai* and *C. c. rogersi*) depend on a small threatened staging area in Bohai Bay, China. Emu 110:307–315

Rubega MA (1997) Surface tension prey transport in shorebirds: how widespread is it? Ibis 139:488–493

Rubega MA, Obst BS (1993) Surface-tension feeding in phalaropes: discovery of a novel feeding mechanism. Auk 110:169–178

Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. Am Zool 37:621–632

Saint-Béat B, Dupuy C, Bocher P, Chalumeau J, De Crignis M, Fontaine C, Guizien K, Lavaud J, Lefebvre S, Montanié H, Mouget J-L, Orvain F, Pascal P-Y, Quaintenne G, Radenac G, Richard P, Robin F, Vézina AF, Niquil N (2013) Key features of intertidal food webs that support migratory shorebirds. PLoS One 8:e76739

Sawai Y, Horton BP, Kemp AC, Hawkes AD, Nagumo T, Nelson AR (2016) Relationships between diatoms and tidal environments in Oregon and Washington, USA. Diat Res 31:17–38

Schneider DC, Harrington B (1981) Timing of shorebird migration in relation to prey depletion. Auk 98:801–811

Shepherd PCF, Boates JS (1999) Effects of a commercial baitworm harvest on semipalmated sandpipers and their prey in the bay of Fundy hemispheric shorebird reserve. Conserv Biol 13:347–356

Shepherd PCF, Partridge VA, Hicklin PW (1995) Changes in sediment types and invertebrate fauna in the intertidal mudflats of the bay of Fundy between 1977 and 1994. Technical report series 237. Environmental Conservation Branch, Canadian Wildlife Service, Atlantic Region, 49 p

Smit J, Piersma T (1989) Numbers, midwinter distribution, and migration of wader populations using the East Atlantic flyway. In: Boyd H, Pirot J-Y (eds) Flyways and reserve networks for water birds. IWRB, Slimbridge, pp 24–63

Spurgeon J (1999) The socio-economic costs and benefits of coastal habitat rehabilitation and creation. Mar Pollut Bull 37:373–382

St. Clair CT, Baird P, Ydenberg R, Elner R, Bendell LI (2015) Trace elements in Pacific dunlin (*Calidris alpina pacifica*): patterns of accumulation and concentrations in kidneys and feathers. Ecotoxicology 24:29–44

Stal LJ (2003) Microphytobenthos, their extracellular polymeric substances, and the morphogenesis of intertidal sediments. Geomicrobiol J 20:463–478

Stonik V, Stonik I (2015) Low-molecular-weight metabolites from diatoms: structures, biological roles and biosynthesis. Mar Drugs 13:3672–3709

Struyf E, Van Damme S, Meire P (2004) Possible effects of climate change on estuarine nutrient fluxes: a case study in the highly nutrified Schelde estuary (Belgium, the Netherlands). Estuar Coast Shelf Sci 60:649–661

Studds CE, Kendall BE, Murray NJ, Wilson HB, Rogers DI, Clemens RS, Gosbell K, Hassell CJ, Jessop R, Melville DS, Milton DA, Minton CDT, Possingham HP, Riegen AC, Straw P, Woehler EJ, Fuller RA (2017) Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. Nat Commun 8:14895

Sutherland TF, Shepherd PCF, Elner RW (2000) Predation on meiofaunal and macrofaunal invertebrates by western sandpipers (*Calidris mauri*): evidence for dual foraging modes. Mar Biol 137:983–993

Sutherland TF, Elner RW, O'Neill JD (2013) Roberts Bank: ecological crucible of the Fraser River estuary. Prog Oceanogr 115:171–180

Tang B, Zhang D, Ge B, Zhang H (2013) Sustainable utilization of biological resources from coastal wetlands in China. China Sci Bull 58:2270–2275

Taylor CM, Laughlin AJ, Hall RJ (2016) The response of migratory populations to phenological change: a migratory flow network modelling approach. J Anim Ecol 85:648–659

Twining CW, Brenna JT, Hairston NG, Flecker AS (2016) Highly unsaturated fatty acids in nature: what we know and what we need to learn. Oikos 125:749–760

Underwood GJC, Paterson DM (2003) The importance of extracellular carbohydrate production by marine epipelic diatoms. In: Callow JA (ed) Advances in botanical research, vol 40, pp 183–240

van de Kam J, Ens B, Piersma T, Zwarts L (2004) Shorebirds: an illustrated behavioural ecology. KNNV, Utrecht, 368 p

van de Kam J, Jonkers B, Piersma T (2016) Marathon migrants: celebrating the birds that connect places and people across our planet. Bornmeer, Gorredijk, 208 p

van den Hout PJ, van Gils JA, Robin F, van der Geest M, Dekinga A, Piersma T (2014) Interference from adults forces young red knots to forage for longer and in dangerous places. Anim Behav 88:137–146

van den Hout PJ, Piersma T, ten Horn J, Spaans B, Lok T (2017) Individual shifts toward safety explain age-related foraging distribution in a gregarious shorebird. Behav Ecol 28:419–428

van der Geest M, Sall AA, Ely SO, Nauta RW, van Gils JA, Piersma T (2014) Nutritional and reproductive strategies in a chemosymbiotic bivalve living in a tropical intertidal seagrass bed. Mar Ecol Prog Ser 501:113–126

van der Heide T, Govers LL, de Fouw J, Olff H, van der Geest M, van Katwijk MM, Piersma T, van de Koppel J, Silliman BR, Smolders AJP, van Gils JA (2012) A three-stage symbiosis forms the foundation of seagrass ecosystems. Science 336:1432–1434

van der Meer J, Piersma T, Beukema JJ (2001) Population dynamics of benthic species on tidal flats: the possible roles of shorebird predation. Ecol Stud 151:317–335

van Gils JA, Dekinga A, Spaans B, Vahl WK, Piersma T (2005) Digestive bottleneck affects foraging decisions in red knots *Calidris canutus.* II. Patch choice and length of working day. J Anim Ecol 74:120–130

van Gils JA, van der Geest M, Jansen EJ, Govers LL, de Fouw J, Piersma T (2012) Trophic cascade induced by molluscivore predator alters pore-water biogeochemistry via competitive release of prey. Ecology 93:1143–1152

van Gils JA, van der Geest M, Leyrer J, Oudman T, Lok T, Onrust J, de Fouw J, van der Heide T, van den Hout PJ, Spaans B, Dekinga A, Brugge M, Piersma T (2013) Toxin constraint explains diet choice, survival and population dynamics in a molluscivore shorebird. Proc R Soc B 280:20130861

van Gils JA, Lisovski S, Lok T, Meissner W, Ożarowska A, de Fouw J, Rakhimberdiev E, Soloviev MY, Piersma T, Klaassen M (2016) Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. Science 352:819–821

van Roomen M, Laursen K, van Turnhout C, van Winden E, Blew J, Eskildsen K, Günther K, Hälterlein B, Kleefstra R, Potel P, Schrader S, Luerssen G, Ens BJ (2012) Signals from the

Wadden Sea: population declines dominate among waterbirds depending on intertidal mudflats. Ocean Coast Manag 68:79–88

Vézina F, Williams TD, Piersma T, Morrison RIG (2012) Phenotypic compromises in a long-distance migrant during the transition from migration to reproduction in the high Arctic. Funct Ecol 26:500–512

Wang Y, Zhang Y (1995) Juvenile mollusk production of marine commercial bottom shell in China. J Fish China 19:166–171

Wang W, Liu H, Li Y, Su J (2014) Development and management of land reclamation in China. Ocean Coast Manag 102:415–425

Warnock N, Elphick C, Rubega MA (2002) Shorebirds in the marine environment. In: Schreiber EA, Burger J (eds) Biology of marine birds. CRC, Washington, pp 581–615

Weber JM (2009) The physiology of long-distance migration: extending the limits of endurance metabolism. J Exp Biol 212:593–597

Weber LM, Haig SM (1997) Shorebird-prey interaction in South Carolina coastal soft sediments. Can J Zool 75:245–252

Weerman EJ, Herman PMJ, van de Koppel J (2011) Top-down control inhibits spatial self-organization of a patterned landscape. Ecology 92:487–495

Whitlatch RB (1977) Seasonal changes in community structure of macrobenthos inhabiting intertidal sand and mud flats of Barnstable Harbor, Massachusetts. Biol Bull 152:275–294

Wijnsma G, Wolff WJ, Meijboom A, Duiven P, de Vlas J (1999) Species richness and distribution of benthic tidal flat fauna of the banc d'Arguin, Mauritania. Oceanol Acta 22:233–243

Wilson WHJ (1990) The relationship between prey abundance and foraging site selection by Semipalmated Sandpipers on a Bay of Fundy mudflat. J Field Ornithol 61:9–19

Wilson WHJ, Vogel ER (1997) The foraging behavior of semipalmated sandpipers in the Upper Bay of Fundy: stereotyped or prey-sensitive? Condor 99:206–210

Wilson HB, Kendall BE, Fuller RA, Milton DA, Possingham HP (2011) Analyzing variability and the rate of decline of migratory shorebirds in Moreton Bay, Australia. Conserv Biol 25:758–766

Wolff WJ, Duiven AG, Duiven P, Esselink P, Gueye A, Meijboom A, Moerland G, Zegers J (1993) Biomass of macrobenthic tidal flat fauna of the banc d'Arguin, Mauritania. Hydrobiologia 258:151–163

Yang H-Y, Chen B, Barter M, Piersma T, Zhou C-F, Li F-S, Zhang Z-W (2011) Impacts of tidal land reclamation in Bohai Bay, China: ongoing losses of critical Yellow Sea waterbird staging and wintering sites. Bird Cons Int 21:241–259

Yang H-Y, Chen B, Ma Z-j, Hua N, van Gils JA, Zhang Z-W, Piersma T (2013) Economic design in a long-distance migrating molluscivore: how fast-fuelling red knots in Bohai Bay, China, get away with small gizzards. J Exp Biol 216:3627–3636

Yang H-Y, Chen B, Piersma T, Zhang Z, Ding C (2016) Molluscs of an intertidal soft-sediment area in China: does overfishing explain a high density but low diversity community that benefits staging shorebirds? J Sea Res 109:20–28

Ydenberg RC, Butler RW, Lank DB, Guglielmo CG, Lemon M, Wolfe N (2002) Trade-offs, condition dependence and stopover site selection by migrating sandpipers. J Avian Biol 33:47–55

Zharikov Y, Skilleter GA (2003) Depletion of benthic invertebrates by bar-tailed godwits *Limosa lapponica* in a subtropical estuary. Mar Ecol Prog Ser 254:151–162

Zwarts L, Drent RH (1981) Prey depletion and the regulation of predator density: oystercatchers (*Haematopus ostralegu*s) feeding on mussels (*Mytilus Edulis*). In: Jones NV, Wolff WJ (eds) Feeding and survival srategies of estuarine organisms. Springer US, Boston, pp 193–216

Zwarts L, Wanink JH (1993) How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. Neth J Sea Res 31:441–476

Zweers GA, Gerritsen AFC (1997) Transitions from pecking to probing mechanisms in waders. Neth J Zool 47:161–208

Chapter 13
Mudflat Fishing

Peter G. Beninger

> *He was a bold man who first swallowed an oyster*
> *— James VI of Scotland/James I of England*

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Abstract Mudflat fishing is certainly one of the oldest human activities, and it probably contributed heavily to both our cognitive development and the settlement pattern of human populations still evident today. It is characterized by simple gear for raking or digging, individual effort, relatively small catches, and micro-regulation. It may be divided into two broad categories: professional fishing (catches are sold) and recreational/subsistence fishing (catches are not sold). The recreational fishery may be likened to the sport fishing industry, in that the economic impact of mudflat fishing

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includes a substantial tourism component. Although difficult to evaluate precisely, methods used in the tourism and sport fishing industries allow ball-park evaluations of the economic impact of recreational mudflat fishing in developed countries.

Environmental impacts of mudflat fishing include resource depletion, as well as reduced densities of non-target macrofauna, altered spatial distributions of both macro-and meiofauna, and geochemical modifications in the sediment. Mudflat fishing impacts are likely to be site- and intertidal level-specific, and choice of the appropriate scale of study is problematic. Little attention has been paid to the effects of mudflat fishing on high-profile, declining species such as shorebirds, and this is an urgent research need. Given the long history of mudflat fishing, the system seems to have been relatively resilient up to the present time; this may change in the face of increased pressure from an exponentially-increasing world population.

1 History

It is beyond the scope of this chapter to present a detailed account of mudflat fishing throughout history and the world, for this would require a volume in itself, much like the recent 'History of Aquaculture' (Nash 2011). However, it is important to first place mudflat fishing in its historical context, before describing its common features throughout the modern world.

1.1 Prehistoric Fishing

The earliest known shell middens date from approximately 150,000 years BP, from both the tip of South Africa and southern Spain, indicating that it was a widespread practice at this time (Marean 2010; Cortés-Sánchez et al. 2011). Although these were mainly rocky- and sandy-shore species, it shows that hominids were accustomed to foraging for shellfish at this point in their evolution. It is likely that humans consumed shellfish prior to the formation of middens, which are associated with sedentarization. It has been suggested that the cognitive requirements for shellfish fishing were crucial to the origin of behavioral modernity in humans (Jerardino and Marean 2010).

The species most commonly found in the earliest shell middens are rocky and sandy-shore bivalves and gastropods, probably reflecting the relative ease of foraging. More definitely mudflat species are found in European Neolithic and Bronze Age middens (e.g. Coles and Taylor 1969, Table 13.1).

Table 13.1 Mollusc shells found at a small Neolithic-Bronze Age shell midden in the Culbin Sands, Morayshire (UK)

Representation of shell species by weight				
Batch no.	*Cerastoderma edule*	*Mytilus edulis*	*Littorina littorea*	*Ensis Sp.*
TB2 U	6[a]	932	397	15
TB3 U	4	640	166	6
TB6 U	–	531	252	1
TB7 U	2	572	184	4
TA14 U	3	481	236	37
TB1 L	30	7	–	–
TB4 L	87	21	19	–
TB5 L	69	6	6	2
TB8 L	133	111	12	13
TB9 L	94	22	12	4
TB11 L	84	143	13	22
TB12 L	49	8	10	2
TB13 L	27	9	6	2
TA15 L	18	85	2	2
TA16 L	40	5	7	1

The site probably supported <10 individuals. From Coles and Taylor (1969), with permission
U Upper Midden
L Lower Midden
[a] All weights were measured to the nearest gram

1.2 Mudflat Fishing in the Judeo-Christian Tradition

Theologically-derived dietary restrictions have characterized the attitude of the Jewish and Christian worlds toward the consumption of aquatic invertebrate species throughout much of recorded history. In keeping with the 'Paradise Lost' creation theme of the opening chapters of the Book of Genesis, humans were said to have been originally herbivorous/vegetarian (Gn 1: 29–30); becoming totally omnivorous (Gn 9: 3), and then very precisely restricted with respect to the types of animals that could be consumed, with the clear injunction not to consume any aquatic organism other than fish (Lv 11:10–11, re-stated in the same terms in Dt 14: 9–10). Although the neighbouring Mediterranean Sea is bereft of significant mudflats due to its small tidal range, this restriction obviated mudflat fishing for consumption by observant Jews anywhere in the world, and continues to do so today. The Christian tradition, directly derived from the Jewish, could easily have followed this trajectory as well, were it not for St. Peter's vision (Acts 10: 10–15; 11: 4–9), widely interpreted as removing all religious barriers to living food sources, and paving the way for guilt-free consumption of mudflat shellfish in the Christian world and its secular descendants.

1.3 Mudflat Fishing in the Greek and Roman Empires

The Ancient Greeks ate most of the sediment-dwelling bivalves which they continue to consume today, and despite the limited tidal range in the Mediterranean, some species were fished on foot at low tide (probably in the compressed supralittoral and mediolittoral zones, as well as in shallow waters of the infralittoral zone). Probable species described in the ancient texts include the fan mussel, *Pinna nobilis*, two species of razor clams *Solen capensis* (P. Fischer, 1881) (= *S. marginatus* Pulteney, 1799) and *Ensis minor* (Chenu, 1843), two isomyarian clams *Venus verrucosa* (Linnaeus, 1758) and *Chamelea gallina* (Linnaeus, 1758), *Pholas dactylus* (Linnaeus, 1758), the wedge shell *Donax trunculus* (Linnaeus, 1758), and the Lagoon cockle *Cerastoderma glaucum* (Poiret, 1879) (Voultsiadou et al. 2010). Most of these bivalve species are still exploited today, in regions which once formed part of the Greek Empire: Asia Minor (Dogan et al. 2008), Egypt (Farag et al. 1999), and throughout the Mediterranean, Aegean, and Adriatic seas (Poutiers 1987; Katsanevakis et al. 2008). To this day, the most productive area for intertidal bivalve fishing is the Northern Aegean Sea, particularly the Bay of Kaloni (Lesvos island), exactly as Aristotle reported 2300 years ago (Koutsoubas et al. 2007).

A special apparatus called a "pinologio" was used to extract *P. nobilis* from the sediment (Fig. 13.1); in addition to its use as food, this species was highly prized for its byssus threads, which were woven into a fabric called 'sea silk', and its shells were used as shallow containers or tools, as were those of *C. glaucum* (Voultsiadou et al. 2010). All of the sediment-fished species were also considered what we term today as

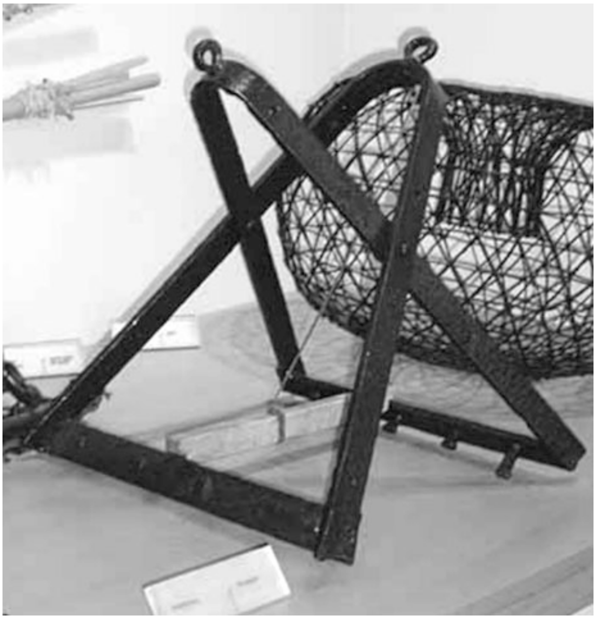

Fig. 13.1 A *pinologio* (foreground), used by Ancient Greeks to extract the fan shell, *Pinna nobilis*, from sediments. Photo taken at the museum of traditional fisheries and shells in Moudania (Chalkidiki, Greece) by D. Koutsoubas.

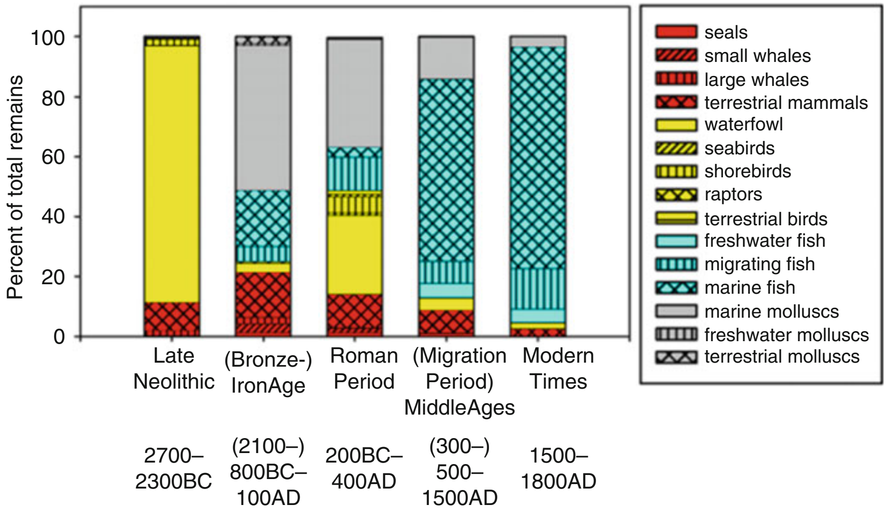

Fig. 13.2 Summary of archaeological remains from 44 sites along the Wadden Sea coast. Percent of remains belonging to each species group (mammals, birds, fish, molluscs) and subgroup as depicted in the legend. Note that fish and molluscs are likely underrepresented in the Late Neolithic period because of missing quantitative information. Cultural periods are identified by name and time. Figure reproduced from Lotze (2007), with permission from Elsevier.

'nutraceuticals', i.e. possessing both nutritive as well as pharmacologic and curative properties (Voultsiadou 2010; Voultsiadou et al. 2010).

1.4 Mudflat Fishing in Europe and the New World

It is impossible to cover the history of mudflat fishing in all of Europe and its offspring in a chapter such as this. However, examples may be studied precisely because of their exemplarity; with its much longer recorded history, Europe is a natural choice for such an enterprise. A case in point is the Wadden Sea (Lotze 2007), which has a history of mudflat fishing since the glacial retreat of the last Ice Age (~7500 BP, Fig. 13.2). In the Bronze-Iron Age (2100 BC–100 AD), molluscs made up half of all identifiable remains at archaeological sites, and these were dominated by species found on the mudflats today: blue mussels *Mytilus edulis*, cockles (*Cerastoderma* spp.), and the clam *Macoma balthica* (Prummel and Heinrich 2005). During the Roman occupation period (200 BC–400 AD), the proportion of these molluscs decreased to 40%, and this decline continued into the Middle Ages (300–1500 AD, 20%) and the Modern era (1500–1800 AD, 10%) (Lotze 2007).

As is so often the case for any unregulated, and many regulated, fisheries (regulation beginning in the twentieth century), exploitation of the common mudflat resource led to the ultimate collapse of most fisheries, with the end result that '*Today,* *the Wadden Sea is among the most degraded estuarine and coastal ecosystems worldwide, together with the Baltic and Adriatic Seas*' (Lotze 2007). At present, only the fisheries for shrimp, blue mussels and cockles are still viable; this is at least partly due to a release from predation, the finfish predators having been driven to functional extinction (Worm and Myers 2003).

2 Contemporary Mudflat Fishing

As mentioned above, subsistence fishing on mudflats is an ancient activity, and it no doubt contributes to the sustenance of many populations worldwide. Due to the difficulty of judging whether this activity is necessary to the survival of the individual fishers, we distinguish only those who sell their catch (professional fishers), and those who do not (recreational fishers). The catch may be for human consumption (bivalves, gastropods, shrimp) or for use as angling bait and aquaculture feeds (polychaetes). Bait fishing is often treated as a separate activity in the literature, but since it shares virtually everything except the end consumer with mudflat fishing, and calls have been made for it to be managed in the same way as mudflat fisheries (Watson et al. 2015, 2017a), it will be included here as a mudflat fishing activity.

2.1 Legal Framework

Mudflat fishing is a type of 'pedestrian fishing', legally defined both in opposition to either ship-based or underwater fishing, and in the requirement that the fisher must at all times have purchase on the substrate (Beurier 2014). Due to strong geographic constraints (i.e. mudflats are all located within territorial waters), there are no international regulations other than the general terms of the 1982 United Nations Convention on the Law of the Sea. At the European Union (EU) level, mudflats as habitats are protected by conservation legislation (SAC—Special Areas of Conservation, and SPA—Special Protection Areas). With respect to the living resources themselves, only EU-wide regulations concerning minimum catch sizes and quality norms exist. Much of the specific regulation is thus to be found at the national or variously local levels; while federal regimes may thus have regulations at the national, state, and local levels, even highly centralized regimes (e.g. France) may have much of their legal framework at the local levels, and it is therefore termed 'micro-regulation' (Boldina 2011).

As mentioned above, mudflat fishing can be further subdivided legally and economically, as either professional or recreational fishing. This distinction may or may not be recognized in law, depending on the jurisdiction. Professional fishing is distinguished primarily by the right to sell fished products, whereas such sale is not permitted for recreational fishers. Professional fishing also carries the obligation of declaring catches, which is somewhat simplified using smartphones (e.g. 'Télécapêche' in France). In

Table 13.2 Types of legal enabling documents for mudflat fishing in France

Enabling document	Activity	Cost
Permit	Fishing	None
Licence	Department	Fee
Stamp	Site/species	Fee

Direction Départementale des Territoires
et de la Mer de la Vendée

PRÉFET DE LA VENDÉE

PERMIS DE PECHE A PIED
PROFESSIONNELLE 2017/2018
n° 2017PAP850000101

Références : Code Rural et de la Pêche Maritime, articles L 961-68 et suivants
Arrêté préfet n° 15/DRCTAJ/2-212 du 19 mars 2015

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Fait à Noirmoutier, le 19 avril 2017
Pour le préfet et par délégation
Patrick LEBLANC
Chef de l'unité régulation
des activités maritimes

COREPEM Licence de pêche à pied professionnelle de
Loire-Atlantique n°98/44/17

Nom : HERY
Prénom : Christophe
Régime : MSA Délivrée le 01/05/2017
Dom. 22, Rue de la Gare
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Timbres	Coque de La Baule			
2017		Moule		Autres Animaux Marins	Licence Huître

COREPEM Licence de pêche à pied professionnelle de
Vendée n°107/85/17

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Licence délivrée le 01/05/2017

Timbre(s)	Palourde	Autres Animaux Marins	
2017	Coque	Huître	Moule

Fig. 13.3 Types of enabling documents for professional intertidal (including mudflat) fishing in France (with consent of M. Christophe Héry, President of the Professional Intertidal Fishers of the Vendée department).

jurisdictions with a complex legal framework (most jurisdictions evolve in this direction), specific regulations may govern professional fishers, e.g. the obligation to fiscally declare the revenues resulting from sales, and contribute to a Social Security fund; in return for payment of licence fees (Table 13.2, Fig. 13.3), the professional fishers then enjoy much higher quotas than the recreational fishers, and may also be allowed to use gear disallowed to recreational fishers (Boldina 2011, Fig. 13.5). All gear is approved at local levels by commissions composed of professional fishermen. In contrast to the professional fishers, recreational fishers do not usually require permits, as this activity is considered a natural extension of the freedom of movement on the seashore, which is common to many jurisdictions worldwide. They must, however, adhere to all regulations governing quotas, gear specifications, minimum sizes, and authorizations based on public health considerations (e.g. areas closed due to bacterial or toxin levels).

Even in countries with relatively ‘advanced’ mudflat fishing regulation, bait fishing tends to largely escape regulation (Watson et al. 2015, 2017a, b)—perhaps simply because the consumers are not people. The result is an activity that is often managed ineffectively, and whose impacts are even more poorly-understood than those of mudflat fishing for human consumption (Watson et al. 2015, 2017a, b).

2.2 Effectiveness of Fishery Regulation

Notwithstanding recent Panglossian professions of ‘resource stewardship’ (e.g. Berkes 2009), all jurists know that an unenforced law is virtually the same as no law at all, and in the case of mudflat fishing, a ‘Tragedy of the Commons’ (Hardin 1968) is the likely result—perhaps even more so with recreational than with professional fishers (who may monitor each other). Given the highly-dispersed nature of intertidal fishing and fishers, the relatively small catches of each fisher, the large geographic areas to cover, and the difficulty of moving about on mudflats, regulatory enforcement is especially weak. Funding for enforcement may even come from professional fishers themselves, as in France, where part of the annual licence fee for professional fishers is used to pay inspectors. However, even in these cases, the actual manpower falls far short of the required manpower; for example, along the entire coastline from Le Croisic to Noirmoutier, France, there are only two inspectors, each working a 35-hour week, and approximately 207 days per year. Due to the difficulty of walking on the mudflats, they approach fishers very slowly, and poachers therefore have ample opportunity to dispose of their catch.

Further evidence that the low-enforcement intertidal fishing environment is ineffective comes from a study done in 219 restaurants throughout Greece (Katsanevakis et al. 2011). Nearly half of these restaurants served *protected* shellfish species (i.e. those which should not be on any menu); the reader is left to imagine the situation for species which are not protected, but subject to fishing regulation. The authors plaintively conclude ‘The strategy for enforcement of existing legislation should be greatly improved; otherwise protection of shelled molluscs will remain ineffective.’ And finally, enforcement was shown to be critical to the protection of ‘no-dig’ sites from bait collectors, and to the management of mudflat bait fisheries as a whole (Watson et al. 2015).

It is likely that increased resources for enforcement will only be forthcoming if the value of mudflat fishing is perceived as being worthy of this investment. The value of professional mudflat fisheries can be assessed in the market value of the products fished, as well as the jobs and infrastructure created or maintained by this activity. The value of recreational mudflat fisheries is likely to be much more complex, with much smaller product values, yet incorporating elements of the tourism industry. A recent study of the surplus value of a small mudflat recreational fishery in France estimated an annual value of 1.5 million € (Boldina et al. in preparation). Heightened awareness of the true value, especially of recreational mudflat shellfisheries, should encourage public investment in the enforcement of regulations designed to perpetuate the resources at the base of these activities.

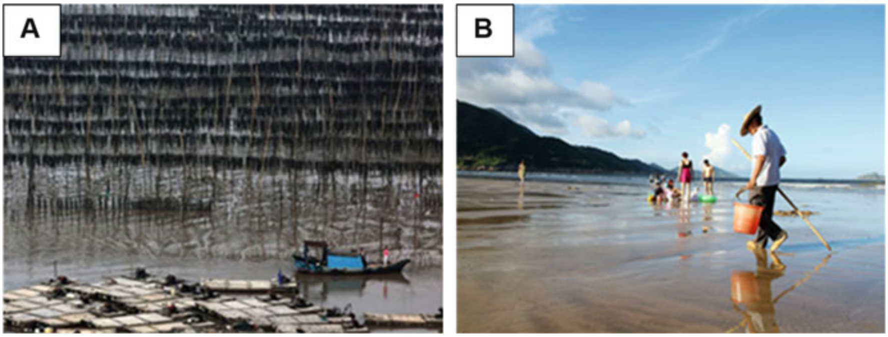

Fig. 13.4 Mytiliculture (**a**) and recreational fishing (**b**) areas on the Xiapu mudflats in Fujian, China. http://www.topchinatravel.com/china-attractions/xiapu-mudflat.htm.

2.3 Conflicts of Use

Mudflat fishing carries the potential for tension and conflict at several levels. Conflicting strategies are evident at the outset, between the above-mentioned legal framework of mudflat conservation, and the very visible habitat perturbation caused by often intensive mudflat fishing.

There are two major mudflat fishery targets: infaunal bivalves (clams, cockles) for human consumption, and polychaete worms (lugworms *Arenicola marina*, sandworms *Nereis virens*, and bloodworms *Glycera dibranchiata*) for the angling bait and aquaculture feed markets (Watson et al. 2017b; Sypitkowski et al. 2009). As these two target groups are largely sympatric, 'clammers' and 'wormers' often overlap on the mudflats, generating usage conflicts. Rigorous research has proven invaluable to the resolution of this conflict, showing that, contrary to the fears of the clammers, worming does not increase clam, and specifically juvenile (*Mya arenaria*) mortality, due to the vertical stratification of these two target groups in the sediment (Beal and Vencile 2001). Similarly, a rapid re-colonization of bait-dug areas has been reported for *Macoma baltica* (van den Heiligenberg 1987). On the other hand, the densities of the clam *Cerastoderma edule* only recovered 5 years after bait digging (Watson et al. 2007), highlighting the need for locally-specific, and even species-specific, research for effective resource management and conflict resolution. The increasing use of bait pumps (see Sect. 2.4), rather than mechanical digging, will probably greatly mitigate such conflicts in the near future.

The second major mudflat usage conflict is between aquaculture and the fishery (Fig. 13.4). Both operations require access to the mudflat; and obviously aquaculturists are loath to have their cultured animals fished by others, while fishers are loath to have areas of the mudflat reserved for exclusive exploitation by aquaculturists. In such a situation, only legal regulation can solve the conflict; ideally, such regulation should proceed from consensus where possible, and this may include other stakeholder perspectives such as habitat and wildlife conservation (e.g. http://www.

frenchmanbaypartners.org/2014/11/conservation-action-planning-mudflat-progress/; http://www.seagrant.umaine.edu/hosting/TB/07TBplan.pdf).

2.4 Types of Fishing Gear

Many types of tools may be seen in use on mudflats, but in countries with advanced legislation, only some of these are legally allowed. Shallow-dwelling bivalves are usually collected using some form of rake; the number and spacing of tines may be legally fixed (Fig. 13.5a, d). Hoes of specified or customary dimensions may be used in finer sediments (Fig. 13.5d). Polychaetes may be fished for bait using tubular hand pumps (Fig. 13.5c). For fragile, rapidly-burrowing species such as the razor clams, the preferred method is to induce them to rise to the sediment surface by pouring salt on their characteristic siphon holes, followed by extraction with a hand shovel. While recreational mudflat fishing generally occurs at low tide, professional fishers may use flat-bottomed boats to access the mudflat at high tide, and use manual drags to recover clams and cockles (Fig. 13.6a, b).

Amateur fishers can check minimum sizes using inexpensive measuring devices (Fig. 13.5b), while professional fishers may use larger, more robust devices (Fig. 13.6c). Indeed, professional fishers often use gear which selects the regulation sizes at several steps of the fishing process (Figs. 13.5d and 13.6e).

2.5 Economic Assessment

It is important to distinguish between the value of a particular species catch, often estimated for commercial fisheries (e.g. the ‘seaworm’ or polychaete commercial fishery, estimated in 1999 to be worth over 200 million € in the European market alone, with a global value of 7.4 billion €—Olive 1999; Watson et al. 2017a), and the total economic value from a fishery, especially in the case of recreational fisheries. As mentioned above, true valuation of mudflat fishing, especially recreational mudflat fishing, is key to justifying the investment needed to protect and sustain the resource upon which it is based. Few studies have addressed this question, and the methodology is still in its infancy. To date, valuations have been based on the individual surplus value, i.e. the economic value added to the local economy by each individual. Two basic approaches are used in the valuation of recreational activities: those based on *revealed preferences,* and those based on *stated preferences* (Hanley et al. 1997; Hicks 2002).

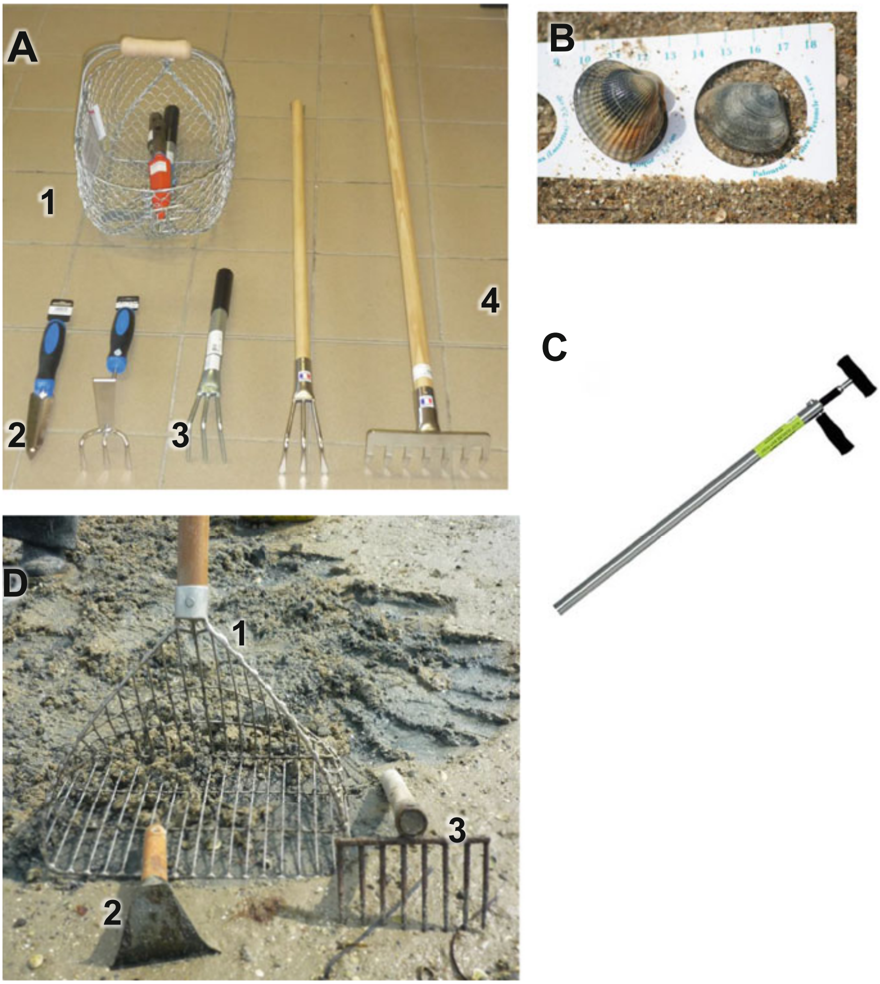

Fig. 13.5 Representative implements used in mudflat fishing. (**a**) French gear for cockle and clam fishing: 1–3, amateur gear: 1, basket allowing drainage of fished animals; 2, narrow shovel which is of practical use only under exceptional conditions when siphon holes can be detected; 3, variety of 3-tined rakes designed to reduce digging impact; 4, multiple-tined rake reserved for professional fishers. (**b**) Simple measuring scale to verify minimum sizes for amateur fishers (France). (**c**) A bait pump used in extracting polychaetes/burrowing shrimp. (**d**) French professional gear: 1, basket allowing both drainage and regulation-compliant size selection; 2, hand hoe for clams and cockles in muddy sediment; 3, hand rake for clams and cockles in coarser sediment. Photos PG Beninger.

2.5.1 Stated vs Revealed Preferences

The stated preference approach incorporates both market and non-market values and can explore hypothetical changes of the environment, sometimes far removed from

Fig. 13.6 Professional mudflat fishing in France. (**a**) Use of a manual drag, (**b**) at high tide on the mudflat, (**c**) sorting container to retain legal-size specimens and (**d**) clam and cockle fishing at low tide. Photos PG Beninger with consentment of M. Christophe Héry.

the reality of existing markets. *Contingent valuation, conjoint analysis,* and *choice experiments* are among the most common techniques used in the stated preferences approach (Hanley et al. 1997; Garrod and Willis 1999). These methods, sometimes combined to produce novel and original models (Brown and Mendelsohn 1984; Cameron 1992; Englin and Cameron 1996; Nunes and van den Bergh 2004; Appéré 2004), have shown limitations in assessing realistic societal values of natural goods and ecosystem services, as demonstrated in the spread between willingness of economic agents to pay for fishing and recreational sites (e.g. Exxon Inc.), and the actual sum awarded by the court (Alaska oil spill—less than four million vs. $US2.5 billion—Hausman et al. 1995).

The revealed preference approach, where individuals reveal their preferences through their choices, presents the advantage of relying on actual facts and indicators such as market prices, rather than on hypothetical and unobservable choices (Hanemann 1994; Alberini and Kahn 2009). Several methods are employed in this approach, such as the *Hedonic Pricing Valuation* (Carter and Liese 2010; Huth and Morgan 2011) and the *Travel Cost Method* (TCM) (Clawson 1959; McConnell and Strand 1981; Carr and Mendelsohn 2003; Nunes and van den Bergh 2004).

The drawbacks of TCM are well known (Pearce et al. 2006; Alberini and Kahn 2009): it only pays attention to (recreational) use values and the real travel cost is often unverifiable (Bockstael et al. 1990; Hanley et al. 1997). Moreover, there may be large inter-individual variations in the perceived value of the trip itself (McConnell and Strand 1981; Cameron 1992; Bontems and Rotillon 2007). It may be countered that these estimations are equally susceptible to under-estimation as to over-estimation, such that for a large enough sample, the errors would tend to cancel each other out. In addition, determining value only from those who actually visit a site cannot take into account those individuals for whom the existence of the site itself has a certain value, without ever actually visiting it. The TCM is thus likely to produce minimum values, which, however, are in themselves quite useful. It is also argued that TCM does not take congestion into account (Deyak and Smith 1978; Jakus and Shaw 1997), thus potentially engendering an omission bias. Attempting to correct for congestion creates its own problem: the potential for endogeneity (correlation of congestion with the risk of error—Bockstael et al. 1990; Leplat 2012).

Despite the drawbacks outlined above, revealed preference methods such as TCM present the distinct advantage of being grounded in actual human actions. The method proved to be particularly helpful in the case of recreational sites whose quality is improved or degraded, resulting in a shift of the demand function (Appéré and Bonnieux 2003; Englin and Cameron 1996; Carr and Mendelsohn 2003; Gürlük and Rehber 2008). Perhaps the overriding virtue of TCM is that it can be combined with the *in situ* methodologies used in studying the natural ecosystems themselves, providing real-time, realistic assessments by actual users of the resource, under the same conditions as those which prevail for the assessments of the other ecosystem dimensions (chemical, physical, and biological). In addition, the TCM method has previously been used in similar contexts, such as the evaluation of recreational fly-fishing sites, or the variation in life quality when intertidal fishing sites are degraded (Bockstael et al. 1990; Hausman et al. 1995; Layman et al. 1996; Appéré and Bonnieux 2003; Appéré 2004; Deronzier and Terra 2006; Johnston et al. 2006), rendering comparison more meaningful. However, TCM valuation results are mostly obtained through ordinary least squares (OLS) or associated regression methods, ignoring several important statistical issues such as the whole and non-negative status of the dependent variable in count data models, or the truncation problem due to *in situ* surveys necessarily starting from the first visit (Grogger and Carson 1991; Cameron and Trivedi 2013).

We recently estimated the economic value of a recreational clam fishery using the TCM approach with a truncated Poisson regression model, and simultaneously collected data from intertidal fishers to create a socio-economic mudflat fisher profile (Boldina et al. in preparation). Independent of the catch value (which is an undeclared, but nonetheless real value added to households), the value injected into the local economy of a small mudflat bivalve fishery in France was estimated at over 1.5 million €. Such numbers could be used to increase regulation enforcement, and to justify on-site investments (e.g. benches, picnic tables), which could increase site attraction and further increase the annual value to the local economy.

2.6 Ecosystem Impact

> *One of the biggest obstacles to sustainable fisheries is likely to be the 'Death by a Thousand Cuts' inflicted in fish habitats by fishing itself…* (Fluharty 2000).

Studies on the ecosystem impact of mudflat fishing have appeared intermittently over the past several decades. Some have focussed on the effects of specific fisheries, such as bait fisheries for lugworms (Blake 1979; Jackson and James 1979; McLusky et al. 1983; van den Heiligenberg 1987; Olive 1993; Harvard and Tindal 1994; Beukema 1995) and bloodworms (Brown and Wilson 1997; Ambrose et al. 1998; Beal and Vencile 2001; Miller and Smith 2012); others have focussed on the effects of fishing human-consumed species [Beal and Vencile (2001), and Masero et al. (2008), which considered the impacts of both bait and shellfish fisheries, Kaiser et al. (2001), Logan (2005), Griffiths et al. (2006), Navedo and Masero (2008)]; and some have looked at the effects of mechanical disturbance, with no specific fishery (Dernie et al. 2003; Whomersley et al. 2010). Much of the thrust of these studies has been concerned with the impact of fishing activities on the mudflat macro- and meiofauna, as well as on feeding shorebirds. Other studies, such as those mentioned below, focussed on the impact of mudflat fishing on sediments, geochemistry, and mudflat fauna as a whole.

Two general types of ecosystem perturbation are conventionally distinguished (Bender et al. 1984): *pulse* (brief and sporadic) or *press* (chronic, continuing). The majority of the mudflats subjected to fishing are thus characterized by sporadic, but nonetheless *press*-type perturbation, depending on the frequency of fishing (itself dependent on time of year, human constraints such as disposable leisure time, etc.).

2.6.1 Geochemical Changes

The mechanical perturbation induced by clam digging or raking modifies sediment granulometry, by exposing finer sediment to erosion, with a resulting increase in grain size, as well as a decrease in sediment organic content (Anderson and Meyer 1986). Studies just below the intertidal zone show that raking to a sediment depth of 15 cm produces a host of changes in sediment characteristics, including the chlorophyll *a* content (Fig. 13.7), P:Fe ratio (Fig. 13.8), HPO_4^{2-}, NH_4^+, NO_3^+, total organic nitrogen, and $Si(OH)_4$ (Falcão et al. 2003). Dramatic changes in sediment geochemistry, notably the $HPO_4{}^{2-}$ concentrations, were also observed at an intertidal site exposed to clam fishing, compared to an undisturbed site (Fig. 13.9, Falcão et al. 2006). Finer-scale study has revealed marked changes in sediment nutrient concentrations within the pools left by fishing depressions in the sediment, compared to adjacent seawater (Van Alstyne et al. 2011).

The removal and associated mortality of infaunal bioturbators in muddy sediments greatly diminishes the oxic sediment layer, resulting in a reducing chemical environment for most of the sediment depth (Norkko and Shumway 2011). Sandy sediments exposed to bivalve fishing are much less affected than are the fished

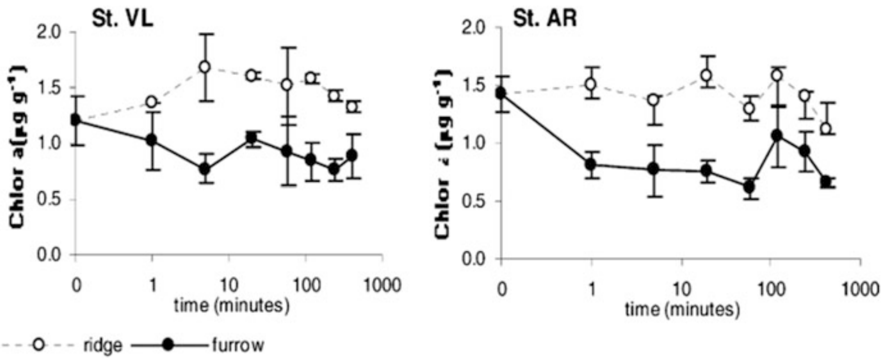

Fig. 13.7 Mean concentrations of chlorophyll a (µg g^{-1}) from the ridge (open circle) and furrow (dark circle) sediment before dredging (0 min); immediately after dredging (1 min) and subsequently (logarithmic time scale), for 2 stations (VL and AR). Ridges and furrows were created by the dredge. From Falcão et al. (2003), reprinted with permission from Elsevier.

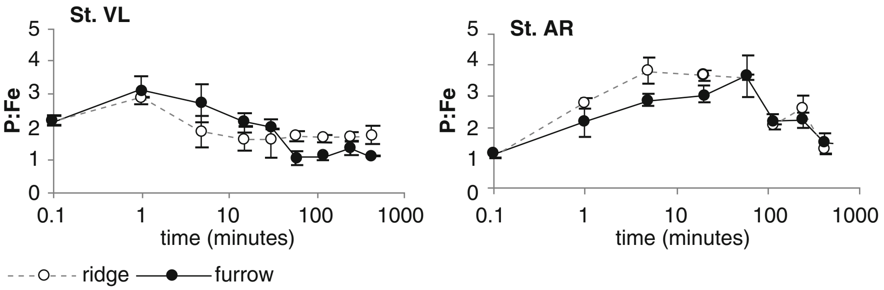

Fig. 13.8 Mean P:Fe ratio from the ridge (open circle) and furrow (dark circle) sediment before dredging (0 min); immediately after dredging (1 min) and subsequently (logarithmic time scale), for two stations (VL and AR). Ridges and furrows were created by the dredge. From Falcão et al. (2003), reprinted with permission from Elsevier.

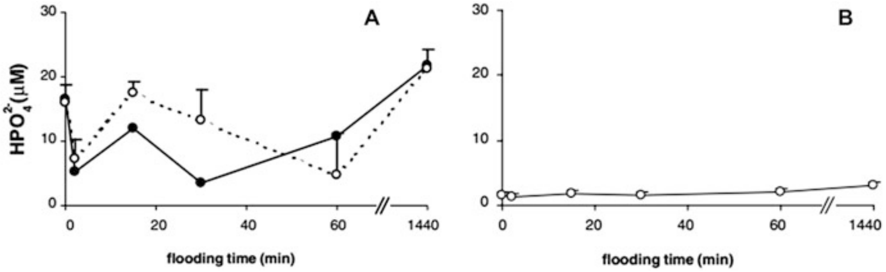

Fig. 13.9. Variation of HPO_4^{2-} in pore water of superficial (0–2 cm, solid line; mean ± SD) and deeper layers (2–8 cm, dotted line; mean ± SD) of muddy sediments (**a**—undisturbed; **b**—reworked), during flooding. From Falcão et al. (2006).

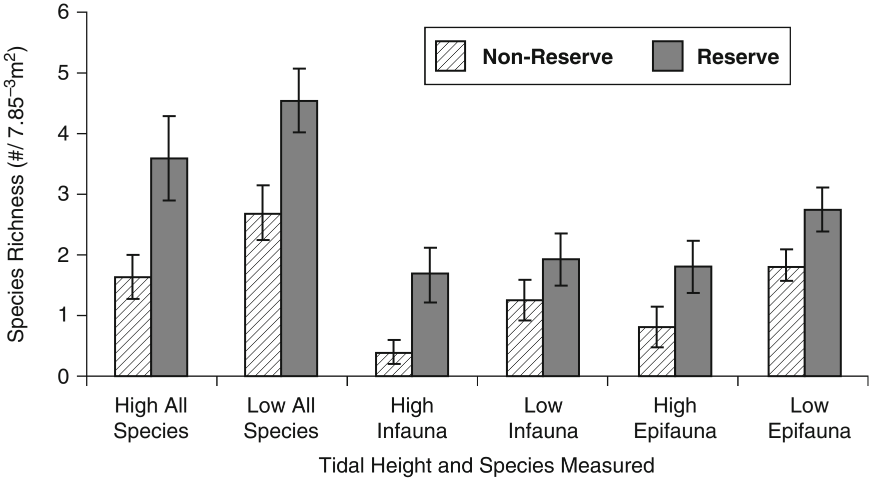

Fig. 13.10 Average non-clam species richness at unfished vs. fished mudflat sites. Species density per core, pooling all unfished and fished sites by tidal height. Bars represent ±1 SE. From Griffiths et al. (2006), with permission from Springer.

mudflat sediments. It is likely that further studies at other sites, focussing on other substances, will also reveal marked geochemical effects on fished mudflats.

2.6.2 Community Changes

Mechanical perturbation on mudflats also affects macrofaunal biomass and composition. This is evident in the overall biomass and community species richness (Fig. 13.10), and/or in the density of both target and non-target species, notably the errant polychaetes which inhabit the upper layers of sediment (Jackson and James 1979; Cryer et al. 1987; van den Heiligenberg 1987; Beukema 1995; Brown and Wilson 1997; Logan 2005; Skilleter et al. 2005; Griffiths et al. 2006; Watson et al. 2007, 2017b; Masero et al. 2008; Toupoint et al. 2016). Macrophytes, which are minor epibenthic species on mudflats, are also affected by mudflat fishing; in particular, macrophytic chlorophytes grow more readily and quickly in the depressions left by fishing activity (Van Alstyne et al. 2011 and Fig. 13.11); indeed, backfilling of dug holes is the most consistently-ignored conservation measure (Watson et al. 2015).

The results of mudflat fishing, and/or the presence of fishers, is generally considered to negatively impact the foraging ecology of shorebirds (Logan 2005; Masero et al. 2008; Navedo and Masero 2008; Watson et al. 2017b). Given the worldwide importance of shorebird populations as environmental sentinels (Piersma and Lindström 2004), and their recent precipitous declines (Munro 2017), this aspect deserves careful attention.

Fig. 13.11 Several-day-old excavation (as evidenced by anchored *Enteromorpha intestinalis*) using illegal fishing gear (probably shovels). Red square shows legal hand gear for comparison. Note the growth of *Enteromorpha sp.* in the pool filling the excavation. Photo PG Beninger, Le Gois, France.

Several authors have cautioned that mudflat fishing impacts have been shown to be (and may generally be) quite site-specific, and even intertidal level-specific, rendering generalizations and predictions extremely problematic (Dernie et al. 2003; Whomersley et al. 2010; Watson et al. 2017b). This obviously means that impact studies must be performed at several intertidal levels at each fishing site, with all of the consequent administrative and financial implications.

Although digging, raking, and bait-pumping the sediment bed are conspicuous forms of mechanical perturbation (Fig. 13.11), humans are also the most imposing animals to frequent mudflats, and it may be expected that human trampling itself could constitute an environmental perturbation. Rossi et al. (2007) showed that human trampling did not appear to affect sediment characteristics, but did negatively affect the abundance and population dynamics of the adult clam *Macoma balthica* and the adult cockle *Cerastoderma edule*. Juveniles of both species appeared more resistant than adults to trampling perturbation, and those of *M. balthica* fared better than those of *C. edule,* opening the possibility of eventual domination of the former on the trampled mudflats. Our own exploratory, unpublished work has shown that meiofauna (nematodes in particular) appear to rapidly burrow deeper into the sediment in response to vibrations induced by human trampling, or even casual walking, on the substrate (Fig. 13.12).

A cautionary note should be sounded with respect to the spatial scales at which most mudflat fishing impact studies have been performed. Watson et al. (2017b) draw attention to the potential artefacts involved when small-scale plots of several m^2 are

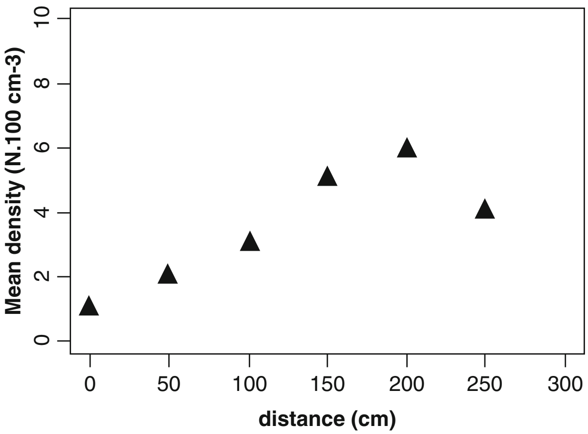

Fig. 13.12 Mean nematode densities (N.100.cm^{-3}) at increasing distances from impact perturbation. Lowest density is found close to the impact, with higher densities further from the impact (P. Beninger, unpublished data).

used, including macrofaunal migration from surrounding areas, and the dependence of recovery rates and effect sizes on plot area. On the other hand, use of their recommended hectare-level spatial scale may well be impossible for many mudflats, due to the inability to obtain permission for, and effective enforcement of, subsequent fisher exclusion. This dilemma is emblematic of the challenges involved in the evaluation of mudflat fishing impacts.

2.6.3 Spatial Distribution Effects

Organism spatial distribution is a structuring characteristic of all ecosystems (Legendre 1993; Borcard et al. 2004; Fortin and Dale 2005). A fine-scale (< several metres) aggregated spatial distribution is the rule for sessile or attached benthic marine organisms, and this may be due both to substrate characteristics, as well as to the selective advantage of proximity to conspecifics (notably for sexual reproduction). A series of recent studies has shown that clam fishing greatly modifies the aggregative spatial distribution characteristics of both targeted (clam, cockle) and untargeted (lugworm) species (Figs. 13.13 and 13.14). In all cases, the aggregative structure broke down at fished sites, resulting in much more contiguous distributions (Boldina and Beninger 2013, 2014; Beninger and Boldina 2014). This effect extended right down to the associated meiofauna (Boldina et al. 2014). In addition to the potential consequences of such attenuation on feeding, reproduction, and recruitment, highlighted in these works, it is important to consider the implications for foraging in non-human predators such as shorebirds, which are major sentinels of environmental status (Huettmann and Czech 2006; Piersma and Lindström 2004), and which probably rely heavily on Levy walk-type foraging strategies (Elliott et al. 2009). Similarly, the important role of sediment reworkers/enrichers such as the lugworm *Arenicola marina* suggest that it would be worthwhile to study the effects of mudflat fishing on this function (Wendelboe et al. 2013), especially in light of the often intense lugworm fishery.

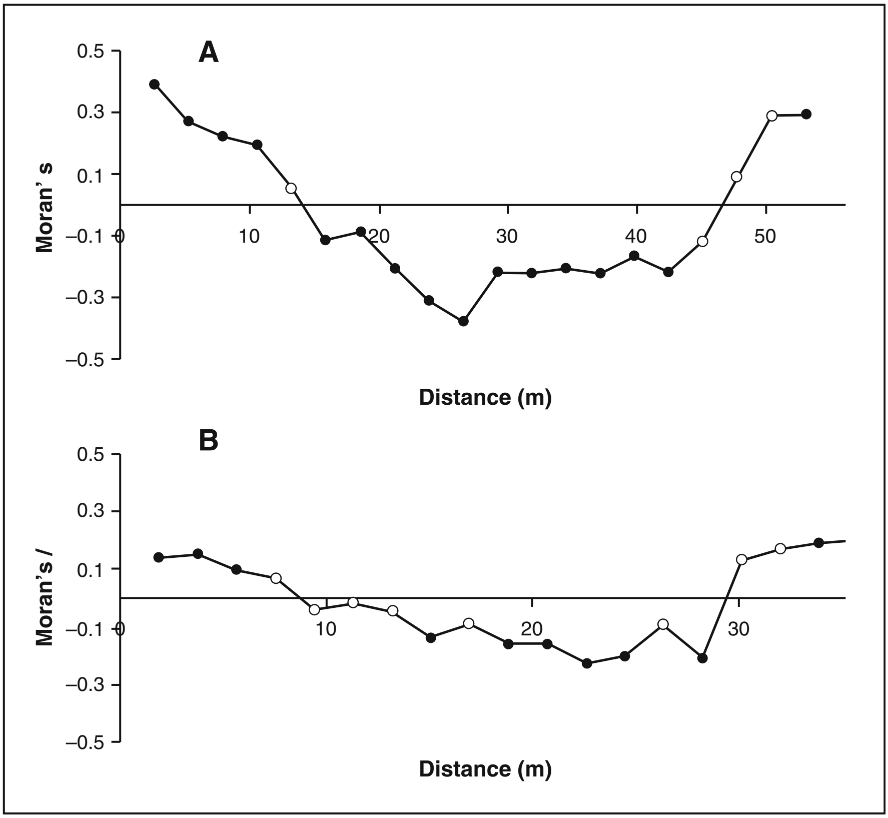

Fig. 13.13 *Arenicola marina*. All-directional spatial autocorrelogram for quadrat-count transformed data using 20 equidistant classes. Statistically significant values are represented by black symbols; non-significant values are represented by empty symbols. (**a**) Non-impacted site. (**b**) Clam-fishing impacted site. From Boldina and Beninger (2014), reprinted with permission from Elsevier.

Although most studies on the effects of ecosystem perturbation tend to report the values of the ecosystem processes themselves, a promising, and more sensitive, approach may be the detection of changes in the variability of these processes. This approach may allow the early detection of ecosystem changes which would otherwise be overlooked in more conventional studies (Fraterrigo and Rusak 2008).

Finally, it should be noted that disturbance effects within spatial patches may extend beyond the patches themselves, and that disturbed patch dynamics may also be affected by feedback from the surrounding community (terHorst and Dudgeon 2009).

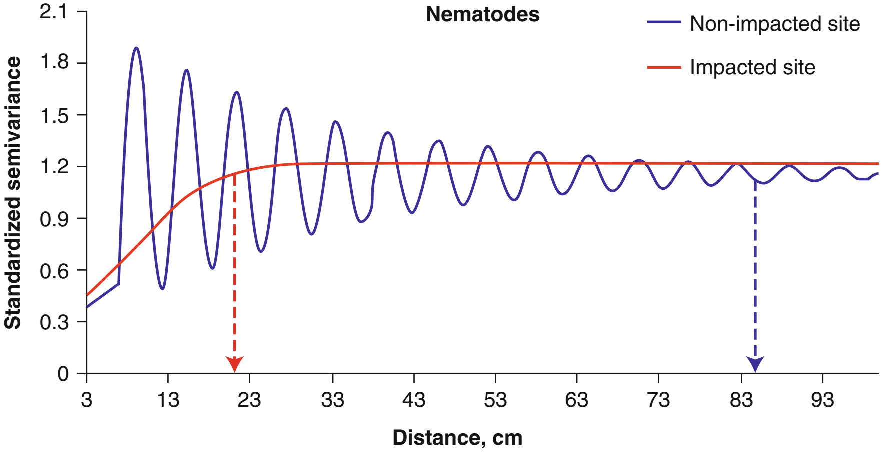

Fig. 13.14 A convenient variogram model of nematode density *vs* distance (extrapolated) for a non-impacted and a clam fishing-impacted site. Note the strong oscillations characterizing the non-impacted site, indicative of spatial aggregation patterning at scales of several centimeters up to over 80 cm, and the virtual absence of such patterning at the clam-fished site. From Boldina et al. (2014), reprinted with permission from Elsevier.

2.6.4 Mudflat Fishers as Sentinels of Resource Problems and Partners in Research

Those directly and continuously in contact with a fished resource are often the first to detect problems with the resource (e.g. Wiber et al. 2012; Bender et al. 2014; www.invasivespeciesinfo.gov/aquatics/mittencrab.shtml). This specialised local ecological knowledge (LEK—Berkes et al. 2000), also referred to as indigenous ecological knowledge or traditional ecological knowledge (TEK—Hamilton and Walter 1999) is frequently the initiator of fishery research, which is usually reactive rather than proactive. A recent case in point is the discovery of the current ribbonworm problem in the Maine mudflat fishery on the American north-east coast (www.mainecoastfishermen.org/single-post/2016/09/28/A-Changing-Climate-in-Our-Mud-Flats-Ribbon-Worms). Collaboration with professional fisherman can be invaluable, as in the series of studies on the effects of mudflat fishing on organism spatial distribution (Boldina and Beninger 2013, 2014; Beninger and Boldina 2014; Boldina et al. 2014), which relied heavily on the LEK of the local President of the Professional Intertidal Fishers Association, without whom it would have been impossible to locate (and access) a non-fished (control) site, and who provided essential information on the types of fishers at the fished sites. While it is important to educate fishers about the concerns of conservation and habitat protection (Watson et al. 2015, 2017a), it is equally important that they feel valued as partners, rather than as adversaries, in such endeavours.

3 Conclusion

We have seen (Chap. 1) that mudflats were probably the cradle of human evolution, since it is very likely that the present distribution of human populations is a cascade result of initial human settlements along coastlines where access to food in the intertidal zone was much easier, consistent, and profitable than hunting or gathering berries (Jackson et al. 2001). Mudflat fishing pressure has been applied irregularly but continuously for at least 150,000 years, and, despite the adverse effects mentioned above, it is a testament to the resilience of the shallow sediment ecosystem (Constantino et al. 2009), that not only recreational/subsistence, but also commercial mudflat fishing is still possible today. It is likely that the continued recruitment of fished species is in fact heavily dependent on larvae arriving in the intertidal zone from the sublittoral zone, which is often subjected to far less infaunal fishing pressure. In this respect, wild food harvested from the mudflats may truly be considered a 'gift from the sea'. Whether this will endure in the face of the increased pressure from an exponentially-increasing human population, is indeed an open question.

References

Alberini A, Kahn J (2009) Handbook on contingent valuation. Edward Elgar, Northampton, 448 p

Ambrose WG, Dawson M, Gailey C, Ledkovsky P, O'Leary S, Tassinari Bvogel H, Wilson C (1998) Effects of baitworm digging on the soft-shelled clam *Mya arenaria*, in Maine: shell damage and exposure on the sediment surface. J Shellfish Res 17:1043–1049

Anderson FE, Meyer LM (1986) The interaction of tidal currents on a disturbed intertidal bottom with a resulting change in particulate matter quantity, texture and food quality. Estuar Coast Shelf Sci 22:19–29

Appéré G (2004) L'évaluation des actifs à usage récréatif: la méthode contingente des coûts de transport. Revue d'Économie Régionale et Urbaine 2004(1):81–106

Appéré G, Bonnieux F (2003) Pêche récréative et risques sanitaires: le cas des coquillages. INRA Sciences Sociales: Recherches en Economie et Sociologie Rurales N° 3/02:1–4

Beal BF, Vencile KW (2001) Short term effects of commercial clam (*Mya arenaria*) and worm (*Glycera dibranchiata*) harvesting on the survival and growth of juveniles of the soft-shell clam. J Shellfish Res 20:1145–1157

Bender EA, Case TJ, Gilpin ME (1984) Perturbation experiments in community ecology: theory and practice. Ecology 65:1–13

Bender MG, Machado GR, Silva PJA, Floeter S, Monteiro-Netto C, Luiz OJ, Ferreira CEL (2014) Local ecological knowledge and scientific data reveal overexploitation by multigear artisanal fisheries in the southwestern Atlantic. PLoS One 9:e110332

Beninger PG, Boldina I (2014) Fine-scale spatial distribution of the temperate infaunal bivalve *Tapes (=Ruditapes) philippinarum* (Adams and reeve) on fished and unfished intertidal mudflats. J Exp Mar Biol Ecol 457:128–134

Berkes F (2009) Revising the commons paradigm. J Nat Resour Policy Res 1:261–264

Berkes F, Colding J, Folke C (2000) Rediscovery of traditional ecological knowledge as adaptive management. Ecol Appl 10:1251–1262

Beukema JJ (1995) Long-term effects of mechanical harvesting of lugworms *Arenicola marina* on the zoobenthic community of a tidal flat in the Wadden Sea. Neth J Sea Res 33:219–227

Beurier JP (2014) Droits maritimes, $3^{\text{ième}}$ edn. Dallioz Action, Paris

Blake RW (1979) Exploitation of a natural population of *Arenicola marina* (L.) from the North-East Coast of England. J Appl Ecol 16:663–670

Bockstael NE, Strand IE, McConnell KE, Arsanjani F (1990) Sample selection bias in the estimation of recreation demand functions: an application to sportfishing. Land Econ 66:40–49

Boldina I (2011) Cadre juridique des activités de la pêche à pied des coquillages sur le littoral atlantique français. Annuaire de droit maritime et océanique 29:143–179

Boldina I, Beninger PG (2013) Fine-scale spatial structure of the exploited infaunal bivalve *Cerastoderma edule* on the French Atlantic coast. J Sea Res 76:193–200

Boldina I, Beninger PG (2014) Fine-scale spatial distribution of the common lugworm *Arenicola marina*, and effects of intertidal clam fishing. Estuar Coast Shelf Sci 143:32–40

Boldina I, Beninger PG, Le Coz M (2014) Effect of long-term mechanical perturbation on intertidal soft-bottom meiofaunal community spatial structure. J Sea Res 85:85–91

Bontems P, Rotillon G (2007) Economie de l'environnement, 3ème édn. Editions La Découverte, Collections Repères, Paris, 120 p

Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H (2004) Dissecting the spatial structure of ecological data at multiple scales. Ecology 85:1826–1832

Brown G Jr, Mendelsohn R (1984) The hedonic travel cost method. Rev Econ Stat 66:427–433

Brown B, Wilson WH Jr (1997) The role of commercial digging of mudflats as an agent for change of infaunal intertidal populations. J Exp Mar Biol Ecol 218:49–61

Cameron TA (1992) Combining contingent valuation and travel cost data for the valuation of nonmarket goods. Land Econ 68:302–317

Cameron AC, Trivedi PK (2013) Regression analysis of count data, 2nd edn. Cambridge University Press, Cambridge

Carr L, Mendelsohn R (2003) Valuing coral reefs: a travel cost analysis of the great barrier reef. AMBIO J Hum Environ 32:353–357

Carter DW, Liese C (2010) Hedonic valuation of sportfishing harvest. Mar Resour Econ 25:391–407

Clawson M (1959) Methods of measuring the demand for and value of outdoor recreation. Reprint no 10. Resources for the Future, Washington

Coles JM, Taylor JJ (1969) The excavation of a midden in the Culbin Sands, Morayshire. Proc Soc Antiq Scot 102:87–100

Constantino R, Gaspar MB, Tata-Regala J, Carvalho S, Cúrdia J, Drago T, Taborda R, Monteiro CC (2009) Clam dredging effects and subsequent recovery of benthic communities at different depth ranges. Mar Environ Res 67:89–99

Cortés-Sánchez M, Morales-Muñiz A, Simón-Vallejo MD, Lozano-Francisco MC, Vera-Peláez JL, Finlayson C, Rodríguez-Vidal J, Delgado-Huertas A, Jiménez-Espejo FJ, Martínez-Ruiz F, Martínez-Aguirre MA, Pascual-Granged AJ, Bergadà-Zapata MM, Gibaja-Bao JF, Riquelme-Cantal JA, López-Sáez JA, Rodrigo-Gámiz M, Sakai S, Sugisaki S, Finlayson G, Fa DA, Bicho NF (2011) Earliest known use of marine resources by Neanderthals. PLoS One 6(9):e24026. https://doi.org/10.1371/journal.pone.0024026

Cryer MC, Whittle GN, Williams R (1987) The impact of bait collection by anglers on marine intertidal invertebrates. Biol Conserv 42:83–93

Dernie KM, Kaiser MJ, Warwick RM (2003) Recovery rates of benthic communities following physical disturbance. J Appl Ecol 72:1043–1056

Deronzier P, Terra S (2006) Etude sur la valorisation des aménités du Loir. Rapport à la Direction des Etudes Economiques et de l’Evaluation Environnementale—Ministère de l’Ecologie, de l’Energie, du Développement durable et de l’Aménagement du territoire, 84 p

Deyak TA, Smith VK (1978) Congestion and participation in outdoor recreation: a household function production approach. J Environ Econ Manag 5:63–80

Dogan AE, Dağlı T, Özcan K, Bakır ZE, Önen M, Katağan T (2008) Commercially important invertebrates inhabiting the Turkish seas. Turk J Aquat Life 3–5(5–8):36–44

Elliott KH, Bull RD, Gaston AJ, Davoren GK (2009) Underwater and above-water search patterns of an Arctic seabird: reduced searching at small spatiotemporal scales. Behav Ecol Sociobiol 63:1773–1785

Englin J, Cameron TA (1996) Augmenting travel cost models with contingent behavior data. Environ Resour Econ 7:133–147

Falcão M, Gaspar MB, Caetano M, Santos MN, Vale C (2003) Short-term environmental impact of clam dredging in coastal waters (south of Portugal): chemical disturbance and subsequent recovery of seabed. Mar Environ Res 56:649–664

Falcão M, Caetano M, Serpa D, Gaspar M, Vale C (2006) Effects of infauna harvesting on tidal flats of a coastal lagoon (ria Formosa, Portugal): implications on phosphorus dynamics. Mar Environ Res 6:136–148

Farag EA, Dekinesh SI, El-Odessy HM (1999) Taxonomical studies on edible bivalve molluscs inhabiting the coastal zones of Alexandria, Egypt. Pak J Biol Sci 2:1341–1349

Fluharty D (2000) Habitat protection, ecological issues, and implementation of the sustainable fisheries act. Ecol Appl 10:325–337

Fortin MJ, Dale MRT (2005) Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge

Fraterrigo JM, Rusak JA (2008) Disturbance-driven changes in the variability of ecological patterns and processes. Ecol Lett 11:756–770

Garrod G, Willis KG (1999) Economic valuation of the environment. Edward Elgar, Cheltenham

Griffiths J, Dethier M, Newsom A, Byers J, Meyer J, Oyarzun F, Lenihan H (2006) Invertebrate community responses to recreational clam digging. Mar Biol 149:1489–1497

Grogger JT, Carson RT (1991) Models for truncated counts. J Appl Econ 6:225–238

Gürlük S, Rehber E (2008) A travel cost study to estimate recreational value for a bird refuge at Lak Manyas, Turkey. J Environ Manag 88:1350–1360

Hamilton R, Walter R (1999) Indigenous ecological knowledge and its role in fisheries research design: a case study from Roviana lagoon, Western Province, Solomon Islands. SPC Trad Mar Resour Manag Knowl Inform Bull 11:13–25

Hanemann WM (1994) Valuing the environment through contingent valuation. J Econ Perspect 8:19–43

Hanley N, Shogren J, White B (1997) Environmental economics in theory and practice. Oxford University Press, 764 p

Hardin G (1968) The tragedy of the commons. Science 162:1243–1248

Harvard MSC, Tindal TE (1994) The impacts of bait digging on the polychaete fauna of the swale estuary, Kent, UK. Polychaete Res 16:32–36

Hausman JA, Leonard GK, McFadden D (1995) A utility-consistent, combined discrete choice and count data model: assessing recreational use losses due to natural resources damage. J Public Econ 56:1–30

Hicks RL (2002) Stated preference methods for environmental management: recreational summer flounder angling in the Northeastern United States. Final report prepared for the US National Marine Fisheries Service. Virginia Institute of Marine Science. 73 p. http://web.vims.edu/GreyLit/VIMS/Hicks2002.pdf

Huettmann F, Czech B (2006) The steady-state economy for global shorebird and habitat conservation. Endanger Species Res 2:89–92

Huth WL, Morgan OA (2011) Measuring the willingness to pay for cave diving. Mar Resour Econ 26:151–166

Jackson MJ, James R (1979) The influence of bait digging on cockle, *Cerastoderma edule*, populations in North Norfolk. J Appl Ecol 16:671–679

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LV, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638

Jakus P, Shaw WD (1997) Congestion at recreation areas: empirical evidence on perceptions, mitigating behaviour et management preferences. J Environ Manag 50:389–401

Jerardino A, Marean CW (2010) Shellfish gathering, marine paleoecology and modern human behavior: perspectives from cave PP13B, pinnacle point, South Africa. J Hum Evol 59:412–424

Johnston RJ, Ranson MH, Besedin EY, Helm EC (2006) What determines willingness to pay per fish? A meta-analysis of recreational fishing values. Mar Resour Econ 21:1–32

Kaiser MJ, Broad G, Hall SJ (2001) Disturbance of intertidal soft-sediment benthic communities by cockle hand raking. J Sea Res 45:9–130

Katsanevakis S, Lefkaditou E, Galinou-Mitsoudi S, Koutsoubas D, Zenetos A (2008) Molluscan species of minor commercial interest in Hellenic seas: distribution, exploitation and conservation status. Mediterr Mar Sci 9:17–32

Katsanevakis S, Poursanidis D, Issaris Y, Panou A, Petza D, Vassilopoulou V, Chaldaiou I, Sini M (2011) “Protected” marine shelled molluscs: thriving in Greek seafood restaurants. Mediterr Mar Sci 12:429–438

Koutsoubas D, Galinou-Mitsoudi S, Katsanevakis S, Leontarakis P, Metaxatos A, Zenetos A (2007) Bivalve and gastropod molluscs of commercial interest for human consumption in the Hellenic seas. In: Papakostantinou C, Tserpes G, Zenetos A (eds) State of the Hellenic Fisheries, 2007. HCMR, Athens, pp 23–43

Layman RC, Boyce JR, Criddle KR (1996) Economic value of Chinook Salmon sport fishery of the Gulkana river, Alaska, under current and alternative management plans. Land Econ 72:113–128

Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659–1673

Leplat M (2012) La congestion: une variable clé dans les modèles de choix de sites récréatifs. Économie et Prévision 200–201:185–204

Logan JM (2005) Effects of clam digging on benthic macroinvertebrate community structure in a Maine mudflat. Northeast Nat 12:315–324

Lotze HK (2007) Rise and fall of fishing and marine resource use in the Wadden Sea, southern North Sea. Fish Res 87:208–218

Marean CW (2010) Pinnacle point cave 13B (western Cape Province, South Africa) in context: the cape floral kingdom, shellfish, and modern human origins. J Hum Evol 59:425–443

Masero JA, Castro M, Estrella SM, Perez-Hurtado A (2008) Evaluating impacts of shellfish and baitworm digging on bird populations: short-term negative effects on the availability of the mudsnail *Hydrobia ulvae* to shorebirds. Biodivers Conserv 17:691–701

McConnell KE, Strand I (1981) Measuring the cost of time in recreation demand analysis: an application to sportfishing. Am J Agric Econ 63:153–156

McLusky DS, Anderson FE, Wolfe-Murphy S (1983) Distribution and population recovery of *Arenicola marina* and other benthic fauna after bait digging. Mar Ecol Prog Ser 11:173–179

Miller RJ, Smith SJ (2012) Nova Scotia’s bloodworm harvest: assessment, regulation and governance. Fish Res 113:84–93

Munro M (2017) What’s killing the world’s shorebirds? Nature 541:16–20

Nash CE (2011) The history of aquaculture. Wiley-Blackwell, Ames, 227 p

Navedo JG, Masero JA (2008) Effects of traditional clam harvesting on the foraging ecology of migrating curlews (*Numenius arquata*). J Exp Mar Biol Ecol 355:59–65

Norkko J, Shumway SE (2011) Bivalves as bioturbators and bioirrigators. In: Shumway SE (ed) Shellfish aquaculture and the environment. Wiley-Blackwell, Singapore, pp 297–317

Nunes PALD, van den Bergh CJM (2004) Can people value protection against invasive marine species? Evidence from a joint TC-CV survey in the Netherlands. Environ Resour Econ 28:517–532

Olive PJW (1993) Management of the exploitation of the lugworm *Arenicola marina* and the ragworm *Nereis virens* (Polychaeta) in conservation areas. Aquat Conserv Mar Freshw Syst 3:1–24

Olive PJ (1999) Polychaete aquaculture and polychaete science: a mutual synergism. Hydrobiologia 402:175–183

Pearce D, Atkinson G, Mourato S (2006) Analyse coûts-bénéfices et environnement: développements récents. Editions OCDE, Paris, 355 p

Piersma T, Lindström A (2004) Migrating shorebirds as integrative sentinels of global environmental change. Ibis 146(Suppl 1):61–69

Poutiers JM (1987) Bivalves. In: Fiches FAO d'identification des espèces pour les besoins de la pêche. Méditerranée et Mer Noire. vol I. Végétaux et Invertébrés. FAO, Rome, pp 370–512

Prummel W, Heinrich D (2005) Archaeological evidence of former occurrence and changes in fishes, amphibians, birds, mammals and molluscs in the Wadden Sea area. Helgoland J Mar Res 59:55–70

Rossi F, Forster RM, Montserrat F, Ponti M, Terlizzi A, Ysebaert T, Middelburg JJ (2007) Human trampling as short-term disturbance on intertidal mudflats: effects on macrofauna biodiversity and population dynamics of bivalves. Mar Biol 151:2077–2090

Skilleter GA, Zharikov Y, Cameron B, McPhee DP (2005) Effects of harvesting callianassid (ghost) shrimps on subtropical benthic communities. J Exp Mar Biol Ecol 320:133–158

Sypitkowski E, Ambose WG Jr, Bohlen C, Warren J (2009) Catch statistics in the bloodworm fishery in Maine. Fish Res 96:303–307

Terhorst CP, Dudgeon SR (2009) Beyond the patch: disturbance affects species abundances in the surrounding community. J Exp Mar Biol Ecol 370:120–126

Toupoint N, Barbier P, Tremblay R, Archambault P, McKindsey CW, Winkler G, Meziane T, Olivier F (2016) Influence of intertidal recreational fisheries and 'bouchot' mussel culture on bivalve recruitment. Mar Environ Res 117:1–12

Van Alstyne KL, Flanagan JC, Gifford SA (2011) Recreational clam harvesting affects sediment nutrient remineralization and the growth of the green macroalga *Ulva lactuca*. J Exp Mar Biol Ecol 401:57–62

van den Heiligenberg T (1987) Effects of mechanical and manual harvesting of lugworms *Arenicola marina* L. on the benthic fauna of tidal flats in the Dutch Wadden Sea. Biol Conserv 39:165–177

Voultsiadou E (2010) Therapeutic properties and uses of marine invertebrates in the ancient Greek world and early Byzantium. J Ethnopharmacol 130:237–247

Voultsiadou E, Koutsoubas D, Achparaki M (2010) Bivalve mollusc exploitation in Mediterranean coastal communities: an historical approach. J Biol Res Thessaloniki 13:35–45

Watson GJ, Farrell P, Stanton S, Skidmore LC (2007) The effects of bait collection on *Nereis virens* populations and macrofaunal communities in the Solent, UK. J Mar Biol Assoc UK 87:703–716

Watson GJ, Murray JM, Schaefer M, Bonner A (2015) Successful local marine conservation requires appropriate educational methods and adequate enforcement. Mar Policy 52:59–67

Watson GJ, Murray JM, Schaefer M, Bonner A (2017a) Bait worms: a valuable and important fishery with implications for fisheries and conservation management. Fish Fish 18:374–388

Watson GJ, Murray JM, Schaefer M, Bonner A, Gillingham M (2017b) Assessing the impacts of bait collection on inter-tidal sediment and the associated macrofaunal and bird communities: the importance of appropriate spatial scales. Mar Environ Res 130:122–133

Wendelboe K, Egelund JT, Flindt MR, Valdemarsen T (2013) Impact of lugworms (*Arenicola marina*) on mobilization and transport of fine particles and organic matter in marine sediments. J Sea Res 76:31–38

Whomersley P, Huxham M, Bolam S, Schratzberger AJ, Ridland D (2010) Response of intertidal macrofauna to multiple disturbance types and intensities—an experimental approach. Mar Environ Res 69:297–308

Wiber MG, Young S, Wilson L (2012) Impact of aquaculture on commercial fisheries: fishermen's local ecological knowledge. Hum Ecol 40:29–40

Worm B, Myers RA (2003) Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology 84:162–173

Chapter 14
Mudflat Aquaculture

Peter G. Beninger and Sandra E. Shumway

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Abstract It was probably an easy and inevitable transition from mudflat fishing to mudflat aquaculture in prehistoric times. Historical references date from the first century AD, and mudflat aquaculture is now practiced worldwide. Culture consists primarily of infaunal and epifaunal bivalve species, with the Manila clam (*Tapes philippinarum*), followed by the Pacific oyster *Crassostrea gigas,* as the most important species worldwide. In this chapter, production statistics and rearing practices are reviewed, and placed in context with environmental issues.

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1 Historical Context

It is difficult to ascertain when mudflat aquaculture actually began, because without archaeological evidence (e.g. vestiges of barriers), wild-fished bivalve shells in prehistoric middens cannot be distinguished from wild-fished juveniles which were then re-seeded in protected plots on the mudflat. Evidence of such 'transitional' mudflat aquaculture has been documented in North America from the first century AD (Lepofsky et al. 2015; Jenkins 2017). The *vivarae piscinarae* which appeared, beginning in the first and second centuries AD, and which were an integral part of the estates of wealthy Roman nobles, may have contained shellfish (Nash 2011). However, the undisputed presence of husbanded marine shellfish dates from the third or fourth century AD, with the depiction of a labelled '*Ostrearia'* on a blown glass bottle (Günther 1897; Fig. 14.1). By the thirteenth century on the French Atlantic coast, mussel spat began to be caught on wooden stakes between which a network of branches were strung, giving rise to the 'bouchot' tradition which has continued, in modified form, to this day. The Japanese began to use a similar system for capturing oyster spat on bamboo poles during the Shogun period beginning in the thirteenth century. By the nineteenth century, juveniles were being reared in net bags attached to the poles, increasing the production per pole. With the development of the hanging-culture technique in the 1920s, bivalve aquaculture was able to expand beyond the mudflats to the sublittoral zone (Nash 2011).

Official interest in European shellfish aquaculture on mudflats increased with the work of Professor Coste in France in the nineteenth century, who developed the technique of capturing oyster spat on modified ceramic roofing tiles. It was at this time (the 'Second Empire', 1852–1870) that Emperor Napoleon III decreed the creation of two Imperial Oyster Parks in Arcachon Bay, which has remained a major site of oyster production to this day (Nash 2011). Mudflat culture of oysters, clams, and mussels increased steadily throughout the twentieth and early twenty-first centuries, both in Europe and the New World, despite recurrent epizooties among the oyster populations and, more recently, the Manila clam populations.

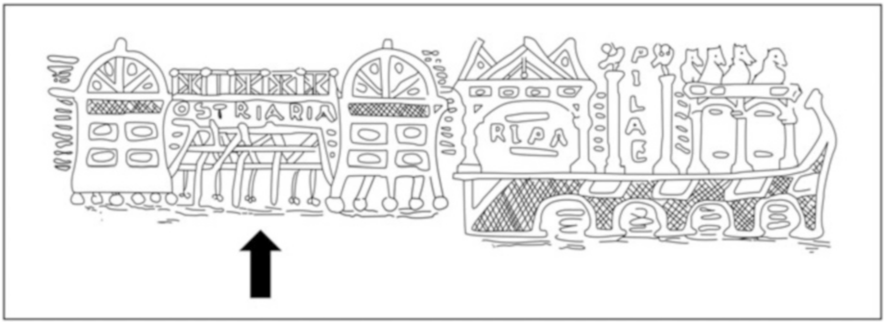


Fig. 14.1 Line drawing from the Roman 'Populina Bottle', dating from the third to fourth century AD. Note the '*Ostrearia*' for rearing juvenile oysters to adults. The slight difference in spelling may be the artist's mistake, or an accepted variation; despite the impressions of many students, Latin was a relatively fluid language. Redrawn from Günther (1897).

2 Major Taxa Reared: Endobenthic (Clams, Cockles) and Epibenthic (Mussels, Oysters)

The major taxa reared (i.e. those for which a declared world production is $\geq 3 \times 10^5$ metric tons) are oysters, clams, and blood cockle (which is in fact an arkshell), of which by far the dominant species are *Tapes philippinarum*, *Crassostrea gigas*, and *Tegillarca granulosa*, respectively (Figs. 14.2, 14.3, 14.4 and 14.5). All three species grow quickly under mudflat conditions, and are accustomed to regular tidal exposure.

In addition to these three dominant species, mussels (*Mytilus* spp.) are important cultured species in some countries, e.g. France and the Netherlands; in both

Fig. 14.2 Basket of Littleneck (= Manila) clam, *Tapes philippinarum*, showing the great degree of heterogeneity in shell pigmentation. Photo PG Beninger.

Fig. 14.3 Pacific oyster, *Crassostrea gigas*. Photo PG Beninger.

Fig. 14.4 Blood cockle, *Tegillarca granulosa.* Note the bright red mantle pigmentation due to the presence of the hemoglobin respiratory pigment. Photos S. Shumway.

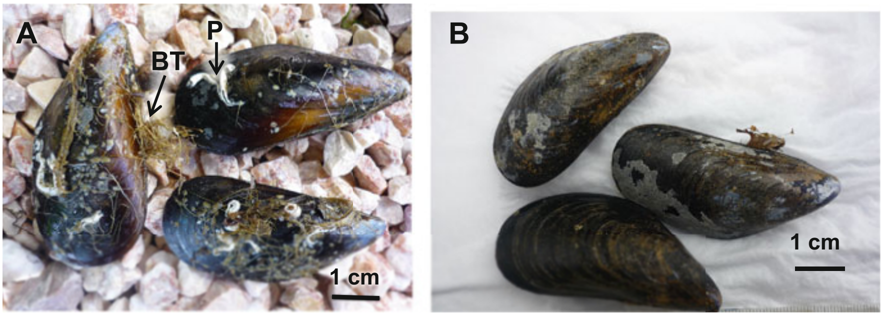


Fig. 14.5 Mussels, *Mytilus spp.* (**a**) Wild-caught *Mytilus edulis*, showing byssus threads (BT) and epibionts such as serpulid polychaetes (P). (**b**) Cultured *Mytilus galloprovincialis*, showing few epibionts (bryozoan *Flustra* sp.). Photos PG Beninger.

countries, the link to the mudflat is indirect, since in the Netherlands only the broodstock are protected on the mudflat, and in France the bouchot culture is either on more sandy substrate in the intertidal, or below low-water mark on muddy sediments. The northern quahog *Mercenaria mercenaria* and the cockle *Cerastoderma edule* are also important local mudflat-cultured species.

3 Global Production and Value

The global aquaculture production and value of the dominant mudflat species are shown in Tables 14.1 and 14.2. The aggregate category of infaunal bivalves ‘Clams, cockles, arkshells’ leads in both production and value, at 5,360,280 metric tons and USD 5,352,922, respectively, in 2014. The epibenthic oysters follow, with 5,155,257 metric tons and USD 4,174,258, respectively. The aggregate category of ‘mussels’, which includes *Mytilus* spp., *Perna* spp.,and *Aulacomya* spp., has a

Table 14.1 World aquaculture production of intertidal bivalves, 2005–2014

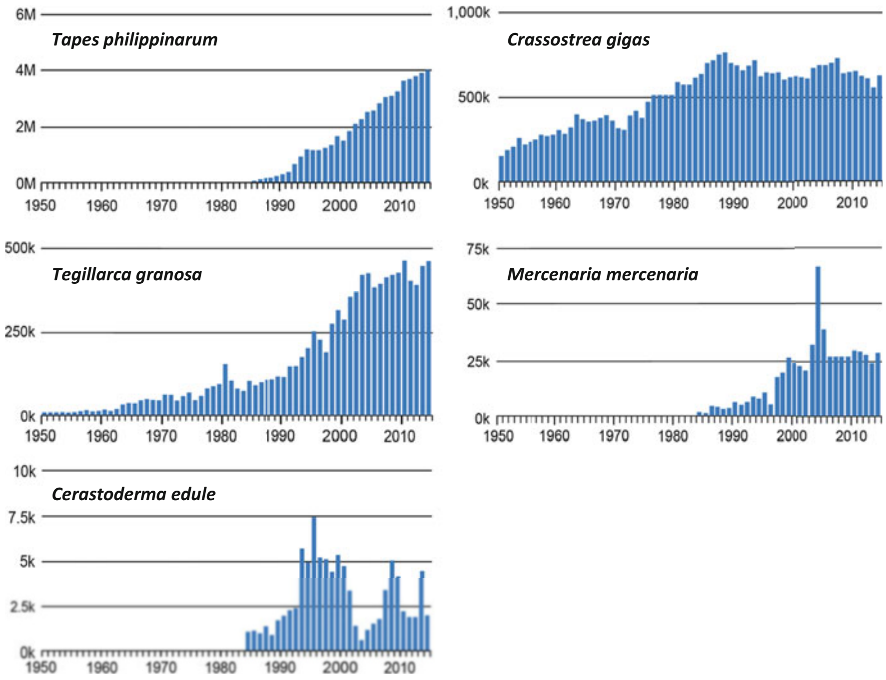
Species group			2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
53	Oysters	Q	4,155,840	4,312,197	4,402,618	4,144,379	4,309,291	4,489,002	4,503,836	4,727,722	4,951,880	5,155,257
		V	2,859,899	2,965,131	2,963,478	3,272,369	3,341,686	3,604,936	3,828,020	3,856,475	4,090,723	4,174,258
54	Mussels	Q	1,718,513	1,659,132	1,598,339	1,585,316	1,729,425	1,806,557	1,877,781	1,828,116	1,768,129	1,901,962
		V	1,044,899	1,195,219	1,627,854	1,629,202	1,516,764	1,592,661	2,310,101	2,201,240	3,352,803	4,070,629
56	Clams, cockles arkshells	Q	3,677,841	3,903,823	4,202,065	4,364,985	4,454,119	4,887,543	4,926,407	4,999,075	5,163,552	5,360,280
		V	3,418,954	3,762,954	3,978,820	4,266,420	4,361,591	4,777,884	4,923,933	4,953,620	5,170,635	5,352,922

Species group 56 is predominantly infaunal species (clams, cockles, and arks—the latter also called cockles in Asia) yet inhabiting predominantly sandy sediments or even the epibenthos, and species groups 53 and 54 are epibenthic species (oysters and mussels), which may also be reared in the sublittoral. Some clams can/are also cultured in the sub-tidal, e.g. *Mercenaria*). *Q* quantity in metric tons, *V* value in USD. Note the steady increase in tonnage, with the exception of mussels, and the steady increase in value for all groups. Source: ftp://ftp.fao.org/FI/STAT/summary/b-1.pdf

Table 14.2 World aquaculture production from 2006–2014 of the three top-ranking cultured bivalve species

Species		2006	2007	2008	2009	2010	2011	2012	2013	2014
Tapes philippinarum	Q	2,807,042	3,045,702	3,110,042	3,249,381	3,604,232	3,676,394	3,786,908	3,896,746	4,010,703
	V	2,965,131	2,786,579	2,877,917	3,041,365	3,353,406	3,478,337	3,546,820	3,644,762	3,744,222
Crassostrea gigas	Q	697,155	728,436	640,020	645,144	652,183	616.745	607,808	552,665	625,925
	V	962,132	971,575	1,156,293	1,128,710	1,222,870	1,397,473	1,283,217	1,321,997	1,343,591
Tegillarca granosa	Q	394,171	413,173	419,299	427,205	465,871	404,896	389,850	450,957	451,446
	V	420,311	4 54,264	466,540	462,657	510,901	483,602	478,526	566,523	580,260

Q quantity in metric tons, *V* value in USD. Source: http://www.fao.org/3/a-i5716t.pdf


Tapes philippinarum

Crassostrea gigas

Tegillarca granosa

Mercenaria mercenaria

Cerastoderma edule

Fig. 14.6 World aquaculture production for species usually grown on mudflats. k = 1000 metric tons, M = 10^6 metric tons. Re-drawn from http://www.fao.org/fishery/species/search/en.

combined production and value of 1,901,962 metric tons and USD 4,070,629, respectively, representing a much greater value per kg than the oysters. It is of course difficult to distinguish between intertidal and subtidal aquaculture production of oysters and mussels without resorting to more local statistics; the same is true of species with a production $<3 \times 10^5$ metric tons, as is the case with the 'mussel' category, since they are all merged in this single category, despite the fact that some, such as *Aulacomya* spp., are mostly grown on floating lines in the subtidal zone.

From Table 14.2 and Figs. 14.6 and 14.7, it is evident that all three of the top-ranking cultured bivalves worldwide are primarily mudflat species (*Tapes philippinarum*, *Crassostrea gigas*, *Tegillarca granosa*). In terms of both tonnage and value, cultured *T. philippinarum* is by far the top-ranking bivalve compared to all other fished and cultured bivalves in the world. The culture of *T. philippinarum* began as the fishery production declined in the 1990s, and was immediately successful, outstripping fishery production in the mid-1990s; in 2002, 97.4% of world production was carried out in China alone. In Europe, the most similar native cultured clam species, *Ruditapes decussatus*, is now a minor product, although gastronomically appreciated (especially in Spain and Portugal).

The second-ranking mudflat-cultured species, *Crassostrea gigas,* has been introduced for successful aquaculture around the world (Fig. 14.12), such that culture production now dwarfs the very low and irregular wild fishery capture (Fig. 14.13).

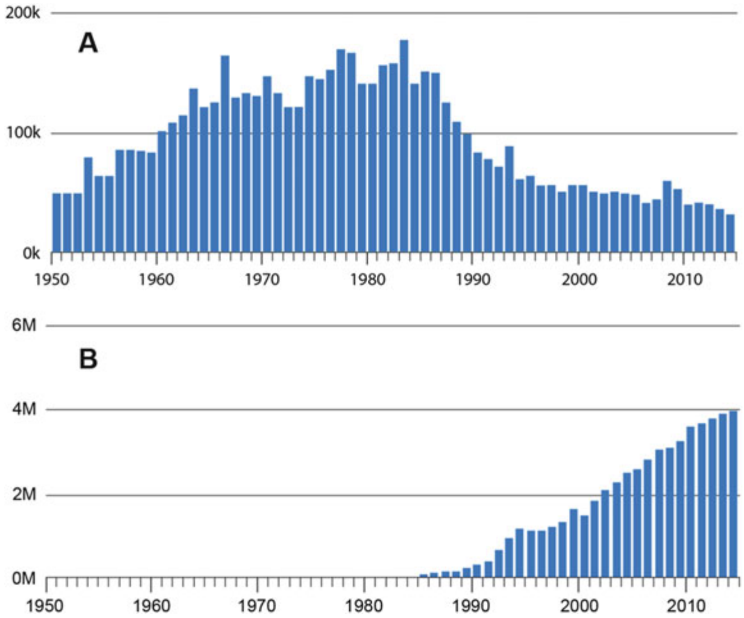


Fig. 14.7 *Tapes philippinarum*. (**a**) Global fishery captures and (**b**) global aquaculture production. Aquaculture production began as fishery captures declined in the 1990s, and far outstrips fishery captures since the mid-90s. *T. philippinarum* is by far the top-ranking bivalve aquaculture species worldwide. k = 10^3 metric tons, M = 10^6 metric tons. Re-drawn from http://www.fao.org/fishery/species/search/en.

The northern quahog or hard clam *Mercenaria mercenaria* and the cockle *Cerastoderma edule* have comparatively small worldwide levels of aquaculture production (Fig. 14.6); this is partly due to their as-yet limited geographic distributions, especially for *C. edule*, restricted to the North-East Atlantic—Baltic—Barents mudflats. The cockle *C. edule* is a true mudflat species, and with or without introductions to new habitats, the margin of progression would seem to be large, since it grows at least as well as *T. philippinarum*, and usually better (higher density).

4 Clam Culture

In addition to its several common names, the Littleneck or Manila clam has had a plethora of scientific names since the original description of Linnaeus (Fischer-Piette and Métivier 1971). Originally an Indo-Pacific species, *Tapes philippinarum* was accidentally introduced from Japan into North America in 1936, along with the intended species, *Crassostrea gigas* (Quayle 1964). Its North American range now extends from Alaska to Baja California, where it is both fished and cultured (Chew 1989; Manzi and Castagna 1989). From the North American Pacific, it was introduced to both Atlantic and Mediterranean Europe in the 1970s and 1980s, specifically for aquaculture (Beninger and Lucas 1984; Shpigel and Fridman 1990; Flassch and Leborgne 1992; Pranovi et al. 2006). As was the case for *C. gigas* (see below), the aquaculture goal was amply fulfilled, and *T. philippinarum* rapidly expanded outside of the culture sites. Whereas this was perceived as a negative ecological and socio-economic development in some areas such as the Venice lagoon (Pranovi et al. 2006), it contributed to a vigorous recreational fishery in France (see Chap. 13), and a commercial fishery in Britain (Jensen et al. 2004).

The northern quahog or hard clam *Mercenaria mercenaria* is locally important as a mudflat culture species in the Eastern USA, where the dominant production site is Chesapeake Bay (https://vaseagrant.org/impacts-of-clam-aquaculture/), with other concentrated areas of production throughout New England (McHugh 2001).

Clam culture consists of seeding spat (wild or hatchery-supplied) or juveniles directly onto the mudflat. The Manila clam *Tapes philippinarum* grows best in the muddier sediments, whereas *Mercenaria mercenaria* prefers a somewhat more sandy sediment bed. Where predation is a problem, the young stages are protected by netting placed over the seeded areas (Fig. 14.8). Harvesting is usually mechanized, using a tractor fitted with a blade and a sorting mechanism to allow sub-sized animals to fall back onto the mudflat (Fig. 14.9a). Subsequent conditioning for market involves further cleaning and sizing, which is also mechanized (Fig. 14.9b).

Fig. 14.8 Installation of predator exclusion nets over seeded clam beds (Hull, Massachusetts, USA). Photo Sandy MacFarlane.

Fig. 14.9 (**a**) Manila clam (*Tapes philippinarum*) harvesting using a tractor-drawn rig which scoops the top few centimeters of mudflat (1), conveying the sediment and clams (2) to a flat, oscillating mesh (3), which allows the sediment and sub-sized clams to be returned to the mudflat. (**b**) Mechanized sorting of harvested clams. The clams are conveyed (1) to a submerged shaking mesh (2), which moves the clams forward (3). The holes in the mesh increase in size distally, so that the smaller clams fall through the mesh first; the larger clams fall through more distally, allowing them to be size-graded. Chellet-Bertheau Productions Ltd., Le Croisic, France. Photo Stewart Beattie.

5 Cockle and Arkshell Culture

Cerastoculture (cockle culture) and venericulture (clam culture) are often performed on the same mudflats, in different sectors, depending on the fine-grain content of the sediment. The cockle *Cerastoderma edule* grows best in finer sediment than that preferred by *Tapes philippinarum*, but there is considerable overlap. The cockle *C. edule* is a major parasite reservoir (see Chap. 8), and this species is also damaged by mechanical perturbation even in its adult stages (Toupoint et al. 2016); despite these drawbacks, it thrives in the aquaculture operations where it is currently grown.

Arcaculture (*Tegillarca granosa*) is an important activity in the Malaysian communities of Penang, Perak, and Selangor. The greatest development of this industry is in Perak, where about 1200 ha of mudflat are under arcaculture (http://www.fao.org/fishery/species/3503/en).

6 Mussel Culture

Two genera dominate world mussel aquaculture: *Mytilus* and *Perna*. Only the mytilids are cultured on mudflats (in addition to the subtidal), where they naturally attach to any solid substrate, large or small, including other mussel shells. The blue mussel *Mytilus edulis* is the most common species, and probably the world's largest mudflat production area is the Wadden Sea, with 58,000 metric tons and a total value of 55.5 million € in in 2005–2006 (http://www.fao.org/fishery/countrysector/naso_netherlands/en#tcN70085). This is more a type of 'ranching' than true mudflat aquaculture: the vast natural intertidal beds (Fig. 14.10) are protected from exploitation, primarily for the sake of migrating shorebirds which use them as a food resource (see also Chap. 12); this protection also allows the intertidal beds to provide a source of spat for suspended mytiliculture in the sub-tidal waters (Nehls et al. 2009).

French mussel production is much more geographically dispersed than that of the Netherlands, totalling 74,100 metric tons. French 'bouchot' mussel culture consists of simple structures such as stakes or poles inserted into the sediment, optionally with either interspersed cords for spat settlement, or wrapped with long mesh

Fig. 14.10 Protected intertidal mussel beds in the Netherlands used for seeding the exploited sublittoral zone. Photo Aad Smaal.

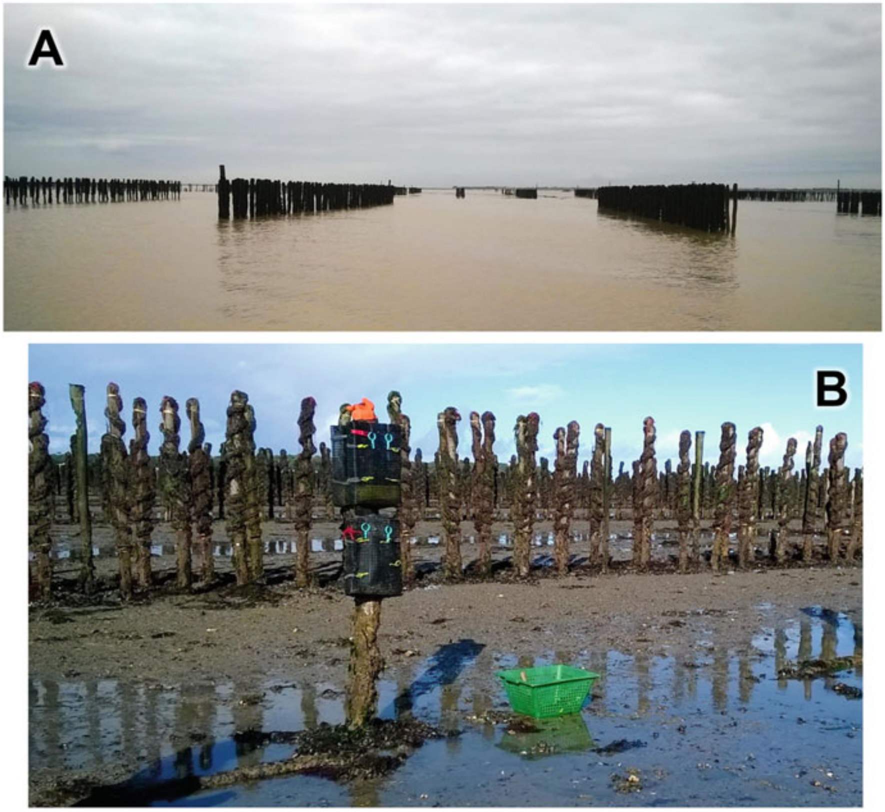


Fig. 14.11 Bouchot culture of *Mytilus edulis* in France. (**a**) Mud substrate (all operations performed from a flat-bottomed boat) and (**b**) mixed substrate. Photos Philippe Glize.

‘sleeves’ containing mussel seed (spat or juveniles—Fig. 14.11a, b). In addition to rearing the mussels to market size, this simple system actually promotes primary recruitment (the first byssal attachment) of mussel spat (Toupoint et al. 2016). Beyond the intertidal zone, mussels are commonly reared on cords suspended from floating lines or rafts.

7 Oyster Culture

As its common name implies, *Crassostrea gigas* was originally a Western Pacific species, introduced to France in 1966 for aquaculture in the wake of the *Ostrea edulis* and later *Crassostrea angulata* epizooties (*C. angulata* is so closely related to *C. gigas* that they hybridize readily in the wild). The Pacific oyster was not expected to reproduce naturally in French Atlantic waters, which were reputed to be too cold for gonad maturation; spat was to be supplied by hatcheries. The species has since established itself as an invasive pest on the French coast, and has moved northward as far as the Baltic and Shetland Islands, due to both larval drifting and introduction (including hatchery spat introduction—Meistertzheim et al. 2013; Lallias et al. 2015; Anglès d'Auriac et al. 2017; Batista et al. 2017; Shelmerdine et al. 2017). Localized coastal warming in sheltered bays has probably contributed to the spread (Dutertre et al. 2009a, b, 2010), but it is also probable that cold-resistant strains have emerged. This species now has the double status of 'desired species' (for aquaculture, as well as for coastal engineering—La Peyre et al. 2015) and 'pest species' (everywhere else) (Troost 2010; Padilla 2010; Moehler et al. 2011). It has been introduced in temperate and cold-temperate waters for aquaculture purposes around the world (Figs. 14.12 and 14.13). In comparison, the American Eastern Oyster *Crassostrea virginica* has a diminutive aquaculture production (Fig. 14.14).

Oysters grow naturally on the benthos, attaching to any solid substrate, including other oyster shells, and in the wild several species tend to form variably-massive reefs (Fig. 14.14a). Their excellent growth above the sediment has led to different forms of three-dimensional culture; on mudflats, these vary from the familiar 'oyster bags' set on 'oyster tables' (Fig. 14.15) to more recent 'hanging cages' (Fig. 14.16).

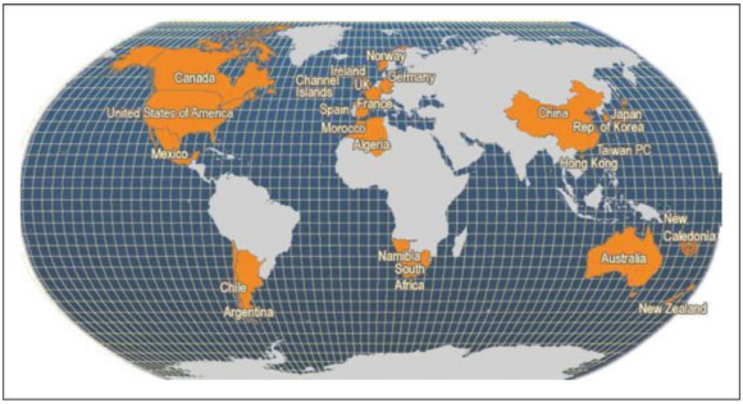


Fig. 14.12 Main producers of cultured *Crassostrea gigas*. Aquaculture of this species has been very successful in temperate and cold-temperate waters globally. Source: http://www.fao.org/fishery/culturedspecies/Crassostrea_gigas/en.

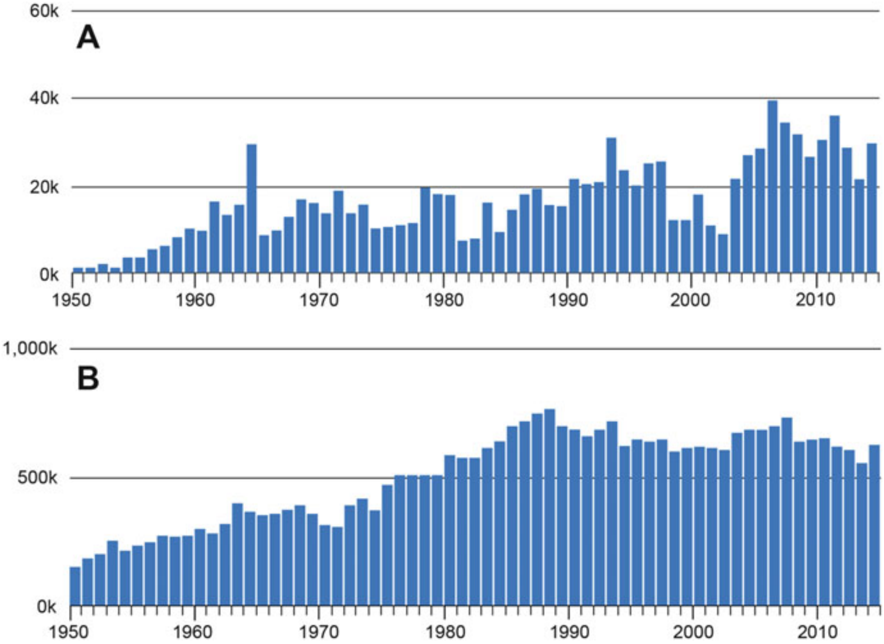


Fig. 14.13 *Crassostrea gigas* (**a**) global fishery captures and (**b**) global aquaculture production; k = 10^3 metric tons. Aquaculture production far surpasses fishery captures. Re-drawn from http://www.fao.org/fishery/culturedspecies/Crassostrea_gigas/en.

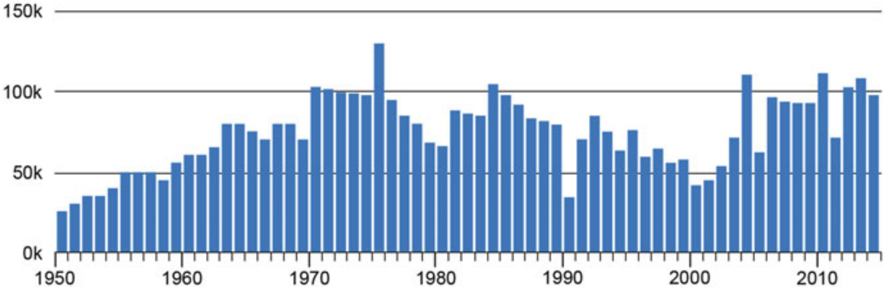


Fig. 14.14 *Crassostrea virginica* aquaculture production. Current levels are similar to those of the 1970s. Re-drawn from http://www.fao.org/fishery/species/2669/en.

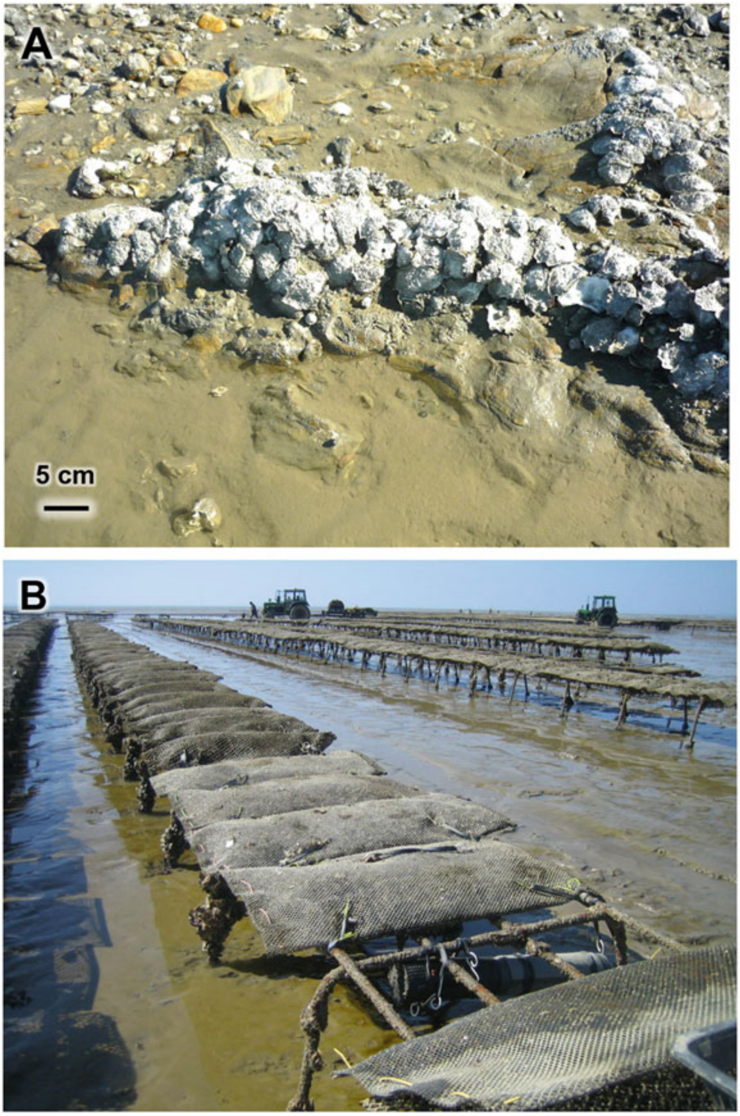


Fig. 14.15 (**a**) Small *Crassostrea gigas* reef, La Bernerie, France, photo PG Beninger. (**b**) *Crassostrea gigas* reared in oyster bags on metallic tables directly on the mudflat in France. Note the microphytobenthic biofilm on the sediment surface directly beneath the tables. Photo Philippe Glize, Syndicat Mixte pour le Développement de l'Aquaculture et de la Pêche en Pays de la Loire.

Fig. 14.16 Off-bottom mudflat cage culture of oysters in the Gulf of Mexico. Photo courtesy of NOAA.

8 Environmental Issues

Just as agriculture has profoundly modified terrestrial environments, it is to be expected that aquaculture will modify marine environments, both positively and negatively. Early documentation emphasized the fate and effects of inputs in fish aquaculture (Ritz et al. 1989; Bjoerklund et al. 1990; Hansen et al. 1990; Beveridge et al. 1991; Handy and Poxton 1993; Wu 1995); however, aquaculture inputs are not an issue in mudflat aquaculture. Additional environmental issues were subsequently addressed, including particle dynamics, bioturbation, pest/pathogen introduction, and habitat alteration. The rapidly-growing literature was brought together in a synthesis by Shumway (2011), and a 'checklist' of problems and possible solutions was supplied by Klinger and Naylor (2012).

It is of course difficult to define what constitutes a ‘positive’ or ‘negative’ environmental effect. In the strict arithmetic sense, a given activity may be considered to have a positive effect if it increases any environmental measure. In real life, however, evaluations of environmental effect invariably incorporate some conscious or unconscious anthropic bias; hypoxia or anoxia in surface sediments are not likely to be looked upon favourably, regardless of how much this is appreciated by prokaryotic anaerobes. Thus environmental outcomes which promote aerobic conditions and eukaryotic (especially metazoan) diversity are favoured, and conditions which preserve or enhance the number and diversity of charismatic vertebrates, such as migratory shorebirds (see Chap. 12), tend to be looked upon most favourably.

Most impacts of mudflat aquaculture can be considered either positive or negative, depending on both degree and on the anthropic viewpoint. Some of these will be examined in the following paragraphs.

Mudflats are subjected to frequent tidal emersion, and this attenuates several problems encountered in subtidal aquaculture, such as hypoxia/anoxia of surface sediments due to excessive biodeposition. The same constraint reduces the available periods of suspension-feeding, such that particle depletion will also be attenuated. Mudflat aquaculture thus has a built-in reducer of some environmental problems, in the form of the tidal cycle.

8.1 Turbidity and Particle Dynamics

The effects of increased filtration, respiration, biodeposition (feces and pseudofeces), and dissolved nutrient release have been explored in bivalve aquaculture operations in the past four decades (Mattson and Lindén 1983; Smaal and Prins 1993; Hatcher et al. 1994; Prins et al. 1996; Newell 2004). The concept of 'carrying capacity' emerged first in relation to the suspensivore-driven depletion of particulate food in the water column, and ultimately reflected the awareness of the constraints imposed by all of the processes generated by shellfish aquaculture (Dame and Prins 1998; McKindsey et al. 2006; Newell 2007). Although difficult to measure precisely, due to the difficulty of accurately determining phytoplankton biomass, as well as the standing crops, filtration rates, and productions of all of the attendant suspension feeders not under culture, application of the concept of 'carrying capacity', within more general management models, is considered essential to the success of bivalve aquaculture operations (Ferreira et al. 2011).

Moderate particle depletion may limit phytoplankton blooms and associated nocturnal fish kills. It has been suggested that shellfish growers receive a form of remuneration in recognition for the roles of cultured bivalves in nutrient cycling and suspended-particle regulation (Ferreira et al. 2011). Conversely, it is intuitively obvious that severe particle depletion will be accompanied by near-simultaneous high rates of biodeposition on poorly-flushed mudflats, and this must be taken into consideration when planning aquaculture operations (Rice 2008).

8.2 Eutrophication

Although shellfish aquaculture operations can be expected to increase nitrogen and phosphorus loads (Bouwman et al 2011), in a review of the impact of shellfish aquaculture with respect to eutrophication, Burkholder and Shumway (2011) stressed that only 7% of the systems examined showed severe eutrophication impact related to the aquaculture operation. These were all located in poorly-flushed, shallow lagoons. In general, bivalve aquaculture actually remediates, albeit to a small extent, the effects of terrestrial inputs which promote eutrophication (e.g. sewage, fertilizers), through the grazing of phytoplankton that would otherwise bloom, including toxin-producing species. Regular harvesting of cultured bivalves, however, is a practice with some potential for reducing the amount of eutrophic substances in coastal ecosystems (Lindhal 2011).

8.3 Biodiversity

Well-known in agricultural systems, the negative relationship between aquaculture (especially fish culture) and biodiversity was identified and explored in the early 1990s (Beveridge et al. 1994). While some of the identified drivers of biodiversity decline, as a result of fish aquaculture, are absent or not limiting in bivalve aquaculture (feed, water, waste accumulation, chemotheraputants), others are present, such as increased microorganism and parasite loads, reduction in macrofauna, alteration of population genetic structure (Arnold et al. 2004, 2009; Hargrove et al. 2015; Filgueira et al. 2015), and loss of habitat and niche space.

Conversely, biodiversity may be improved simply through the well-known positive effect of increased tridimensional complexity. For example, mudflat aquaculture infrastructure may act as refugia for the early life stages of various non-target species, including those of commercial interest (DeAlteris et al. 2004; Tallman and Forrester 2007), as well as generate an increase in the densities of grazing molluscs and juvenile fish which feed upon the fouling organisms (Spencer et al. 1996).

8.4 Habitat Disturbance

Habitat disturbance is a major driver of alterations in biological and demographic processes, spatial and temporal variation in habitat suitability, and natural selection and evolution (Banks et al. 2013). Habitat disturbance includes very real and concrete aspects such as the circulation of shellfish farmers and their tractors and rigs on the mudflat (Fig. 14.9a), as well as the installation of rearing infrastructure (e.g. racks, bouchots, antipredator netting, etc.—Figs. 14.8 and 14.11). It is well-known that mere human trampling can negatively impact sediment-dwelling organisms, including mudflat infauna (Rossi et al. 2007; Reyes-Martínez et al. 2015), so it can be expected that heavy vehicular traffic will exacerbate this impact. There is a pressing need for more research on this topic.

Whereas extensive aquaculture infrastructure has been installed on mudflats in countries such as China, with little or no resistance from the local inhabitants, a definite NIMBY (‘not in my back yard’) tendency has emerged in countries where public contestation is possible and prevalent. As Rice (2008) has observed, ‘*…relatively affluent coastal populations often express reservations over the loss of recreation and aesthetic values that are often articulated in the rhetoric of* *environmental protection*'; it is true that, if one sets aside the positive environmental impacts, the negative environmental impacts of aquaculture provide convenient, ostensibly objective grounds for contestation. In such situations, the 'social carrying capacity' of a given site is often attained well before the ecological carrying capacity (McKindsey et al. 2006).

9 Toward an Integrated Mudflat Management Approach

It is today considered a mark of true enlightenment when the social sciences become involved in ecosystem management (e.g. Cranford et al. 2012), and a veritable apotheosis when they then assume the dominant role. Abundant opportunities arise for devising forms and having them filled out, of writing weighty reports with attractive graphics, hiring many bureaucrats, mediators, ombudspeople, facilitators, outreach specialists, and their indispensable assistants, and of inviting politicians of all levels to engage their own bureaucracies to formulate new laws and regulations. As this process tends toward the cumbersome, it is somewhat simpler to look to other systems for examples of integrated (or at least diverse, which is often the same thing) mudflat management incorporating aquaculture. The Jiangsu mudflat, encompassing nearly 900 km of Chinese coastline, with an area of 6500 km^2 (Anonymous 1986), supports diverse economic activities, of which aquaculture occupies 37% (Fig. 14.17). Aquaculture production has steadily risen on this mudflat, surpassing the natural production of shellfish in 2007 and 2008 (Table 14.3).

In the end, the continued growth of mudflat aquaculture will depend on the area yet undeveloped, and the public resolve to allow such development will vary greatly by country. There is currently very little growth margin in densely-populated

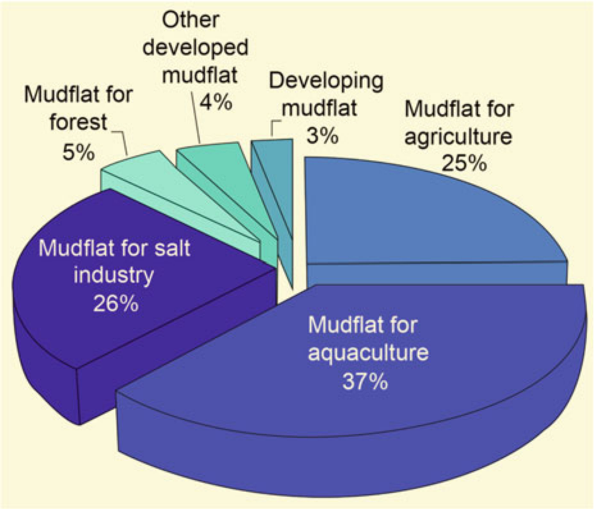


Fig. 14.17 Economic uses of the Jiangsu mudflat in mainland China [re-drawn from Wang and Wall (2010), with permission from Elsevier].

Table 14.3 Estimated natural production, aquaculture production, and aquaculture product value for mudflat-produced shellfish on the Jiangsu mudflat, mainland China

Year	Nature product ($\times 10^3$ tons)	Aquaculture product ($\times 10^3$ tons)	Aquaculture product value ($\times 10^9$ USD)	Aquaculture area (km^2)
1990	306.8	31.7	–	668.7
1995	567	83.8	–	879.4
2000	660	248.7	–	1441.8
2005	582.8	551.5	1.768	1729.5
2006	575	396.7	2.003	1454.7
2007	573.5	625.6	2.087	1481.6
2008	578.1	674.4	2.515	1600.9

Aquaculture production surpassed natural production in 2007 and 2008 [re-drawn from Wang and Wall (2010), with permission from Elsevier]

countries such as in Europe, where new permits have been generally frozen in the past decade, and private use of intertidal space for commercial activities has met with considerable opposition in many developed nations. Similarly, there is little margin for growth in the competing human and non-human uses for mudflats, and in that of the human population itself. As they have in the past, epizooties will probably decimate cultures with little or no premonition, and this must be considered an inevitable risk of the trade. Alternative species may not always be locally-available, so the issue of species introductions (frequent in previous decades, and increasingly prohibited) and subsequent invasion control (see Chap. 11) will also emerge. It is likely that worldwide mudflat aquaculture production will reach a plateau well before the human population does.

References

Anglès D'Auriac MB, Rinde E, Norling P, Lapègue S, Staalstrøm A, Hjermann DØ, Thaulow J (2017) Rapid expansion of the invasive oyster *Crassostrea gigas* at its northern distribution limit in Europe: naturally dispersed or introduced? PLoS One 12(5):e0177481. https://doi.org/10.1371/journal.pone.0177481

Anonymous (1986) Jiangsu Province integrated expedition of coastal zone and mudflat resources integrated report on coastal zone and mudflat resources in Jiangsu Province. Ocean Press, Beijing [in Chinese]

Arnold WS, Walters SL, Fajans SJ, Peters SC, Bert TM (2004) Influence of congeneric aquaculture on hard clam (*Mercenaria* spp.) population genetic structure. Aquac Int 12:139–160

Arnold WS, Geiger SP, Stephenson SP (2009) *Mercenaria mercenaria* introductions into Florida, USA, waters: duration, not size of introduction, influences genetic outcomes. Aquat Biol 5:49–62

Banks SC, Cary GJ, Smith AL, Davies ID, Driscoll DA, Gill AM, Lindenmayer DB, Peakall R (2013) How does ecological disturbance influence genetic diversity? Trends Ecol Evol 28:670–679

Batista FM, Fonseca VG, Ruano F, Boudry P (2017) Asynchrony in settlement time between the closely related oysters *Crassostrea angulata* and *C. gigas* in ria Formosa lagoon (Portugal). Mar Biol 164:110

Beninger PG, Lucas A (1984) Seasonal variations in condition, reproductive activity, and gross biochemical composition of two species of adult clam reared in a common habitat: Tapes decussatus L. (Jeffreys) and Tapes philippinarum (Adams & Reeve). J Exp Mar Biol Ecol 79 (1):19–37

Beveridge MCM, Phillips MJ, Clarke RM (1991) A quantitative and qualitative assessment of wastes from aquatic animal production. In: Brune DE, Tomasso JR (eds) Aquaculture and water quality. The World Aquaculture Society, Baton Rouge, pp 506–533

Beveridge MCM, Ross LG, Kelly LA (1994) Aquaculture and biodiversity. Ambio 23:497–502

Bjoerklund H, Bondestam J, Bylund G (1990) Residues of oxytetracycline in wild fish and sediments from fish farms. Aquaculture 86:359–367

Bouwman AF, Pawlowski M, Liu C, Beusen AHW, Shumway SE, Gilbert PM, Overbeek CC (2011) Global hindcasts and future projections of coastal nitrogen and phosphorous loads due to shellfish and seaweed aquaculture. Rev Fish Sci 19:331–357

Burkholder JM, Shumway SE (2011) Bivalve shellfish aquaculture and eutrophication. In: Shumway SE (ed) Shellfish aquaculture and the environment. Wiley-Blackwell, Singapore, pp 155–215

Chew KK (1989) Manila clam biology and fishery development in western North America. In: Manzi JJ, Castagna M (eds) Clam Mariculture in North America. Elsevier, Amsterdam, pp 243–261

Cranford PJ, Kamermans P, Krause G, Mazurie J, Buck BH, Dolmer P, Fraser D, Van Nieuwenhove K, O'Beirn FX, Sanchez-Mata A, Thorarinsdottir GG, Strand O (2012) An ecosystem-based approach and management framework for the integrated evaluation of bivalve aquaculture. Aquac Environ Interact 2:193–213

Dame RF, Prins TC (1998) Bivalve carrying capacity in coastal ecosystems. Aquat Ecol 31:409–421

Dealteris JT, Kilpatrick BD, Rheault RB (2004) A comparative evaluation of the habitat value of shellfish aquaculture gear, submerged aquatic vegetation and a non-vegetated seabed. J Shellfish Res 23:867–874

Dutertre M, Barillé L, Beninger PG, Rosa P, Gruet Y (2009a) Variations in the pallial organ sizes of the invasive oyster, *Crassostrea gigas*, along an extreme turbidity gradient. Estuar Coast Shelf Sci 85:431–436

Dutertre M, Beninger PG, Barillé L, Papin M, Rosa P, Barillé AL, Haure J (2009b) Temperature and seston quantity and quality effects on field reproduction of farmed oysters, *Crassostrea gigas*, in Bourgneuf Bay, France. Aquat Living Resour 22:319–329

Dutertre M, Beninger PG, Barillé L, Papin M, Haure J (2010) Rising water temperatures, reproduction and recruitment of an invasive oyster, *Crassostrea gigas*, on the French Atlantic coast. Mar Environ Res 69:1–9

Ferreira JG, Hawkins AJS, Bricker SB (2011) The role of shellfish farms in provision of ecosystem goods and services. In: Shumway SE (ed) Shellfish aquaculture and the environment. Wiley-Blackwell, Singapore, pp 155–215

Filgueira R, Comeau LA, Guyondet T, McKindsey CW, Byron CJ (2015) Modelling carrying capacity of bivalve aquaculture: a review of definitions and methods. Encyclopedia of sustainability science and technology. Springer Science and Business Media, New York, pp 1–33

Fischer-Piette J, Métivier B (1971) Révision des Tapetinae (Mollusques bivalves). Mémoires du Muséum National d'Histoire Naturelle, Série A, Zoologie 71:1–106 (+141 plates)

Flassch JP, Leborgne Y (1992) Introduction in Europe, from 1972 to 1980, of the Japanese manila clam (*Tapes philippinarum*) and effects on aquaculture production and natural settlement. ICES Mar Sci Symp 194:92–96

Günther RT (1897) The oyster culture of the ancient romans. J Mar Biol Assoc U K 4:360–365

Handy RD, Poxton MG (1993) Nitrogen pollution in mariculture: toxicity and excretion of nitrogenous compounds by marine fish. Rev Fish Biol Fish 3:205–241

Hansen PK, Pitman K, Ervik A (1990) Effects of organic waste from marine fish farms on the sea bottom beneath the cages. ICES, Copenhagen, 14 p

Hargrove JS, Sturmer L, Scarpa J, Austin JD (2015) Assessment of genetic diversity in wild and aquaculture stocks of *Mercenaria mercenaria* in Florida. J Shellfish Res 34:355–365

Hatcher A, Grant J, Schofield B (1994) Effects of suspended mussel culture (*Mytilus* spp.) on sedimentation, benthic respiration and sediment nutrient dynamics in a coastal bay. Mar Ecol Prog Ser 115:219–235

Jenkins JA (2017) Methods for inferring oyster mariculture on Florida's Gulf Coast. J Archaeol Sci 80:74–82

Jensen AC, Humphreys J, Caldow RWG, Grisley C, Dyrynda PEJ (2004) Naturalization of the manila clam (*Tapes philippinarum*), an alien species, and establishment of a clam fishery within Poole harbour. Dorset J Mar Biol Assoc 84:1069–1073

Klinger D, Naylor R (2012) Searching for solutions in aquaculture: charting a sustainable course. Annu Rev Environ Resour 37:247–276

Lallias D, Boudry P, Batista FM, Beaumont A, King JW, Turner JR, Lapègue S (2015) Invasion genetics of the Pacific oyster Crassostrea gigasin the British Isles inferred from microsatellite and mitochondrial markers. Biol Invasions 17:2581–2595

La Peyre MK, Serra K, Joyner TA, Humphries A (2015) Assessing shoreline exposure and oyster habitat suitability maximizes potential success for sustainable shoreline protection using restored oyster reefs. Peer J 3:e1317. https://doi.org/10.7717/peerj.1317

Lepofsky D, Smith NF, Cardinal N, Harper J, Morris M, Gitla (Elroy White), Bouchard R, DID K, Salomon AK, Puckett M, Rowell K (2015) Ancient shellfish mariculture on the northwest coast of North America. Am Antiq 80:236–259

Lindhal O (2011) Mussel farming as a tool for re-eutrophication of coastal waters: experiences from Sweden. In: Shumway SE (ed) Shellfish aquaculture and the environment. Wiley-Blackwell, Singapore, pp 217–237

Manzi JJ, Castagna MA (eds) (1989) Clam Mariculture in North America. Elsevier, Amsterdam, 461 pp

Mattson J, Lindén O (1983) Benthic macrofauna succession under mussels, *Mytilus edulis* L. (Bivalvia), cultured on hanging long lines. Sarsia 68:97–102

McHugh JL (2001) Management of hard clam stocks, *Mercenaria mercenaria*. In: Kraeuter JN, Castagna M (eds) Biology of the hard clam. Elsevier, Amsterdam, pp 631–649

McKindsey CW, Thetmeyer H, Landry T, Silvert W (2006) Review of recent carrying capacity models for bivalve culture and recommendations for research and management. Aquaculture 261:451–462

Meistertzheim A-L, Arnaud-Haond S, Boudry P, Thébault M-T (2013) Genetic structure of wild European populations of the invasive Pacific oyster *Crassostrea gigas* due to aquaculture practices. Mar Biol 160:453–463

Moehler J, Wegner KM, Reise K, Jacobsen S (2011) Invasion genetics of Pacific oyster *Crassostrea gigas* shaped by aquaculture stocking practices. J Sea Res 66:256–262

Nash CE (2011) The history of aquaculture. Wiley-Blackwell, Ames

Nehls G, Witte S, Buttger H, Dankers N, Jansen J, Millat G, Herlyn M, Markert A, Kristensen PS, Ruth M, Buschbaum C, Wehrmann A (2009) Beds of blue mussels and Pacific oysters. Thematic report no 11. In: Marencic H, de Vlas J (eds) Quality status report 2009. Wadden Sea ecosystem no 25. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Wilhelmshaven

Newell RIE (2004) Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. J Shellfish Res 23:51–61

Newell RIE (2007) A framework for developing "ecological carrying capacity" mathematical models for bivalve mollusc aquaculture. Bull Fish Res Agency 19:41–51

Padilla DK (2010) Context-dependent impacts of a non-native ecosystem engineer, the Pacific oyster *Crassostrea gigas*. Integr Comp Biol 50:213–225

Pranovi F, Franceschini G, Casale M, Zucchetta M, Torricelli P, Giovanardi O (2006) An ecological imbalance induced by a non-native species: the Manila clam in the Venice lagoon. Biol Invas 8:595–609

Prins TC, Smaal AC, Pouwer AJ, Dankers N (1996) Filtration and resuspension of particulate matter and phytoplankton on an intertidal mussel bed in the Oosterschelde estuary (SW Netherlands). Mar Ecol Prog Ser 142:121–134

Quayle DB (1964) Distribution of introduced marine Mollusca in British Columbia waters. J Fish Res Board Can 21:1155–1181

Reyes-Martínez MJ, Ruíz-Delgado MC, Sanchez-Moyano JE, García-García FJ (2015) Response of intertidal sandy-beach macrofauna to human trampling: an urban vs. natural beach system approach. Mar Environ Res 103:36–45

Rice MA (2008) Environmental effects of shellfish aquaculture in the Northeast. Northeastern Regional Aquaculture Center Publication no 105-2008: 1–6

Ritz DA, Lewis ME, Shen M (1989) Response to organic enrichment of infaunal macrobenthic communities under salmonid seacages. Mar Biol 103:211–214

Rossi F, Forster RM, Montserrat F, Ponti MA, Ysebaert T, Middelburg JJ (2007) Human trampling as short-term disturbance on intertidal mudflats: effects on macrofauna biodiversity and population dynamics of bivalves. Mar Biol 151:2077–2090

Shelmerdine RL, Mouat B, Shucksmith RJ (2017) The most northerly record of feral Pacific oyster *Crassostrea gigas* (Thunberg, 1793) in the British Isles. BioInvas Rec 6:57–60

Shpigel M, Fridman R (1990) Propagation of the Manila clam *Tapes semidecussatus* in the effluent of marine aquaculture ponds in Elat, Israel. Aquaculture 90:113–122

Shumway SE (2011) Shellfish aquaculture and the environment. Wiley-Blackwell, Chichester, 424 pp

Smaal AC, Prins TC (1993) The uptake of organic matter and the release of inorganic nutrients by bivalve suspension feeder beds. In: Dame RF (ed) Bivalve filter feeders in estuarine and coastal ecosystem processes. Springer, Berlin, pp 271–298

Spencer BE, Kaiser MJ, Edwards DB (1996) The effects of Manila clam cultivation on an intertidal benthic community: the early cultivation phase. Aquac Res 27:261–276

Tallman JC, Forrester GE (2007) Oyster grow-out cages function as artificial reefs for temperate fishes. Trans Am Fish Soc 136:790–799

Toupoint N, Barbier P, Tremblay AP, McKindsey CW, Winkler G, Meziane T, Olivier F (2016) Influence of intertidal recreational fisheries and 'bouchot' mussel culture on bivalve recruitment. Mar Environ Res 117:1–12

Troost K (2010) Causes and effects of a highly successful marine invasion: case-study of the introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries. J Sea Res 64:145–165

Wang F, Wall G (2010) Mudflat development in Jiangsu Province, China: practices and experiences. Ocean Coast Manag 53:691–699

Wu RSS (1995) The environmental impact of marine fish culture: towards a sustainable future. Mar Pollut Bull 31:159–166

Chapter 15
Quantitative Considerations in Mudflat Ecology

Peter G. Beninger and Inna Boldina

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Abstract Basic themes relevant to quantitative mudflat ecology are presented and explored, with examples: classical and informed-probability statistics, spatial and temporal analyses, allometric modelling, replication and pseudoreplication. The common thread is the necessity of evaluating evidence to arrive at a judgement of scientific credibility.

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1 Introduction

> *'Not only is our world uncertain, our attempts to explain the world (i.e., Science) are uncertain. And our measurements of our (uncertain) world are uncertain.'* (Cressie and Wikle 2011).

Science is an evidence-based belief system. We believe that the cell, the organism, the world, the universe, all function according to explanations that we have forged using inference, experimentation, inductive and deductive reasoning—all based on one form of evidence: observation. Observations may be direct, as in the examination of a mudflat tardigrade under the optical microscope, or they may be indirect, as in the inference of the existence of a planet or a black hole based on identifiable anomalies in the behaviour of nearby objects. Our evidence-based belief system is constantly revised as new observations, and new interpretations of the meaning and consequences of these observations, are made. For all its explanatory power, science necessarily remains a belief system; and uncertainty is an intrinsic dimension of belief. We do not judge things to be 'true' or 'false'; we judge them to be 'believable' or not, given our analysis of the observations made to this point. It is of the utmost importance for all scientists to consciously realize that we must make judgements every time we assess evidence, whether it be the fixing of a critical probability level in classical statistics, the fixing of prior probabilities in Bayesian statistics, etc. Judgements are not (alas, given the widespread practice in marine ecology, we must say *should not*) be made by statistical procedures, uncoupled from human interpretation and reasoning. Statistics are a precious aid to judgement, but only the researcher can actually make judgements. Relinquishing this duty, under the pretense of 'scientific objectivity', is really an abdication of scientific responsibility (Beninger et al. 2012).

The field of statistics is almost entirely grounded in probability theory, reflecting the 'uncertainties' so appropriately summarized by Cressie and Wikle (2011). It is customary (yet somewhat absurd) to divide the field of statistics into two functional spheres: *descriptive* and *inferential* statistics. The former seeks to present the data in such a way that both the essential data characteristics (central tendency, dispersion, etc.) and any obvious or underlying patterns are clearly and concisely exposed. The latter aims to allow conclusions to be drawn from the sample data to the statistical population, usually with respect to hypotheses. Yet inferences can certainly be made from descriptive data, and many techniques of *descriptive statistics* lead directly to the formulation of *post-hoc* hypotheses, so despite the clamour which is sometimes still heard, we may accept that there is a great degree of overlap between these two spheres.

It will not have escaped the notice of most readers that reviewers often show a proclivity to haggle with authors over their statistical treatment of data. Indeed, when we delve deeper into the issues surrounding virtually every statistical procedure, from a 'simple' *t*-test to more esoteric spatial and temporal analyses, we are struck by the multiplicity of conflicting considered opinions among statisticians themselves (for reviews, see Beninger et al. 2012; Legendre et al. 2015; Boldina and Beninger

2016). Statistics has evolved very rapidly in recent decades, and there has scarcely been time for the ‘dust to settle’—prompting an eminent statistician to state ‘*Statistics today is in a conceptual and theoretical mess*’ (Royall 2004)!

We must obviously ‘crack on’ with the best scientific work possible, in spite of the current state of flux in statistics. An account of all of the statistical approaches and tools which may be used in mudflat ecology is obviously beyond the scope of a single chapter or even a single book. Our goal here is to highlight the most important approaches to the quantitative analysis of data in mudflat ecology, with examples and recommendations from experience.

Most readers have had a grounding in classical (or frequentist) inferential statistics, which may certainly be used in some contexts; however, field ecology takes place in particular areas (spaces), often over certain time periods, so a familiarity with both spatial and temporal statistics is also important. These burgeoning fields of statistics are presented in great depth in a number of recent works (Fortin and Dale 2005; Finkenstadt et al. 2006; Cressie and Wikle 2011; Diggle 2014; Cressie 2015), and succinctly in others (Dale et al. 2002; Fortin et al. 2002, 2012; James and Fortin 2013), but since these works are often less familiar to marine ecologists, it is important at this point to at least open a window on them. Similarly, many mudflat ecologists face the problem of estimating and even predicting population biomass and production; growth models are obviously at the heart of these concerns, so we delve carefully into the troubled waters of allometric modelling. And finally, given the labour-intensive requirements of fieldwork amenable to statistical analyses, the very pragmatic questions of replication and pseudoreplication are considered and contextualized.

2 Statistics for Non-spatio-temporal Data

The classical or *frequentist* inferential approach in marine ecology is by far the most common in the published literature. This ubiquity is the product of academic tradition (many would use the term ‘inertia’) since the foundational works of Fisher, Neyman, Pearson, and Gosset (aka ‘Student’). Over the years, a paradigm of *null hypothesis significance testing* (NHST) has emerged, which often conflates two historically and epistemologically distinct paradigms: that of Fisher and that of Neyman-Pearson (Hubbard and Bayarri 2003; Beninger et al. 2012); note that the Neyman-Pearson paradigm itself has been deemed ‘*neither fish nor fowl*’ (Christensen 2005). The statistical literature is replete with accounts of the misuse of NHST, as well as of its inadequacy to generate valid conclusions under the conditions usually practiced; defenders of NHST generally fault the users rather than the approach itself [see Beninger et al. (2012) for review, as well as more recent high-profile contributions such as Hewitt et al. (2016) and Phillips (2016)]. Recent suggestions for improvement to the NHST paradigm include the drastic reduction of the customary Type 1 error critical threshold from 0.05 to 0.005 or 0.001 (Johnson 2013). While this measure would help, it is hardly a solution to the multiple ways in which NHST is routinely misused. Most regrettably, this suggestion itself falls prey to one of the basic 'significance fallacies', i.e. the obsession with *statistical* significance, while ignoring *biological* significance, and, more generally, effect size (Beninger et al. 2012).

Alternative inferential approaches include Bayesian, likelihood, and information-theoretic analysis, all of which are predicated upon comparisons of probability of model fit to data; the probabilities may be revised as new or additional data are included. For brevity, I will refer to these as 'informed probability' approaches. The use of statistical techniques shows a definite 'fashion' effect which is probably a deep-rooted principle of the human psyche, and which does not spare scientists; Bayesian inference is emerging as a new 'favourite' alternative to frequentist statistics (Efron 2013; Owhadi et al. 2015). Enlightened use of the most appropriate statistical tools for the job is the crux of the recent *evidentiary approach* based on the evaluation of evidence (which, as we stated previously, is what scientific judgement should be about). Taper and Ponciano (2016) concluded their account of this approach by saying

> *'. . .there is no magic wand for scientists in statistics. If one wants to use statistics effectively in science, then one needs to learn how to clarify scientific arguments with statistical arguments. To do that one needs to understand how the statistical arguments work. In many ways, this is a much harder task than mastering statistical methods.'*

—to which we add an emphatic 'Amen'.

Both the frequentist and informed-probability statistical approaches require independence of observations; however, there are two broad dimensions of ecology in which observations are often not independent: the spatial and temporal dimensions. The spatial aspect is acutely important on mudflats, in which many of the organisms are not visible (because they are infaunal, and may also be too small to see readily with the naked eye), such that to even sample correctly, we must know something about their spatial distribution. The temporal aspect is important because we often wish to know if our observations capture recurrent phenomena. Spatial and temporal variations may also confound each other if they are not adequately accounted for (Thrush et al. 1994). These two aspects will be considered in turn.

3 Spatial Statistics

From the subatomic to the cosmic scales, matter and energy in the universe are not regularly, nor even randomly, distributed. While some types of events might be subject to randomness, or even to regularity at some scale (e.g. the distribution of ions in a crystal lattice), at other scales they are not (e.g. the distribution of diamond crystals in the Earth's crust). It is therefore reasonable to assume that the distribution of organisms on a mudflat may also present patchiness; and if so, this distribution will affect our sampling methods and our estimations of biomass, production, and all ecological processes stemming from these estimations. Furthermore, the spatial patterning of organisms may vary depending on the scale of study, such that a complete picture can only be obtained from the study of spatial structure at multiple spatial scales (Murphy et al. 2008; Chapman et al. 2010). Aggregative distribution implies spatial autocorrelation, as explained below.

3.1 Autocorrelation: Boon and Bane

Observations which are not independent are *autocorrelated.* In ecological studies, autocorrelation can be either a dangerous elephant in the room, or the basis of a very useful tool. In the former case, despite its obviousness, we are unaware of it, and this naïvety can easily invalidate our statistical treatment of the data, and thus our entire study—whether it is already published or not. In the latter case, not only are we aware of it, but we seek to exploit it, usually to estimate and describe ecological phenomena.

Many marine researchers have unknowingly worked with autocorrelated data, and performed classical statistical tests and comparisons, which supply test-statistics and probability values, remaining unaware that these numbers may be more or less valid, depending on the degree of spatial autocorrelation, and on the type of study. To the bane of these workers, autocorrelated data may have invalidated, or at least cast doubt upon, their analyses. Conversely, other researchers, acutely aware of the properties of autocorrelation, seek to harness them in order to properly characterize spatial or temporal processes in marine ecology, or simply to effect samplings which circumvent the biases induced by autocorrelation. The properties of autocorrelation are a boon to these researchers.

In autocorrelated processes, the value of each data point tends to be related to the neighbouring values (in our discussion, either in time, space, or both). Autocorrelation may be positive, as in the above example, when neighboring values tend to be increasingly similar to each other, or negative, as when neighboring values tend to be increasingly dissimilar as they become closer to each other (Getis 2010; Legendre 1993). Often, the variable is probability; for example, the probability of finding a mussel next to another mussel is very high, whereas the probability of finding a single mussel far from any other is much lower.

Although awareness of the existence and importance of autocorrelated processes in nature dates from the beginning of the twentieth century (Hooker 1905; Student 1914), these ideas were only formulated in a clear and striking manner much later by Tobler in his famous First Law of Geography: "Everything is related to everything else, but near things are more related than distant things" (Tobler 1970). From this point onward, quantitative methods involving autocorrelation began to emerge, first in the fields of mining engineering and geology (Cressie 2015) and later in ecology, with the works of Sokal and Oden (1978a, b). Autocorrelation is thus conceptually rooted in geography, i.e. in spatial processes, and therefore spatial autocorrelation has become the basis of modern spatial analysis (Getis 2008).

Almost all ecological processes (species distributions, species richness, biotic and abiotic environmental variables, etc.) are spatially and/or temporally autocorrelated (Fortin and Dale 2009; Legendre and Legendre 2012; Dale and Fortin 2014), so whether they know it or not, most researchers in marine ecology are explicitly or implicitly concerned with autocorrelation.

3.2 Spatial vs. Temporal Autocorrelation

The basic principles of autocorrelation are the same for spatial or temporal processes, but spatial processes are much more complex, since they are one- to three-dimensional, whereas temporal processes are only one-dimensional. In addition, temporal processes can only proceed in one direction of this single dimension. In contrast, spatial processes may proceed in any available direction for each spatial dimension, and the spatial characteristics of each dimension may differ from those of the others. This difference in directionality of process generates a fundamental difference in causality: in temporally-autocorrelated processes, past events cause future events (but the reverse is not true), whereas the causality of spatially autocorrelated processes is reciprocal (Legendre and Legendre 2012). And finally, there is only a single unit of measurement for temporal autocorrelation (time) but several metric units for spatial autocorrelation (distance, point density, links, etc.) (Getis 2007).

3.3 The Perils of Ignoring Spatial Autocorrelation

As so aptly put by Fortin and Dale (2009), *'...knowledge of the characteristics of spatial structure is almost always the first step to understanding ecological complexity'*. Many marine benthic studies require knowledge of organisms' biomass and density, and therefore involve field sampling, either at sea or in the intertidal. We often read that organisms, sediment, etc. were 'randomly sampled', which usually means that the sampling device was deployed a number of times, with no specific, pre-determined spatial pattern. Such an approach compounds two frequent, yet very different sources of error:

1. mistaking 'haphazard' sampling for 'random' sampling (the former may easily include both systematic and erratic biases, whereas all classical statistical testing, and many descriptive statistical tools, rely on true random samples). The consequences for confidence in the reported results are obvious.
2. failure to account for spatial autocorrelation in the distribution of the objects of study. Even a truly random spatial sampling pattern can fail to capture the spatial distribution of the objects of interest, and hence fail to accurately estimate the parameter of interest (e.g. biomass, density, etc.—Fortin and Jacquez 2000; Fortin et al. 2002; Hawkins 2012). The same argument applies, *a fortiori*, when

an arbitrary, regular spatial sampling pattern is used (e.g. a sampling grid, or a transect with samplings spaced at regular intervals).

Some classical statistical tests are less affected by spatial autocorrelation in some types of study, notably in bivariate studies, in which a response variable (e.g. species abundance) is related to an explanatory variable (e.g. sediment grain size) (Legendre et al. 2002). Moreover, some procedures have been developed to attenuate the effects of spatial autocorrelation in some bivariate statistical tests (Fortin and Jacquez 2000; Dale and Fortin 2009; Fortin and Dale 2009—note that they require sophisticated understanding of the techniques themselves, and may involve careful selection of sample size, so that they must be decided prior to sampling!). For univariate studies, in which the data are tightly dependent on the spatial distribution (e.g. biomass or production of a given mudflat—there are no response or explanatory variables), **unless we accurately take into account the spatial distribution (and thus the autocorrelation) of the objects of interest, we cannot trust the results of our samplings.** In the latter case, there is only one way to ensure that our sampling adequately takes into account the spatial pattern of the object of interest: first, determine what that pattern is, and second, determine what spatial sampling strategy will capture that pattern (Fig. 15.1).

At this point, readers may well exclaim that they will never have the time or the financial resources to do the often long and painstaking work involved in spatial analyses, especially in situations where the objects of interest are not readily visible, e.g. shipboard sampling of epibenthic organisms, infauna sampling on mudflats, or meiofaunal sampling anywhere. We can only reply that we empathize completely, but unless they find the necessary time and resources, confidence in their study results will suffer from the failure to have done so. The next-best approach is simply to sample such a large number of randomly-selected points that it is virtually impossible not to capture the spatial pattern. However, this is usually both infeasible and unverifiable.

3.4 The Essential Spatial Statistics Toolbox

3.4.1 Sampling Considerations

Several parameters must be selected correctly in order to characterize a spatial pattern: sample size (number of sampling points), grain (size of the sampling unit) and spatial lag (distance between sampling points) (Dungan et al. 2002; Fortin and Dale 2005). The minimum recommended sample size is 30 (Legendre and Fortin 1989; Fortin and Dale 2005), but a greater number of points may be needed to detect certain spatial processes, or, on the contrary, 20 points may be sufficient to capture spatial variability if the spatial pattern is very clear (Fortin and Dale 2005). The choice of sampling grain is basically dictated by organism size and convention. A sampling grain of 0.1 m^2 (0.4×0.25 m), is frequently used in benthic macrofaunal

Fig. 15.1 Determining the spatial distribution of the polychaete *Arenicola marina* using recent fecal casts. The presence of these casts allows us to easily locate each animal, contrary to most other mudflat infauna. Complete procedure is detailed in Boldina and Beninger (2014). Photo I. Boldina.

studies (McIntyre et al. 1984; Southwood and Henderson 2000; Boldina and Beninger 2013), while a 3.14 cm^2 (2 cm diameter) grain has been used in meiofaunal studies (Boldina et al. 2014).

The choice of spatial lag is often more difficult than that of sample size and grain, because prior data may be lacking for the spatial distribution of the organisms studied. Nevertheless, this choice is very important; if the spatial lag (inter-point distance) is too large compared to the patch size, the spatial distribution will appear to be uniform, even if in reality it is clustered (Fortin et al. 1989). In such cases, a

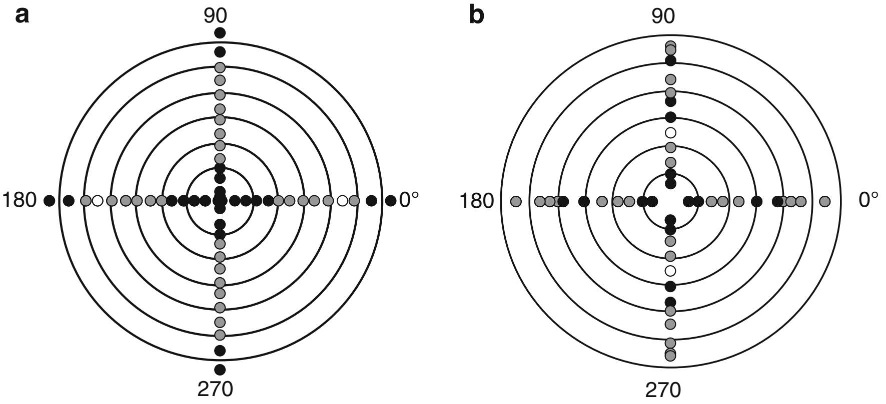

Fig. 15.2 Bearing correlogram for verification of isotropy assumption for the spatial distribution of *Cerastoderma edule* at two mudflat sites (**a** and **b**). Black circles indicate significant positive correlation; gray circles indicate significant negative correlation, white circles indicate statistically non-significant correlation. Note how the results are symmetric about the graph axes. From Boldina and Beninger (2013), with permission from Elsevier publishers.

very fine lag preliminary study must be performed to determine the ideal spatial lag for larger-scale sampling (Boldina and Beninger 2013).

3.4.2 Isotropy Assumption

An important requirement for the characterization of spatial distribution is that we must know whether the spatial distribution has the same characteristics in all directions, a property called *isotropy*. In other words, spatial autocorrelation should depend only on the distance between observations, and not on their orientation with respect to each other. In geographically or geologically complex environments (e.g. mountain ranges, estuaries), the environment itself is heterogeneous, and this may easily affect the characteristics of species spatial distribution. Fortunately for mudflat ecologists, the physical environment is usually quite simple and homogeneous, such that the isotropy condition is likely to be the norm. Isotropy is usually verified by performing two sampling transects at right angles, and plotting the resulting correlograms (see below). An isotropic spatial distribution will be symmetrical about the planes of the graph (Fig. 15.2).

3.4.3 Statistical Tools

It has long been known that variance between samples changes with spatial scale, and this has been the basis for using variance to detect spatial aggregation (Greig-Smith 1952). Early (and, unfortunately, persistent) use of the variance: mean ratio have repeatedly been shown to be suboptimal in this regard, as well as with respect to characterizing such aggregations (see Kershaw 1973). More sensitive variance-based indices have been developed, and these are described in detail in Fortin and Dale (2005), Finkenstadt et al. (2006), Cressie and Wikle (2011), Diggle (2014), and Cressie (2015). The minimum toolset for basic spatial analysis consists of procedures which define the strength of autocorrelation. These procedures also provide the basic descriptive elements of spatial pattern: patch width and inter-patch distance. Two types of such spatial tools are frequently used in ecology: (1) the semivariance and (2) Moran's *I* spatial coefficient (Fortin and Dale 2005), the latter being an extension of the familiar Pearson correlation coefficient (Legendre and Legendre 2012). The semivariance can be used to study processes that do not meet the assumption of second order stationarity, i.e. non-stationarity of the mean and variance (i.e. the means and variances are not constant over the entire area studied) (Glover et al. 2011). Although Moran's *I* cannot be calculated for non-second-order stationarity processes, it is easily interpreted, it enables cross-comparisons with other studies (Kraan et al. 2009), and it can be tested for significance (Legendre and Legendre 2012). The mathematical background for these techniques is described in Cliff and Ord (1981), Haining (2003), Fortin and Dale (2005), and Legendre and Legendre (2012). Briefly, Moran's *I* measures the similarity between two values of the same variable, and the semivariance measures the dissimilarity. A plot of Moran's *I* coefficients *vs* distances separating the measures (lag distance) is referred to as a *correlogram*, whereas a plot of semivariance versus lag distance is called an *experimental semivariogram* or *variogram*. The correlogram and variogram methods are complementary; under certain conditions we can consider correlograms and variograms as different descriptions of the same thing.

3.4.4 Moran's *I* and Correlograms

The main assumption for the use of correlograms is second-order stationarity, i.e. the process is stationary and it can be assessed if the mean and variance remain constant over the entire study area (Fortin and Dale 2005; Legendre and Legendre 2012). However, this method can be greatly biased by the presence of outliers (Fortin et al. 2002).

The correlogram shape indicates the patch sizes and the spatial lags (inter-patch distance) with negative and positive autocorrelation. An example of a correlogram is given in Fig. 15.3.

3.4.5 Semivariance and Variograms

The semivariance $\gamma(h)$ is simply the variance in organism abundance at each distance class in a sampling transect. There is no valid reason to term it 'semivariance' rather than 'variance' [the term was first coined in Matheron (1965)], but the misnomer has persisted to the point where the two terms, and their associated graphs 'semivariogram' and 'variogram', have become interchangeable (Bachmaier and Backes 2008). Where spatial structure (i.e. aggregation) exists, the value of $\gamma(h)$ will increase from a minimum

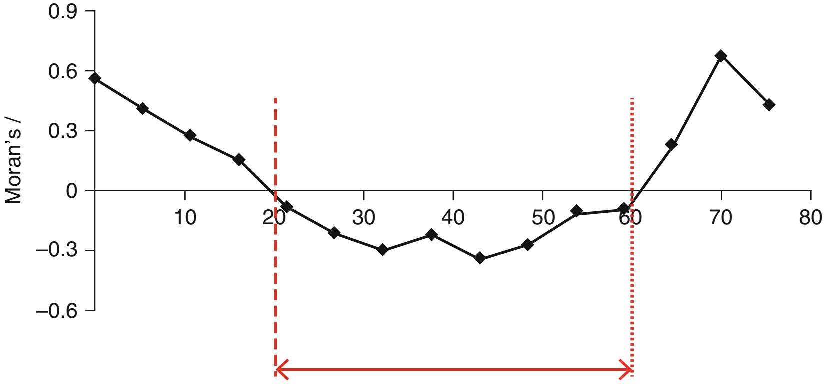

Fig. 15.3 All-directional spatial autocorrelogram for cockle (*Cerastoderma edule*) densities using 15 equidistant classes. Statistically-significant values are represented by black circles. A statistically-significant Moran's *I* first crosses the distance axis at approx. 20 m, representing the spatial range (i.e. patch width). The values next cross the axis at approx. 60 m, indicating a spatial lag (inter-patch distance) of approx. 40 m. The second peak, at approx. 70 m, indicates that a second patch was revealed by the sampling scheme. After Boldina and Beninger (2013), with permission from Elsevier publishers.

at small distances (within-patch) to progressively greater values at larger distances (beyond-patch). More complex patterns may be superimposed on this (Flanagan et al. 2018); for example, a declining oscillating pattern has been observed for the spatial patterning of meiofauna (Fig. 15.4).

Contrary to correlograms, variograms can be computed for spatial processes that only satisfy the intrinsic hypothesis, i.e. the mean is constant over the study area, and the increment of variance between two different locations depends only on the distance between locations (Oliver et al. 1989). This is a less restrictive assumption than second-order stationarity (Fortin et al. 1989). Furthermore, the theoretical variogram obtained by modelling the experimental variogram allows us to predict the spatial structure of unsampled areas of the studied space (i.e. behaviour of the semivariance beyond the spatial data set), a process called *kriging* (Fortin et al. 2002). This requires finding mathematical models which best fit the data, a process which is initially intuitive (mathematical approximations of given curve shapes), and which may be refined using the Akaike Information Criterion (AIC—Akaike 1981; Burnham and Anderson 2002). Most variogram models are spherical, but the less common 'hole-effect' variogram model is also useful for detecting and illustrating the presence of cyclic spatial processes (Fig. 15.4).

Another very useful characteristic of the semivariance technique is that it is one of the ways to calculate fractal dimension. This is discussed below.

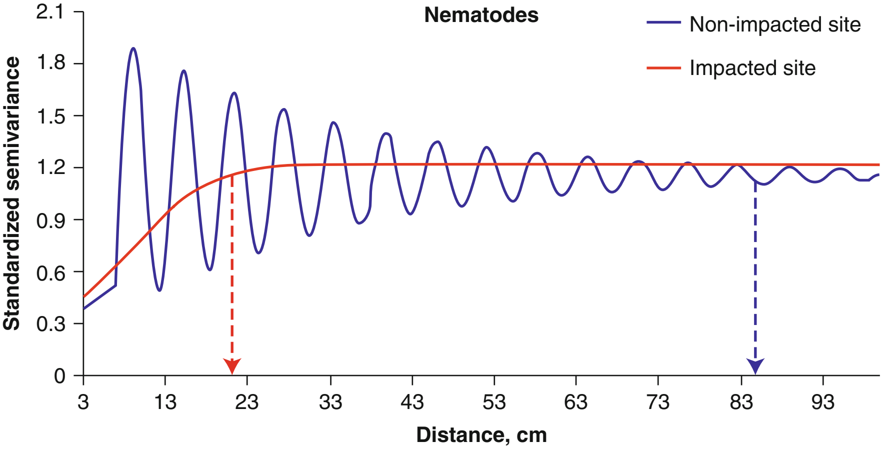

Fig. 15.4 Hole-effect variogram models of nematode density vs distance (extrapolated) for a non-fishing-impacted *vs* a fishing-impacted mudflat site. The non-impacted site shows an exponential-cosine composite cyclic variation at distances ≥8 cm, persisting to 85 cm, whereas the impacted site shows no such cyclicity, but rather a stabilization at distances ≥20 cm. From Boldina and Beninger (2014), with permission from Elsevier publishers.

3.4.6 Fractal Dimension

For an eminently readable presentation of fractal foundations and ecological applications, Seuront (2010) cannot be too highly recommended. Briefly, a set of points (or *events*, as real objects are called, to avoid confusion with the mathematical abstraction) may be distributed in such a manner that it occupies only a very small part of the study area (e.g. one or two dense, compact patches); or, on the other hand, events (which for biologists are often *organisms*) may be spread over the entire surface area. The fractal dimension of such sets quantifies the extent to which they occupy the available area; for the two-dimensional surface of a mudflat, the smallest possible fractal dimension value is 1, and the greatest possible fractal dimension value is 2. These extremes also correspond to degrees of spatial structure, with the lower values signifying highly ordered structure, and the higher values signifying lack of structure. With respect to the spatial distribution of organisms on a mudflat, a low fractal dimension indicates a high level of aggregation with a small number of patches, and thus less space-filling, while a high fractal dimension corresponds to low aggregation and greater space-filling (Pitt and Ritchie 2002; Seuront and Spilmont 2002).

If a double logarithmic plot of the semivariance *vs* the lag distance is linear, the fractal dimension can be calculated from the slope of $D = 2 – S/2$, where S is the slope estimated from the log–log plot of the experimental variogram, as in the example below (Fig. 15.5).

The fractal dimension characterizing a particular spatial distribution may be particularly useful in understanding predation strategies on these organisms. As

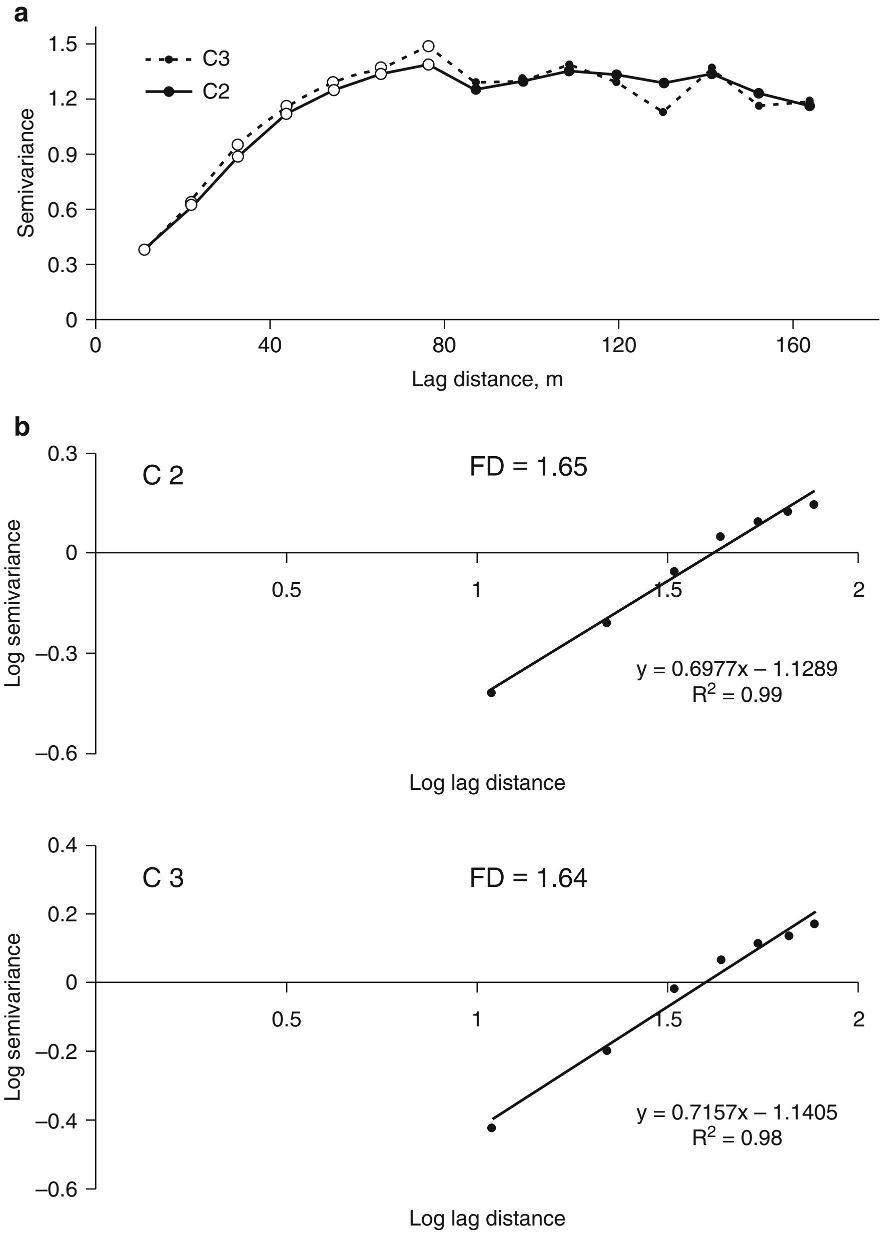

Fig. 15.5 Utilization of semivariance to calculate fractal dimension. (**a**) Experimental variograms (as opposed to the model variograms of Fig. 15.4) for two cohorts (C2 and C3) of the infaunal mudflat bivalve *Tapes philippinarum* at a non-fished site. Open circles show the points used for plotting the log semivariance *vs* the lag distance, in order to calculate the fractal dimension. (**b**) Variogram data plotted on a log-log scale. The fractal dimensions (FD) are calculated from the slopes of the regression lines. The calculated FD (1.64–1.65) show values consistent with a patchy spatial distribution on this non-fished mudflat, in comparison to a much more homogeneous

pointed out in Beninger and Boldina (2014), given a moderate to high prey detection ability, such as in spiny rays (at high tide), shorebirds, or intertidal clam fishers, a Brownian or correlated random walk strategy is most appropriate for prey spatial distributions with little aggregation and high space-filling (high FD—Seuront and Lagadeuc 2001). In contrast, a Lévy walk predation strategy is best suited to patchy prey distributions with much less spacefilling (low FD—Elliott et al. 2009). As FD increases, predators are expected to shift from a Lévy walk to a more random strategy. Of course, prey quality may also impact foraging strategy, resulting in different surviving prey size profiles within patches (Sutherland 1982).

4 Beyond Single Time-Point Studies: Temporal Analysis

4.1 Autocorrelation: The Persistent Foe

Many marine studies are concerned with how processes change over time. The goals of time-series analysis may be summarized as (1) *description,* the characterization of the properties of the time-series, e.g. the periodicity of photoperiod, (2) *explanation*, the study of how the variables in one time series affect those in a parallel series, e.g. how the values of temperature affect the values of salinity, (3) *prediction*, the ability to forecast future values from past and present values, (4) *control*, the extent to which we may influence a time-series, e.g. the building of polders and doors to control water depth at high tide.

The most commonly-overlooked source of autocorrelation comes from the confusion between time, some process which itself takes place over time, and another process which takes place within the first process. A classic example is seasonality; the passage of seasons is a process embedded within time, and a seasonal physiological response (migration, reproduction etc.) is a process embedded within seasonality. Ecological processes may be embedded in either time itself (e.g. ageing), in a process which itself is embedded in time (e.g. seasonal gametogenesis), or both at once (e.g. seasonal gametogenesis following a transition to sexual maturity).

While it is perfectly legitimate to study how processes change with respect to time or some other process embedded in time, it is essential to ensure that we do not use statistical tools based on the independence of observations (i.e. the value of one observation does not influence the value of another observation), when in fact the data are autocorrelated. When studying temporal processes, the data are far more often than not autocorrelated, either through their relation to time itself (e.g. ageing), or to another process embedded in time (e.g. seasonality). Such data may therefore not be analyzed using tools which require data independence—yet, alas, they often

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Fig. 15.5 (continued) distribution (FD 1.78–1.83, not shown) on a nearby fished mudflat. From Beninger and Boldina (2014), with permission from Elsevier Publishers.

are. Examples in the environmental science literature are plethoric, e.g. seasonal variations in biomass, in biochemical composition, in isotopic composition, in pollutant content, etc.

Most commonly, temporally-autocorrelated data are mistakenly analyzed using some form of frequentist (classical) statistical test, whether simply comparing confidence intervals, or some type of multiple comparison such as ANOVA. Some workers feel a sense of statistical invulnerability by choosing a non-parametric test, which quite obviously cannot alleviate the problem of autocorrelation. So, given that temporally-sequential data are virtually always autocorrelated, **how can comparisons be made between sampling dates when the data are autocorrelated? In almost all cases, the answer is simple: they cannot ever be compared using a statistic (including comparing 'error bars'—standard deviations, standard errors of the mean, or confidence intervals) or a statistical test.** The impediment introduced by temporal autocorrelation is so fundamental, and in the overwhelming majority of cases so unquantifiable, that no statistical comparison of any kind may be made—including the informed—probability approaches. At best, qualitative comparisons may be made, keeping in mind (and in print) that for a given geographic location, it is normal for the data of one time period to influence that of a later time period, and conversely, that the data of one time period was very probably influenced by that of an earlier time period—although whether they actually were, and to what extent, will remain unknown.

4.2 Time-Series Analysis: What We Can Do with Autocorrelated Data

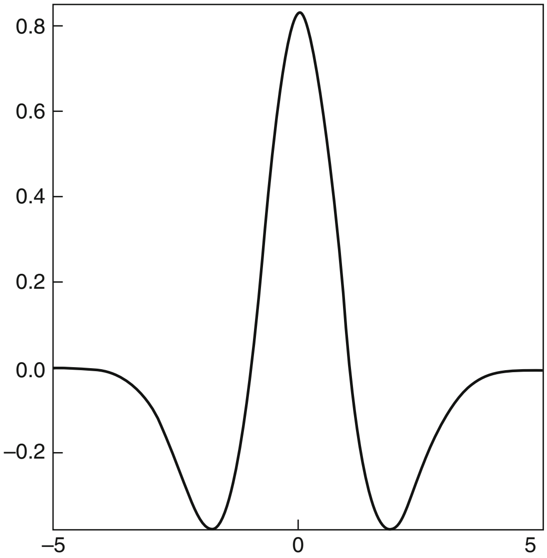
Is there anything else we can usefully do with autocorrelated temporal data? The answer is definitely yes, and there are a number of excellent works which explain this in great depth (e.g. Cressie and Wikle 2011; Chatfield 2016), but it is not what ecologists often wish to do (i.e. statistically compare values from different time periods). The most obvious goal we may accomplish is an accurate description of the temporal process. Visual analysis of time series graphics is a necessary starting point ('*Anyone who tries to analyze a time series without plotting it first is asking for trouble*'—Chatfield 2016). However, such analyses are approximate (despite efforts to reduce variance and non-normal biases via data transformations), and do not allow firm conclusions to be drawn. For example, if the data contains many random fluctuations (noise), it may be difficult to visually identify systematic patterns within the data. We also cannot simply compare data from the same period of the year between different years, since visual inspection may both lack precision, and fail to account for random fluctuations within the data. Random fluctuations may vary considerably over the studied time period, and should be taken into account when analysing both trend and seasonal components of a time series. In particular, if the magnitude of the random component of a time series is strong compared to the trend component, erroneous conclusions about the trend direction may be made if we do not account for the random component.

Inexact conclusions can also be made if the turning point of a time series is not correctly identified. Consider the example of parasite abundances in the mudflat bivalve *Cerastoderma edule*. Following parasitological convention, parasite abundance is defined as the mean number of parasites found in all animals sampled (Margolis et al. 1982). If parasite abundance is higher in October 2019 than in October 2018, simple visual inspection of the abundance graph may lead us to conclude that there was an increase in the level of parasite abundance over the one-year time period. However, the parasite abundance may increase up to a turning point in August 2018 and then decrease rapidly to October 2018. While the initial conclusion is not false, it is seriously incomplete and even misleading, since in reality there was a steady decrease for 2–3 months. It is thus clear that to compare data from the same months between different years we not only need to compare the values of these months, but also the dynamics of the variable before and after these months—while also taking into consideration the dynamics of the random component. Neither simple visual inspection of abundance curves nor classical statistical techniques can accomplish these necessary analyses. Only time series analysis accounts for the complex internal structure of time series data, allowing a more accurate description of the studied process.

Most time-series analyses involve observations made at approximately equal-interval periods; these are called *discrete* time series. In cases where the data appear to follow an oscillatory pattern, we can determine the basic properties of the oscillation, such as its periodicity, frequency, and amplitude. Two approaches are classically used for the characterization of biological time series: analysis of correlation between values of the time series (and subsequent construction of models) (Cryer and Chan 2008; Shumway and Stoffer 2011) and *spectral (=Fourier)* analysis, which decomposes the time series into sinusoidal components (Chatfield 2016; Broughton and Bryan 2009). The former optimizes temporal resolution while the latter optimizes frequency resolution. We refer the reader to these works for a detailed treatment of these techniques, which have become standards in the ecological literature.

A more recent approach in biology, *wavelet analysis*, optimizes both temporal and frequency resolution. This method was first applied in forest canopy research (Bradshaw and Spies 1992), and has since been extended to other areas of ecology and biology (Dale and Mah 1998; Lark and Webster 2001; Mi et al. 2005; Rouyer et al. 2008a, b; Hassler et al. 2011; James et al. 2011; Blauw et al. 2012). Wavelet analysis defines temporal structure as a function of scale and position (Daubechies 1988). It allows us to decompose the signal and thereby to detect periodicities which are not visible to the naked eye. We will describe in detail an example using the time-series of abundances of the trematode parasite *Himasthla quissetensis* in the mudflat bivalve *Cerastoderma edule.*

Fig. 15.6 Second-order derivative of the Gaussian wavelet (Mexican hat wavelet) used to characterize the time-series of trematode abundances in the mudflat bivalve *Cerastoderma edule*. Unpublished data, I. Boldina.



4.2.1 A Wavelet Example

As its name implies, a wavelet is a mathematical function with limited duration and an average value of zero. The choice of a reference wavelet (mother wavelet) is arbitrary and depends primarily on the characteristics of the data (Nason and von Sachs 1999). For the example given below, we chose the second order derivative of a Gaussian wavelet (also called the Mexican hat wavelet, because of its characteristic shape—Fig. 15.6), because it is particularly efficient at isolating peaks and discontinuities (Torrence and Compo 1998; Sheng 2010):

$$\Psi(t) = \frac{2}{\sqrt{3}}\pi^{-\frac{1}{4}}\left(1 - t^2\right)e^{-t^2/2}$$

Each mother wavelet may be stretched or shrunk (Fig. 15.7), thereby defining its scale. For each scale the wavelet function is then shifted over the data function (here the time series of trematode abundance) and a coefficient of wavelet transformation is computed and placed in the wavelet power spectrum according to the colour scale for each time position (Bradshaw and Spies 1992; Flandrin et al. 2010). If the wavelet function matches the data well (similar shape and dimension), the absolute value of the coefficient of wavelet transformation is high, and conventionally appears as red regions of the wavelet power spectrum (Fig. 15.7); if the wavelet and data do not match well, the wavelet coefficient is low and appears as blue regions in the wavelet power spectrum. The same procedure is repeated for each wavelet scale. Thus the positions of red regions on the abscissa (time) axis indicate the temporal position of periodicity peaks, i.e. in which months these periodicities occur. The periodicity peaks should not be interpreted as spectral regions with high

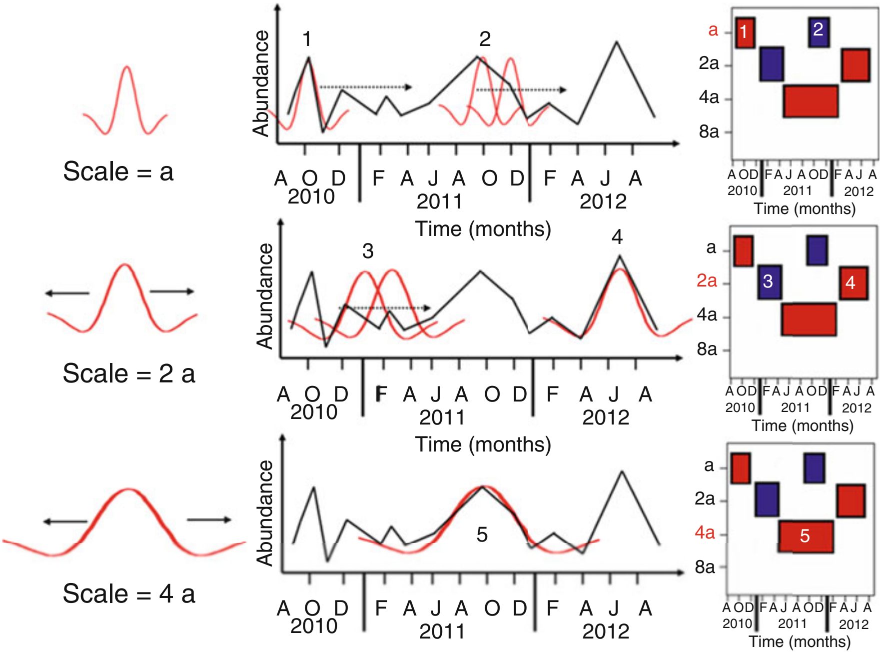


Fig. 15.7 Schematic representation of wavelet transforms for trematode abundance data in the mudflat bivalve *Cerastoderma edule*. Unpublished data, I. Boldina.

trematode abundances, but rather as the time periods in which the mother wavelet corresponds particularly well with the data.

The position of the red spectral regions along the time axis indicates the scales (or duration) of abundance peaks. For example, Peak 1 in Fig. 15.7 has a period of ‘a’ (= 1 month) and occurs in October 2010. Peak 4 is identified at scale ‘2a’ (= 2 months), occurring between June and August 2012.

To summarize, the graphs of the original unprocessed time series data (trematode abundance *vs* time) and of the wavelet spectrum are complementary, the former allowing the detection of significant points in abundance, the latter allowing the detection of significant periodicities of abundance.

As was noted above, most time-series statistical methods require evenly—spaced data points (discrete time series). Since this is often difficult to achieve for all data points (due to weather conditions, equipment or human health failures, etc.), it is possible to supply missed values using polynomial interpolation (Zeileis and Grothendieck 2005).

In addition to characterizing the time-series (the *description* goal), we may also seek to determine to what extent one set of variables influences another set of variables over the same time period; in this case the relationship between the time series of *H. quissetensis* abundances, on the one hand, and water temperature on the other hand (the *explanation* goal). Visual observation of the similarity between

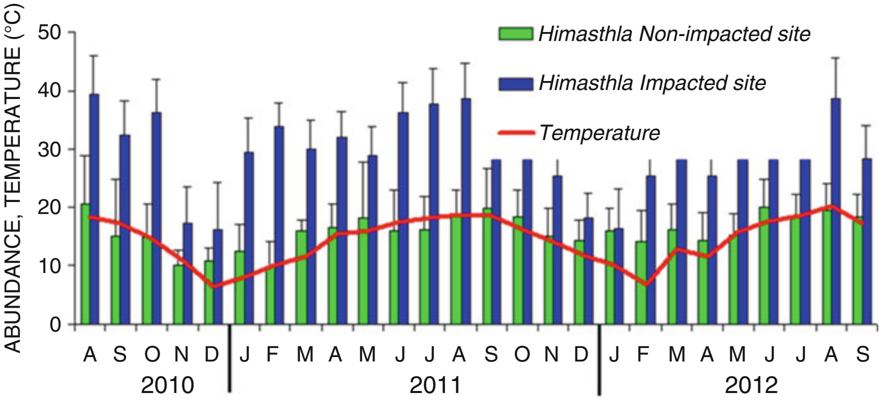


Fig. 15.8 Non-transformed *Himasthla quissetensis* monthly mean abundances in *Cerastoderma edule* at two study sites (impacted vs. non-impacted by mudflat fishing). Bars represent 95% confidence intervals. The series appears to be cyclic, a general correspondence between temperature and abundance is apparent, and the impacted site appears to have a generally greater level of parasite abundance. Unpublished data, I. Boldina and P.G. Beninger.

temporal patterns of different time series (e.g. Fig. 15.8) is not sufficient for conclusions of correlation (Moore et al. 2006). The cross-wavelet power spectrum allows detection of regions of common power (i.e. correspondence) between time series (Grinsted et al. 2004). All analyses may be performed using R software; the cross-wavelet power spectra analyses may be conducted using the biwavelet R package (Gouhier 2014).

Figure 15.9 demonstrates several important characteristics of this time series, which can only be either partially or inconclusively surmised from the graphic representation of Fig. 15.8. The wavelet spectrum was characterized by strong significant peaks at scales from 4 to 15 months over the entire study period (Fig. 15.9 HI). Small-scale fluctuations (<4 months) in the global temporal variations (small number of significant peaks on small scale) were also evident for the *H. quissetensis* abundances on both sites (Fig. 15.9 HN vs HI), but these contributions were quite weak. This information allows us to conclude that samplings approximately every 4 months would therefore suffice to capture the essential periodicity characteristics of parasite abundance, thus allowing an economy of effort.

We can see that *H. quissetensis* abundances fluctuated in phase with water temperature over the entire study period (Fig. 15.9 HN-Temp and HI-Temp), which means that, as was suggested by the graphical data of Fig. 15.8, trematode abundances and water temperature are in fact positively correlated. The data also clearly show that at least a 4-month temperature trend is necessary to produce a considerable change in parasite abundance, so occasional short-term atypical water temperature episodes are not expected to provoke significant oscillations in parasite abundance. None of these conclusions could be reached on the basis of the time-series graphical data (Fig. 15.8) alone.

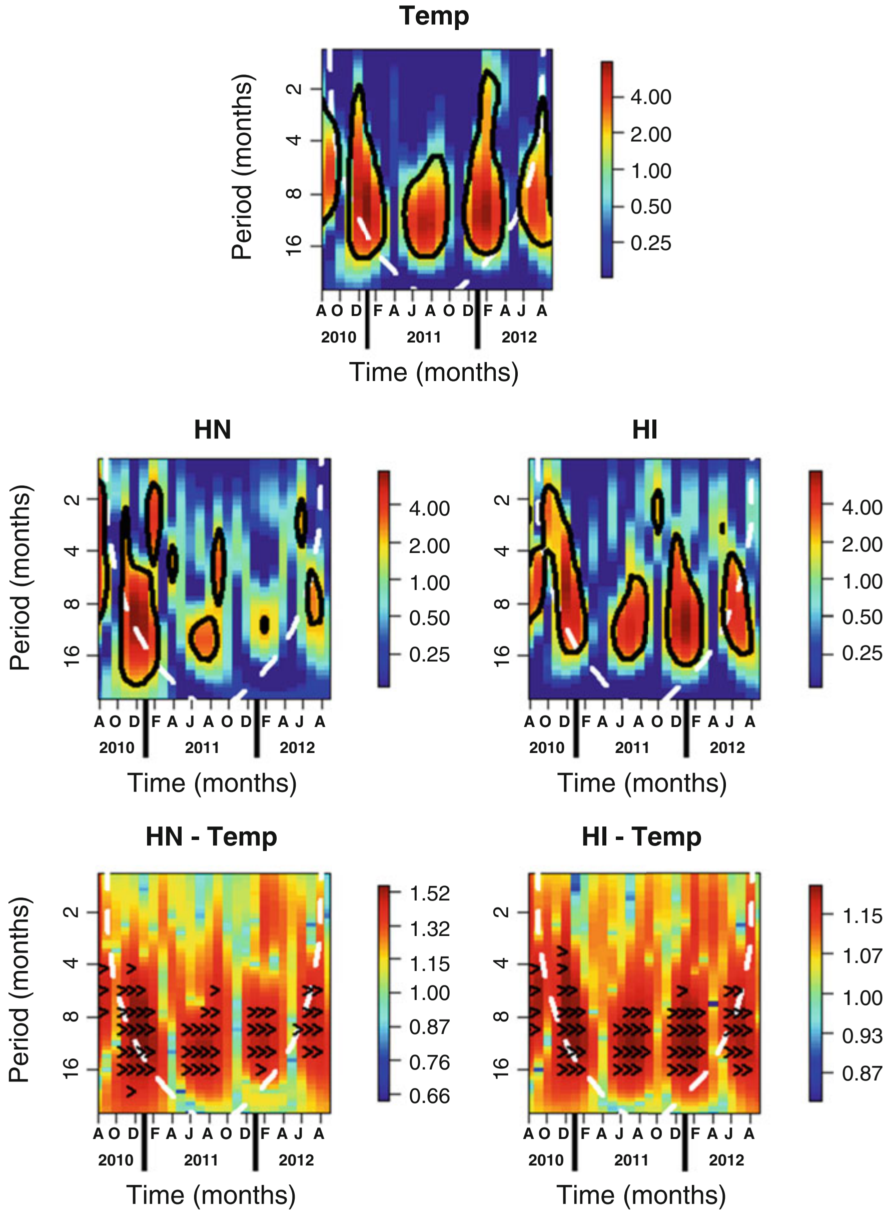


Fig. 15.9 Wavelet power spectra for *Himasthla quissetensis* mean monthly abundance and mean monthly water temperatures. Black lines enclose regions which are statistically significant at the 95% confidence level against background noise (technically termed ‘red’ noise, i.e. random, but autocorrelated time series; not to be confused with the red color of the power spectra, which indicate high level of nonrandom autocorrelated time series). The cone of influence (white dashed lines) shows the region beyond which the results should be interpreted with caution due to edge effects. Color coding indicates the strength of a signal. Black arrows indicate the phase difference between fluctuations of the two analyzed time series. Arrows pointing to the right signify that two time series are in phase, arrows pointing to the left indicate that two time series are in anti-phase. **Temp**:

4.2.2 Prediction from Time-Series Analysis

If the time series is very regular, (i.e. if successive values depend tightly upon previous values, i.e. are strongly autocorrelated), the time-series is *deterministic*. Determinism is a very useful property, because it allows the most accurate and reliable prediction of future values, and prediction is one of the most prized, and useful, scientific goals. If the relation between successive and previous values is weak, (i.e. future values are only partially explained by previous values, i.e. they are weakly autocorrelated), the time-series is *stochastic*. In ecology, this is the most common situation, and it is also the most frustrating: the presence of an unknown degree of autocorrelation prohibits the use of statistics which require independence of variables (classical and informed-probability statistics), such that no inter-date comparisons can be made, and the weakness of the autocorrelation also diminishes our ability to predict future values (e.g. biomass 1 month or 1 year hence). Rather than a firm prediction, we can only calculate a probability distribution for future values, and the properties of this distribution are conditioned by the past or present values (Chatfield 2016; Cressie and Wikle 2011).

5 Allometry-Based Models of Production: The Power Law and Beyond

Suffice it to say that the use of the mathematical term *isometry* is relatively corrupted in biology, where it refers to equal rates of growth of different body parts. *Allometry* refers to the differential growth rates of different body parts. This concept is central to many domains of biology, from physiology to ecology and evolution. Since populations are made up of individuals, population modelling for production estimates always incorporates some model of individual growth, of which the simplest merely account for growth changes in length, as in the familiar Von Bertalanffy growth model. More sensitive models will account for changes in different body parts, such as the shell and the somatic tissue of molluscs. However, by far the most widespread use of allometric modelling in ecology is in the relation between length and weight.

Fig. 15.9 (continued) wavelet power spectrum for mean water temperature. **HN**: wavelet power spectrum for *H. quissetensis* mean monthly abundance data at the non-impacted site. **HI**: wavelet power spectrum for *H. quissetensis* mean monthly abundance data at the impacted site. **HN–Temp**: cross wavelet power spectrum for HN and Temp times series. **HI–Temp**: cross wavelet power spectrum for HI and Temp times series. Unpublished data, I. Boldina and P.G. Beninger.

5.1 Problems with the Power Law Approach

Many relationships between measurable variables are approximated by some form of power law (Ferriere and Cazelles 1999; Farrell-Gray and Gotelli 2005; Newman 2005; Tjørve 2009), and this is also the case for allometric modelling. When applied to the length-weight relation, the process is called *allometric scaling*. This process has been applied from the individual organism level, e.g. metabolic rates (Kleiber 1932; West et al. 1997), feeding and respiration (Newell and Bayne 1980), dynamic energy budget (DEB) models (Sousa et al. 2008; White et al. 2011) and length-biomass allometry (Santos et al. 2002), to the ecosystem level (Allen et al. 2005).

In standard practice, power-law relationships are modelled using the equation $Y = aX^b$. Few equations of such simplicity have been the object of more debate and discussion in biology. Since the function itself is exponential, the component data and the function itself have often been log-transformed [log(y) = log(a) + b log(x)], in order to apply linear regression techniques, and this practice has been largely carried over to the present, in particular with respect to length-weight allometric relationships (e.g. Katsanevakis et al. 2007a; Packard and Birchard 2008; Andrades et al. 2018). The conventional wisdom is that if an allometric relationship follows the power law, it should be approximately linear on a log-log plot (Stumpf and Porter 2012). This condition is far from sufficient, however, since 'approximate' is obviously a subjective evaluation, and especially because large arithmetic deviations may appear insignificant on a log-log plot. The r^2 may even be impressively high and statistically significant for a relationship which does not, in fact, follow the power law, but merely appear to be well-approximated by, or even partly follow, the power law on a log-log plot (Seuront 2010; Harte 2011). In point of fact, r^2 for a straight line fitted to log transformations has little bearing on the strength of relationship between untransformed variables. The issue of back-transformation has generated considerable debate in recent years (Xiao et al. 2011; Packard 2012a, b, 2016; Ballantyne 2013), and led some to conclude that only graphical inspection of the original arithmetic data can be used to determine whether data are appropriately modelled by the power law (Packard 2017).

Compounding the problem of log transformation of data, subsequent back-transformation to the arithmetic domain introduces even further distortions. Even if log transformation allows the data to satisfy assumptions of linearity, normality and homoscedasticity, this does not guarantee that these assumptions will hold upon back-transformation (Packard 2017). Furthermore, linearization does not open a magically simple procedure for modelling an allometric relation, since proper linear regression is a far more complex procedure than many workers seem to believe and practice (Boldina and Beninger 2016). And finally, there are many cases where allometric relationships simply do not fit the power law very well, in either the logarithmic or the arithmetic domains.

In the many cases where relationships do not follow the power law, application of traditional linear regression methods on log-transformed data (i.e. ordinary least squares, OLS, and reduced major axis, RMA) is inappropriate. Special statistical techniques have thus been developed to overcome the weaknesses and limitations of traditional methods, such as multi-model inference (Burnham and Anderson 2002; Katsanevakis 2006; Katsanevakis et al. 2007a, b; Tjørve 2009), rotation regression method (Isler et al. 2002), and heteroscedasticity-consistent standard error estimators for OLS regression (Long and Ervin 2000; Hayes and Cai 2007). However, such techniques suffer from restrictive parametric assumptions which are often not satisfied, and none of them offer consistently effective solutions, such that the statistical approach to modeling allometric relationships is often suboptimal.

5.2 Circumventing the Allometric Modelling Restrictions and Assumption Violations: The Copula Approach

If data do not follow the power law, i.e. log-transformed data continue to present asymmetric dependence or nonlinearity, conventional linear regression methods will fail to adequately characterize the complex underlying dependence structure (de la Peña et al. 2006). In the case of allometry, the dependence structure is often size-related, thus introducing a size-dependent bias, potentially impacting biomass estimates. Copula-based regression, a relatively new concept of dependency originally applied in the field of financial risk management (Carrière 2006), circumvents many drawbacks of conventional regression methods, including those described above. Copula modelling has developed rapidly in the fields of geostatistics, hydrology, and climate modelling (Salvadori and De Michele 2007; Boardman and Vann 2011; Schefzik et al. 2013), and in a few fields of biology such as environmental science (Joe 1994), genetics (Kim et al. 2008), and forestry (Kershaw et al. 2010; Serinaldi et al. 2012). Copula-based models present important advantages, compared to traditional regression methods, of which the most important to the present discussion is that, in contrast to linear regression, copulae are scale-invariant, avoiding the problems of back-transformation (Schmidt 2006).

We are unaware of the copula approach having been used in allometry, with the possible exception of two non-marine studies (specifically, computing wood volume: Wang et al. 2010; Serinaldi et al. 2012). Although we have used this technique to model the length–weight relationships of the mudflat bivalves *Tapes philippinarum* and *Cerastoderma edule* (Boldina and Beninger, unpublished), it is mathematically quite sophisticated, such that the trade-off for fewer restrictions and assumption violations is a relatively esoteric technique which is probably beyond the ken of many mudflat ecologists. Close collaboration with a statistician should overcome this roadblock and allow a wider use of this promising approach.

6 Replication and Pseudoreplication in Mudflat Ecology

One of the most cited articles in ecology is that of Hurlbert (1984) on pseudoreplication. From that date forward, the term “pseudoreplication” has become a “stigmatizing label”, and many ecologists consider that results are unreliable if the number of within-study replications is not sufficient (Oksanen 2001). Pseudoreplication has generated considerable debate, and remains a controversial topic in ecology (Heffner et al. 1996; Oksanen 2001, 2004; Cottenie and De Meester 2003; Hurlbert 2004; Kotze et al. 2004; Millar and Anderson 2004; Davies and Gray 2015; Colegrave and Ruxton 2018). For some authors, the absence of within-study replication is invalidating. However, despite the orthodox views of these scientists, there are exceptions, and they mostly concern field studies. Some examples will be considered below.

There are obvious cases where replication is simply impossible, because the object of study is too rare, e.g. studies of the ecological consequences of earthquakes or volcanic eruptions, studies on Einstein’s preserved brain (Falk et al. 2012; Men et al. 2014) etc. It is also sometimes mutually exclusive to work on appropriate spatial and/or temporal scales and to make the necessary number of replications at the same time—either it is not technically possible, or the cost of replicates is too high. This problem often arises for studies performed at large spatial scales (Carpenter 1990, 1998). In these cases, the choice of an appropriate scale seems more relevant, even though this involves sacrificing the number of replicates and risking criticism because of pseudoreplication (Oksanen 2001; Cottenie and De Meester 2003).

In ecosystem effect studies, especially those on the effect of ‘press’ perturbation in strongly anthropized ecosystems, it is sometimes impossible to find a single non-impacted site (Brown and Herbert Wilson 1997). The only possible solution in this case is to carry out a comparison between sites with different levels of perturbation. The number of sites with a low perturbation level may also be insufficient for true replication, as in Aspden et al. (2004).

Sometimes, only one non-impacted site can be found and in this case the only possible solution is to replicate transects for this control site and for the study site (s) (Hixon and Tissot 2007; Shenko et al. 2012). If the detected size effect is large, and the site characteristics very similar, the causes of this effect can be attributed to the effect of perturbation and not to differences between the sites (Oksanen 2001, 2004; Cleary 2003). If the results obtained seem interesting, replication studies may be performed later, possibly by other researchers. Meta-analysis can also be used to compensate for the lack of replications (Oksanen 2001).

In summary, we advocate the ‘dialling down’ of pseudoreplication concerns on the one hand, and a ‘cards on the table’ approach to reporting field studies, with particular emphasis on outlining the effect size, the importance of past or future convergent results, and obstacles to within-study replication, on the other hand. ‘*When replication is not at all feasible but the size effect is assumed to be large, the clear demonstration of this effect may be considered an indication of a real effect*’ (Oksanen 2001; Cleary 2003). As one of the editors of a well-known marine sciences journal recently wrote to me (PGB), ‘*all studies suffer from lack of true replication at* *some spatial level*'. This is in fact true even for single-point studies: true replication, the only effective means of validation, means repeating the entire study from scratch, preferably by different researchers. This is as rare as frog's teeth in the scientific literature, and is almost never done in ecology, or in any other branch of biology, for reasons outlined in Johnson (1999) and Beninger et al. (2012); furthermore, a large number of such replications would be needed to provide additional certainty (Phillips 2016)! In a recent review of the 'false-positive' problem, Forstmeier et al. (2016) conclude (as do all such studies):

> *…we advocate reallocating some efforts away from seeking novelty and discovery and towards replicating important research findings of one's own and of others for the benefit of the scientific community as a whole. We believe these efforts will be aided by a shift in evaluation criteria away from the current system which values metrics of 'impact' almost exclusively and towards a system which explicitly values indices of scientific rigour.*

As scientists, we can only agree completely with this statement. As practicing scientists, we will all ignore it the next time we design or try to publish a study, and most certainly when we apply for a grant. The reasons are simple: both because all scientific journals put an absolute priority on novelty and discovery, and because as human beings working in a competitive world, we also seek novelty and discovery, where result replication is synonymous with 're-inventing the wheel', and considered, at best, a mark of inferior scientific ability, and usually, a disqualifying production. Perhaps a system of explicit reward for 'indices of scientific rigour' will eventually evolve, but the general current of contemporary science is not headed in that direction.

7 P.S.: Is There Still a Place for Descriptive Studies?

As mentioned above, science is a human activity, and humans, including some scientists, are inclined to follow 'fashion' in accoutrement, gadgets, and their approach to research. Statistics have achieved such an ascendancy in marine ecology (where they are used and misused with at least equal frequency), that, despite the numerous more realistic assessments of the validity of such analyses [see Beninger et al. (2012) for review], some biology research journals continue to look upon purely descriptive scientific studies with a jaundiced eye. The Journal of Plancton Research, for example, states in its 'About the Journal' section: '*Hypothesis-driven work is particularly welcomed; purely descriptive or confirmatory papers will generally not be considered'* (note the outright disqualification of 'confirmatory papers'—i.e. true replication—academic.oup.com/plankt/pages/About).

We must set the record straight: descriptive studies (not experimental ones) are most often the 'cutting-edge' of science. We must first know that something exists before we can do anything else about it, including formulating hypotheses (think black holes, dark energy and matter, subatomic particles, hydrothermal vents and their chemosymbioses, and the Archaea, for a start!). Conversely, we must already know a great deal about something before we can devise an experiment to test a particular aspect of it. Descriptive studies allow science to move forward, while experimental studies often broaden the knowledge of what has been described. There is absolutely no reason to ennoble experimental studies simply because they may include sophisticated statistical analyses. Descriptive studies (which may also have important quantitative components) are at least as, and very often more, deserving of our consideration and respect; without them, we would not know what hypotheses to formulate, or what to design experiments about. Unfortunately, this glaring, fundamental truth will probably continue to be ignored by blinkered scientists and equally-hobbled reviewers and journal editors, well into the future.

References

Akaike H (1981) Likelihood of a model and information criteria. J Econ 16:3–14

Allen AP, Gillooly JF, Brown JH (2005) Linking the global carbon cycle to individual metabolism. Funct Ecol 19:202–213

Andrades R, Joyeux J-C, Andrade JM, Machado FS, Reis-Filho JA, Macieira RM, Giarrizzo T (2018) Filling the gap: length-weight and lengthlength relationships of intertidal endemic fishes of the Brazilian Province Oceanic Islands. J Appl Ichthyol 34(3):720–723

Aspden RJ, Vardy S, Perkins RG, Davidson IR, Bates R, Paterson DM (2004) The effects of clam fishing on the properties of surface sediments in the lagoon of Venice, Italy. Hydrol Earth Syst Sci 8:160–169

Bachmaier M, Backes M (2008) Variogram or semivariogram? Understanding the variances in a variogram. Precis Agric 9:173–175

Ballantyne F (2013) Evaluating model fit to determine if logarithmic transformations are necessary in allometry: a comment on the exchange between Packard (2009) and Kerkhoff and Enquist (2009). J Theor Biol 317:418–421

Beninger PG, Boldina I (2014) Fine-scale spatial distribution of the temperate infaunal bivalve *Tapes (=Ruditapes) philippinarum* (Adams and Reeve) on fished and unfished intertidal mudflats. J Exp Mar Biol Ecol 457:128–134

Beninger PG, Boldina I, Katsanevakis S (2012) Strengthening statistical usage in marine ecology. J Exp Mar Biol Ecol 426-427:97–108

Blauw A, Benincà E, Laane R, Greenwood N, Huisman J (2012) Dancing with the tides: fluctuations of coastal phytoplankton orchestrated by different oscillatory modes of the tidal cycle. PLoS One 7 (11):e49319. https://doi.org/10.41371/journal.pone.0049319

Boardman RC, Vann JE (2011) A review of the application of copulas to improve modelling of nonbigaussian bivariate relationships (with an example using geological data). In: Proceedings of the19th international congress on modelling and simulation. The Modelling and Simulation Society of Australia and NZ, Perth, pp 627–633

Boldina I, Beninger PG (2013) Fine-scale spatial structure of the exploited infaunal bivalve *Cerastoderma edule* on the French Atlantic coast. J Sea Res 76:193–200

Boldina I, Beninger PG (2014) Fine-scale spatial distribution of the common lugworm *Arenicola marina*, and effects of intertidal clam fishing. Estuar Coast Shelf Sci 143:32–40

Boldina I, Beninger PG, Le Coz M (2014) Effect of long-term mechanical perturbation on intertidal soft-bottom meiofunal community spatial structure. J Sea Res 85:85–91

Boldina I, Beninger PG (2016) Strengthening statistical usage in marine ecology: linear regression. J Exp Mar Biol Ecol 474:81–91

Bradshaw GA, Spies TA (1992) Characterizing canopy gap structure in forests using wavelet analysis. J Ecol 80:205–215

Broughton SA, Bryan KM (2009) Discrete Fourier analysis and wavelets. Applications to signal and image processing. Wiley, Hoboken, 360 p

Brown B, Herbert Wilson Jr W (1997) The role of commercial digging of mudflats as an agent for change of infaunal intertidal populations. J Exp Mar Biol Ecol 218:49–61

Burnham K, Anderson D (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, 514 p

Carpenter SR (1990) Large-scale perturbations: opportunities for innovation. Ecology 71:2038–2043

Carpenter SR (1998) The need for large-scale experiments to assess and predict the response of ecosystems to perturbation. In: Groffman P (ed) Successes, limitations, and frontiers in ecosystem science. Springer, New York, pp 287–312

Carrière JF (2006) Copulas. In: Sundt B, Teugels JL (eds) Encyclopedia of actuarial science. Wiley, Chichester, 1944 p

Chapman MG, Tolhurst TJ, Murphy RJ, Underwood AJ (2010) Complex and inconsistent patterns of variation in benthos, micro-algae and sediment over multiple spatial scales. Mar Ecol Prog Ser 398:33–47

Chatfield C (2016) The analysis of time series: an introduction, 6th edn. Chapman & Hall/CRC, Boca Raton, 333 p

Christensen R (2005) Testing Fisher, Neyman, Pearson, and Bayes. Am Stat 59:121–126

Cleary DR (2003) An examination of scale of assessment, logging and ENSO-induced fires on butterfly diversity in Borneo. Oecologia 135:313–321

Cliff AD, Ord JK (1981) Spatial processes: models and applications. Pion, London, 266 p

Cottenie K, De Meester L (2003) Comment to Oksanen (2001): reconciling Oksanen (2001) and Hurlbert (1984). Oikos 100:394–396

Colegrave N, Ruxton GD (2018) Using biological insight and pragmatism when thinking about pseudoreplication. Trends Ecol Evol 33:28–35

Cressie N (2015) Statistics for spatial data, Revised edition. Wiley-Interscience, New York, 928 p

Cressie NK, Wikle CK (2011) Statistics for spatio-temporal data. Wiley, Hoboken, 624 p

Cryer JD, Chan KS (2008) Time series regression models. In: Cryer JD, Chan KS (eds) Time series analysis with applications in R. Springer, New York, pp 249–276

Dale MRT, Fortin MJ (2009) Spatial autocorrelation and statistical tests: some solutions. J Agric Biol Environ Stat 14:188–206

Dale MRT, Fortin M-J (2014) Spatial analysis: a guide for ecologists, 2nd edn. Cambridge University Press, Cambridge

Dale MRT, Mah M (1998) The use of wavelets for spatial pattern analysis in ecology. J Veg Sci 9:805–814

Dale MRT, Dixon P, Fortin MJ, Legendre P, Myers DE, Rosenberg MS (2002) Conceptual and mathematical relationships among methods for spatial analysis. Ecography 25:558–577

Daubechies I (1988) Orthonormal bases of compactly supported wavelets. Commun Pure Appl Math 41:909–996

Davies GM, Gray A (2015) Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). Ecol Evol 5:5295–5304

de la Peña VH, Ibragimov R, Sharakhmetov S (2006) Characterizations of joint distributions, copulas, information, dependence and decoupling, with applications to time series. Lecture Notes-Monograph Series. The Second Erich L. Lehmann Symposium Institute of Mathematical Statistics, Optimality, pp 183–209

Diggle PJ (2014) Statistical analysis of spatial and spatio-temporal point patterns. CRC Press, Boca Raton, 268 p

Dungan JL, Perry JN, Dale MRT, Legendre P, Citron-Pousty S, Fortin MJ, Jakomulska A, Miriti M, Rosenberg MS (2002) A balanced view of scale in spatial statistical analysis. Ecography 25:626–640

Efron B (2013) Bayes' theorem in the 21st century. Science 340:1177–1178

Elliott KH, Bull RD, Gaston AJ, Davoren GK (2009) Underwater and above-water search patterns of an Arctic seabird: reduced searching at small spatiotemporal scales. Behav Ecol Sociobiol 63:1773–1785

Falk D, Lepore F, Noe A (2012) The cerebral cortex of Albert Einstein: a description and preliminary analysis of unpublished photographs. Brain 136(Pt 4):1304–1327. https://doi.org/10.1093/brain/aws295

Farrell-Gray CC, Gotelli NJ (2005) Allometric exponents support a 3/4-power scaling law. Ecology 86:2083–2087

Ferriere R, Cazelles B (1999) Universal power laws govern intermittent rarity in communities of interacting species. Ecology 80:1505–1521

Finkenstadt B, Held L, Isham V (2006) Statistical methods for spatio-temporal systems. CRC Press, Boca Raton, 286 p

Flanagan AM, Flood RD, Frisk MG, Garza CD, Lopez GR, Maher NP, Cerrato RM (2018) The relationship between observational scale and explained variance in benthic communities. PLoS One 13:e0189313. https://doi.org/10.1371/journal.pone.0189313

Flandrin P, Gonçalves P, Abry P (2010) Scale Invariance and Wavelets. In: Abry P, Gonçalves P, Véhel JL (eds) Scaling. Fractals and Wavelets, Wiley Online Library, pp 71–102

Forstmeier W, Wagenmakers EJ, Parker TH (2016) Detecting and avoiding likely false-positive findings—a practical guide. Biol Rev 92:1941–1968. https://doi.org/10.1111/brv.12315

Fortin MJ, Dale MRT (2005) Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge

Fortin MJ, Dale M (2009) Spatial autocorrelation in ecological studies: a legacy of solutions and myths. Geogr Anal 41:392–397

Fortin MJ, Jacquez GM (2000) Randomization tests and spatially auto-correlated data. Bull Ecol Soc Am 81:201–205

Fortin MJ, Drapeau P, Legendre P (1989) Spatial autocorrelation and sampling design in plant ecology. Vegetatio 83:209–222

Fortin MJ, Dale MRT, ver Hoef J (2002) Spatial analysis in ecology. In: El-Shaarawi AH, Piegorsch WW (eds) Encyclopedia of environmetrics. Wiley, Chichester, pp 2051–2058

Fortin MJ, James PMA, MacKenzie A, Melles SJ, Rayfield B (2012) Spatial statistics, spatial regression, and graph theory in ecology. Spatial Stat 1:100–109

Getis A (2007) Reflections on spatial autocorrelation. Reg Sci Urban Econ 37:491–496

Getis A (2008) A history of the concept of spatial autocorrelation: a geographer's perspective. Geogr Anal 40:297–309

Getis A (2010) Spatial Autocorrelation. In: Fischer MM, Getis A (eds) Handbook of applied spatial analysis: software tools, methods and applications. Springer, Berlin, pp 255–278

Glover DM, Jenkins WJ, Doney SC (2011) Modeling methods for marine science. Cambridge University Press, Cambridge, 588 p

Gouhier T (2014) Biwavelet: Conduct univariate and bivariate wavelet analyses (Version 0.14). http://biwavelet.r-forge.r-project.org

Greig-Smith P (1952) The use of random and contiguous quadrats in the study of the structure of plant communities. Ann Bot 16:293–316

Grinsted A, Moore JC, Jevrejeva S (2004) Application of the cross wavelet transform and wavelet coherence to geophysical time series. Nonlinear Process Geophys 11:561–566

Haining R (2003) Spatial data analysis: theory and practice. Cambridge University Press, Cambridge, 452 p

Harte J (2011) Maximum entropy and ecology: a theory of abundance, distribution, and energetics. Oxford University Press, New York, 256 p

Hassler SK, Lark RM, Milne AE, Elsenbeer H (2011) Exploring the variation in soil saturated hydraulic conductivity under a tropical rainforest using the wavelet transform. Eur J Soil Sci 62:891–901

Hawkins BA (2012) Eight (and a half) deadly sins of spatial analysis. J Biogeogr 39:1–9

Hayes AF, Cai L (2007) Using heteroskedasticity-consistent standard error estimators in OLS regression: An introduction and software implementation. Behav Res Methods 39:709–722

Heffner RA, Butler MJ, Reilly CK (1996) Pseudoreplication revisited. Ecology 77:2558–2562

Hewitt C, Campbell ML, Davidson AD (2016) Deciphering p-values: beware false certainty. Science 353:551

Hixon MA, Tissot BN (2007) Comparison of trawled vs untrawled mud seafloor assemblages of fishes and macroinvertebrates at Coquille Bank, Oregon. J Exp Mar Biol Ecol 344:23–34

Hooker RH (1905) On the correlation of successive observations. J R Stat Soc 68:696–703

Hubbard R, Bayarri MJ (2003) Confusion over measures of evidence (p's) versus errors (α's) in classical statistical testing. Am Stat 57:171–182

Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. Ecol Monogr 54:187–211

Hurlbert SH (2004) On misinterpretations of pseudoreplication and related matters: a reply to Oksanen. Oikos 104:591–597

Isler K, Barbour AD, Martin RD (2002) Line-fitting by rotation: a nonparametric method for bivariate allometric analysis. Biom J 44:289–304

James PMA, Fortin M-J (2013) Ecosystems and spatial patterns. In: Leemans R (ed) Ecological systems: selected entries from the encyclopedia of sustainability science and technology. Springer Science+Business Media, New York, pp 101–124

James PMA, Sturtevant BR, Townsend P, Wolter P, Fortin MJ (2011) Two-dimensional wavelet analysis of spruce budworm host basal area in the Border Lakes landscape. Ecol Appl 21:2197–2209

Joe H (1994) Multivariate extreme-value distributions with applications to environmental data. Can J Stat 22:47–64

Johnson DH (1999) The insignificance of statistical significance testing. J Wildl Manag 63:763–772

Johnson VE (2013) Revised standards for statistical evidence. Proc Natl Acad Sci 110:19313–19317

Katsanevakis S (2006) Modelling fish growth: model selection, multi-model inference and model selection uncertainty. Fish Res 81:229–235

Katsanevakis S, Thessalou-Legaki M, Karlou-Riga C, Lefkaditou E, Dimitriou E, Verriopoulos G (2007a) Information-theory approach to allometric growth of marine organisms. Mar Biol 151:949–959

Katsanevakis S, Xanthopoulos J, Protopapas N, Verriopoulos G (2007b) Oxygen consumption of the semi-terrestrial crab *Pachygrapsus marmoratus* in relation to body mass and temperature: an information theory approach. Mar Biol 151:343–352

Kershaw KA (1973) Quantitative and dynamic plant ecology. Edward Arnold, London, pp 128–137

Kershaw JJ, Richards E, McCarter J, Oborn S (2010) Spatially correlated forest stand structures: a simulation approach using copulas. Comput Electron Agric 74:120–128

Kim JM, Jung Y, Sungur EA, Han K, Park C, Sohn I (2008) A copula method for modeling directional dependence of genes. BioMed Central Bioinform 9:225

Kleiber M (1932) Body size and metabolism. Hilgardia 6:315–353

Kotze DJ, Johnson CA, O'Hara RB, Vepsäläinen K, Fowler MS (2004) Editorial: The Journal of Negative Results in Ecology and Evolutionary Biology. J Negat Results Ecol Evol Biol 1:1–5

Kraan C, van der Meer J, Dekinga A, Piersma T (2009) Patchiness of macrobenthic invertebrates in homogenized intertidal habitats: hidden spatial structure at a landscape scale. Mar Ecol Prog Ser 383:211–224

Lark RM, Webster R (2001) Changes in variance and correlation of soil properties with scale and location: analysis using an adapted maximal overlap discrete wavelet transform. Eur J Soil Sci 52:547–562

Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659–1673

Legendre P, Fortin MJ (1989) Spatial pattern and ecological analysis. Vegetatio 80:107–138

Legendre P, Legendre L (2012) Numerical ecology. Developments in environmental modelling, vol 24, 3rd edn. Elsevier, Amsterdam, 1006 p

Legendre P, Dale MRT, Fortin MJ, Gurevitch J, Hohn M, Myers D (2002) The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography 25:601–615

Legendre P, Fortin MJ, Borcard D (2015) Should the Mantel test be used in spatial analysis? Methods Ecol Evol 6:1239–1247

Long JS, Ervin LH (2000) Using heteroscedasticity consistent standard errors in the linear regression model. Am Stat 54:217–224

Margolis L, Esch GW, Holmes JC, Kuris AM, Schad GA (1982) The use of ecological terms in parasitology. J Parasitol 68:131–133

Matheron G (1965) Les variables régionalisées et leur estimation: une application de la théorie des fonctions aléatoires aux sciences de la nature. Masson et Cie, Paris, 305 p

McIntyre AD, Elliot JM, Ellis DV (1984) Introduction: design of sampling programmes. In: Holme NA, McIntyre AD (eds) Methods for the study of marine Benthos. Wiley-Blackwell, Oxford, pp 1–26

Men W, Falk D, Sun T, Chen W, Li J, Yin D, Zang L, Fan M (2014) The corpus callosum of Albert Einstein's brain: another clue to his high intelligence? Brain 137:e268. https://doi.org/10.1093/brain/awt252

Mi X, Ren H, Ouyang Z, Wei W, Ma K (2005) The use of the Mexican Hat and the Morlet wavelets for detection of ecological patterns. Plant Ecol 179:1–19

Millar R, Anderson M (2004) Remedies for pseudoreplication. Fish Res 70:397–407

Moore J, Grinsted A, Jevrejeva S (2006) Is there evidence for sunspot forcing of climate at multi-year and decadal periods? Geophys Res Lett 33:1–5

Murphy RJ, Tolhurst TJ, Chapman MG, Underwood AJ (2008) Spatial variation of chlorophyll on estuarine mudflats determined by field-based remote sensing. Mar Ecol Prog Ser 365:45–55

Nason GP, von Sachs R (1999) Wavelets in time series analysis. Philos Trans A 357:2511–2526

Newell RIE, Bayne BL (1980) Seasonal changes in the physiology, reproductive condition and carbohydrate content of the cockle *Cardium* (= *Cerastoderma*) *edule* (Bivalvia: Cardiidae). Mar Biol 56:11–19

Newman M (2005) Power laws, Pareto distributions and Zipf's law. Contemp Phys 46:323–351

Oksanen L (2001) Logic of experiments in ecology: is pseudoreplication a pseudoissue? Oikos 94:27–38

Oksanen L (2004) The devil lies in details: reply to Stuart Hurlbert. Oikos 104:598–605

Oliver M, Webster R, Gerrard J (1989) Geostatistics in physical geography. Part I: Theory. Trans Inst Br Geogr 14:259–269

Owhadi H, Scovel C, Sullivan T (2015) Brittleness of Bayesian inference under finite information in a continuous world. Electron J Stat 9:1–79

Packard GC (2012a) Is non-loglinear allometry a statistical artifact? Biol J Linn Soc 107:764–773

Packard GC (2012b) Julian Huxley, *Uca pugnax* and the allometric method. J Exp Biol 125:569–573

Packard GC (2016) Relative growth by the elongated jaws of gars: a perspective on polyphasic loglinear allometry. J Exp Zool (Mol Devel Evol) 326B:168–175

Packard GC (2017) The essential role for graphs in allometric analysis. Biol J Linn Soc 120:468–473

Packard GC, Birchard GF (2008) Traditional allometric analysis fails to provide a valid predictive model for mammalian metabolic rates. J Exp Biol 211:3581–3587

Phillips F (2016) Deciphering p-values: defining significance. Science 353:551

Pitt WC, Ritchie ME (2002) Influence of prey distribution on the functional response of lizards. Oikos 96:157–163

Rouyer T, Fromenti JM, Ménard F, Cazelles B, Briand K, Pianet R, Planque B, Stenseth NC (2008a) Complex interplays among population dynamics, environmental forcing, and exploitation in fisheries. Proc Natl Acad Sci 105:5420–5425

Rouyer T, Fromentin J, Stenseth N, Cazelles B (2008b) Analysing multiple time series and extending significance testing in wavelet analysis. Mar Ecol Prog Ser 359:1–23

Royall RM (2004) The likelihood paradigm for statistical evidence. In: Taper ML, Lele SR (eds) The nature of scientific evidence: statistical, philosophical and empirical considerations. The University of Chicago Press, Chicago, pp 119–152

Salvadori G, De Michele C (2007) On the use of copulas in hydrology: theory and practice. J Hydrol Eng 12:369–380

Santos MN, Gaspar MB, Vasconcelos P, Monteiro CC (2002) Weight–length relationships for 50 selected fish species of the Algarve coast (southern Portugal). Fish Res 59:289–295

Schefzik R, Thorarinsdottir TL, Gneiting T (2013) Uncertainty quantification in complex simulation models using ensemble copula coupling. Stat Sci 28:616–640

Schmidt T (2006) Coping with copulas. In: Rank J (ed) Copulas: from theory to application in finance. Risk Books, London, pp 3–34

Serinaldi F, Grimaldi S, Abdolhosseini M, Corona P, Cimini D (2012) Testing copula regression against benchmark models for point and interval estimation of tree wood volume in beech stands. Eur J For Res 131:1313–1326

Seuront L (2010) Fractals and multifractals in ecology and aquatic science. CRC, Boca Raton

Seuront L, Lagadeuc Y (2001) Multiscale patchiness of the calanoid copepod *Temora longicornis* in a turbulent coastal sea. J Plankton Res 23:1137–1145

Seuront L, Spilmont N (2002) Self-organized criticality in intertidal microphytobenthos patch patterns. Phys A 313:513–539

Sheng Y (2010) Wavelet transform. In: Poularikas AD (ed) Transforms and applications handbook. CRC Press, Boca Raton, p 911

Shenko AN, Bien WF, Spotila JR, Avery HW (2012) Effects of disturbance on small mammal community structure in the New Jersey Pinelands, USA. Integr Zool 7:16–29

Shumway RH, Stoffer DS (2011) Time series analysis and its applications with R examples, 3rd edn. Springer, New York, 596 p

Sokal RR, Oden NL (1978a) Spatial autocorrelation in biology: 1. Methodology. Biol J Linn Soc 10:199–228

Sokal RR, Oden NL (1978b) Spatial autocorrelation in biology: 2. Some biological implications and four applications of evolutionary and ecological interest. Biol J Linn Soc 10:229–249

Sousa T, Domingos T, Kooijman SALM (2008) From empirical patterns to theory: a formal metabolic theory of life. Philos Trans R Soc B Biol Sci 363:2453–2464

Southwood TRE, Henderson PA (2000) Ecological methods. Wiley-Blackwell, Oxford, 592 p

Student (1914) The elimination of spurious correlation due to position in time or space. Biometrika 10:179–180

Stumpf MPH, Porter MA (2012) Critical truths about power laws. Science 335:665–666

Sutherland WJ (1982) Spatial variation in the predation of cockles by oystercatchers at Traeth Melynog, Anglesey. II. The pattern of mortality. J Anim Ecol 51:491–500

Taper ML, Ponciano JM (2016) Evidential statistics as a statistical modern synthesis to support 21st science. Popul Ecol 58:9–29

Thrush SF, Pridmore RD, Hewitt JE (1994) Impacts on soft-sediment macrofauna: the effects of spatial variation on temporal trends. Ecol Appl 4:31–41

Tjørve E (2009) Shapes and functions of species–area curves (II): a review of new models and parameterizations. J Biogeogr 36:1435–1445

Tobler WR (1970) A computer movie simulating urban growth in the Detroit region. Econ Geogr 46:234–240

Torrence C, Compo GP (1998) A practical puide to wavelet analysis. Bull Am Meteorol Soc 79:61–78

Wang M, Upadhyay A, Zhang L (2010) Trivariate distribution modeling of tree diameter, height, and volume. For Sci 56:290–300

West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. Science 276:122–126

White CR, Kearney MR, Matthews PG, Kooijman SA, Marshall DJ (2011) A manipulative test of competing theories for metabolic scaling. Am Nat 178:746–754

Xiao X, White E, Hooten M, Durham S (2011) On the use of log-transformation vs. nonlinear regression for analyzing biological power laws. Ecology 92:1887–1894

Zeileis A, Grothendieck G (2005) Zoo: S3 Infrastructure for regular and irregular time series. J Stat Softw 14:1–27

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