# The Microbiome of Coastal Sediments

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## Abstract

Coastal zones are among the most productive marine environments and many are highly impacted by anthropogenic activity. Coastal zones are key regions for the transformation of land-based inputs of nutrients and pollutants and provide many essential ecosystem services for human society. Periods of tidal exposure and submergence, coupled with seasonal variation in land-based inputs, result in intertidal habitats characterized by highly variable environmental conditions that pose crucial adaptive challenges for organisms. This review focuses on the microbiome of coastal sediments consisting of protists (especially diatoms), bacteria, archaea, and fungi. The diversity, distribution, production, adaptations, and interactions between these groups are reviewed. Coastal microbiomes are characterized by high rates of biogeochemical activity. Photoautotrophic diatoms exhibit complex patterns of behavior to cope with a highly variable light climate. Multiple species–species interactions between autotrophs and heterotrophs contribute to the cycling of carbon and nitrogen. In sediments, autotrophic and heterotrophic processes are closely coupled both spatially and temporally. Bacteria and archaea control the nitrogen- and carbon cycles while taxonomic diversity is influenced by gradients of organic matter, nitrogen compounds, sulfide, and oxygen. Fungi are important components of coastal salt marsh sediment microbiomes but their role in unvegetated sediments is less well understood. This review considers the high human impact on coastal sediments and the importance of nutrient gradients and pollution pressures (hydrocarbons) in affecting diversity and species distribution.

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## 12.1 Introduction

Coastal zones are among the most productive marine environments. Located at the interface between marine, freshwater, and terrestrial environments and receiving inputs from both the open ocean and from the land, coastal zones consist of a matrix of diverse habitats positioned along various physical, chemical, and biological gradients. Organisms living within transitional coastal zones have to be adapted to major gradients of conditions that can be subject to seasonal variability. In addition to seasonal changes (particularly present at temperate- and polar latitudes), there is a strong influence of the lunar tidal cycle (bi-weekly) resulting in periods of varying length of aerial exposure and saline water submergence in intertidal environments. These exposure cycles can result in important changes in environmental conditions on an hourly basis. Thus, the coastal zone is characterized by highly variable environmental conditions that pose considerable adaptive challenges for organisms living within it. Despite these challenges, coastal habitats support characteristic microbiomes (defined as a characteristic microbial community with distinct physiological and chemical properties and activities resulting in the formation of specific ecological niches, Berg et al. 2020) that underpin the ecological functioning of these habitats. Coastal microbiomes play crucial roles in biogeochemical cycling, food webs, and habitat modification, resulting in the provision of important ecosystem services to human society.

The coastal zone encompasses a wide range of habitats. Rocky shores are extensive worldwide and are generally characterized by steep spatial gradients from land to sea. Rocky shores host abundant communities of macroscopic organisms but their microbiology is less well described (Maggi et al. 2017). The impervious nature of rocky shores means that the influence of microbes present as thin epilithic biofilms is strongly affected by cycles of desiccation, extreme salinity fluctuations, macroalgal spore settlement and germination, and grazing by macroinvertebrates. This chapter does not focus on these environments and readers are referred to Dal Bello et al. (2017) and Notman et al. (2016).

Estuaries and intertidal flats are among the most productive of the various coastal ecosystems and provide important ecosystem services such as the provisioning of food resources, water purification, carbon storage, and coastal storm surge tidal defense (Waltham et al. 2020). Estuaries are also some of the most human-modified environments because of historic and current concentration of human populations and industries along their coastlines (Henderson et al. 2020; Van Niekerk et al. 2013). This has resulted in a considerable degradation of estuarine ecosystems, which changed the ecological processes that govern their health and ecosystem services (Duarte et al. 2020; Van Niekerk et al. 2019; Waltham et al. 2020). Coastal habitats (salt marsh, mangrove, seagrass, muddy and sandy intertidal flats) are important zones of nutrient cycling (Nedwell et al. 2016) and valuable sites of organic carbon generation and accumulation ("blue carbon," the carbon stored in the sediment, living and non-living above- and below-ground biomass of salt marsh and seagrass habitats (Alongi 2020; Beaumont et al. 2014; Burden et al. 2019; Legge et al. 2020; Waltham et al. 2020). Because coastal environments are located in the transition zone between the land and the sea, they are particularly susceptible to pollution, including excess nutrients (particularly inorganic N and P), heavy metals, pesticides, pharmaceuticals, numerous industrial persistent organic pollutants, and plastics. One of the major types of organic pollutants in coastal ecosystems are petroleum hydrocarbons from crude oil and its many refined products.

Estuarine sedimentary systems are extensively distributed across the globe. All estuaries have their own characteristics influenced by the local geology and catchment features and the local tidal range, from microtidal (<2 m tidal range), mesotidal (2–4 m tidal range), and macrotidal (>4 m tidal range). Tidal range and wind and wave-climate are major factors influencing the geomorphology of a coastal-estuarine system. A typical meso- or macro-tidal estuary is usually characterized by a well-mixed salinity gradient from freshwater to fully marine with fine-grained sediment and mudflats in the sheltered regions of the estuary toward its head and mixed- and sandy sediments toward the mouth where tides and wind-driven waves and currents are stronger (Baas et al. 2019; Green and Coco 2014; Zhu et al. 2020). In agricultural and populous catchments, most nutrient loading is land derived. Hence, an estuarine gradient reflects covarying conditions of increasing salinity, decreasing nutrient loading, increasing sediment particle size, and varying levels of tidal exposure (Nedwell et al. 2016). Approximately perpendicular to this linear gradient is the gradient of tidal exposure with upper shores often colonized by vascular macrophytes (salt marshes in temperate regions and mangroves in the tropics, Alongi 2020) and by sand dune habitats on wind-dominated sandy shores (Galiforni-Silva et al. 2020). Mid-tide level shores tend to be dominated by micro- and macro-algal mats, and the lower shores more physically disturbed, but also colonized by biogenetic reefs of bivalves or polychaete worms. These environmental gradients, the large surface area provided by sediment particles, and accounting for areal and depth dimensions result in an extensive mosaic of habitats that support productive and diverse microbiomes (Heip et al. 1995; Luna et al. 2013; Underwood and Kromkamp 1999).

## 12.2 Coastal Autotrophic Microbiomes: Microphytobenthic Biofilms

On intertidal mud and sand flats and in shallow subtidal systems where sunlight reaches the sediment surface diverse and abundant microbial biofilms occur. Collectively these assemblages are termed microphytobenthos (MPB) or benthic microalgae (BMA) biofilms, terms which emphasize the important role played by the photoautotrophic components of these complex agglomerates of autotrophic and heterotrophic protists, bacteria, archaea, and fungi (An et al. 2020; Chen et al. 2017; Cibic et al. 2019; Pinckney 2018; Sahan et al. 2007; Underwood and Kromkamp 1999). The photoautotrophic diatoms (Stramenopiles, Bacillariophyceae) are major components of most MPB or BMA biofilms with net primary production of 29–314 g C $m^{-2}$ $y^{-1}$ (Pinckney 2018; Underwood and Kromkamp 1999). The primary production of MPB provides the main energy resource to biofilm consumers (protozoans and metazoans) and their predators (Christianen et al. 2017; Green et al. 2012; Herman et al. 2000; Hope et al. 2020), while heterotrophic bacteria and archaea are the primary remineralizers of MPB-derived organic material, including volatile compounds and detrital organic matter present in the sediment (Acuña Alvarez et al. 2009; Bohórquez et al. 2017; Gaubert-Boussarie et al. 2020; Luna et al. 2013; Nedwell et al. 2016).

Two types of microphytobenthic biofilms are recognized: transient microbial biofilms that form and reform over daily and weekly timescales and more permanent microbial mats. Microbial mats are characterized by higher biomass and are usually dominated by cyanobacteria. Microbial mats show long-term temporal persistence (months to years) such that a macroscopic structure is formed, and they are often closed systems with much internal recycling of nutrients (Long et al. 2013; Stal et al. 2019). Stromatolites are a particular type of microbial mat that possess a laminated calcified structure, which is considered to be the outcome of an intense coupling between microbial (cyanobacteria, heterotrophic bacteria, archaea, eukarya) and geochemical processes leading to a remnant geological formation. A specialized type of a coastal microbial mat is the supratidal microbialite. These microbialites have been found in the supratidal zone of rocky shores in South Africa, Australia, and the U.K., where there is a freshwater input (Rishworth et al. 2020). Microbial mats and stromatolite microbiomes have been reviewed by Stal (2016), Stal et al. (2019), and Rishworth et al. (2020) and are not considered further here.

### 12.2.1 Diversity of Microphytobenthos in Coastal Sediments

Transient marine benthic biofilms have a high potential species richness of photoautotrophs. Although both photosynthetic and heterotrophic microeukaryotes such as flagellates and ciliates are present (Chen et al. 2017; Gong et al. 2015; Massana et al. 2015), their ecology and importance in intertidal biofilm is in most cases unresolved. A few genera of cyanobacteria (e.g., *Lyngbya, Oscillatoria*) and motile euglenophytes (e.g., *Euglena deses, E. proxima*) are found and are often in high abundance in transient biofilms (Bellinger et al. 2005; Kingston 1999; Perkins et al. 2002; Underwood et al. 2005) (Table 12.1). However, the dominant group of MPB in terms of biomass and activity are benthic diatoms with well over 1500 benthic diatom (morpho)species described from different geographical regions (Witkowski et al. 2000). Within a particular environment however, especially on estuarine intertidal mudflats it is more usual to find only a few (20+) species that are numerically dominant within MPB assemblages (Forster et al. 2006; Park et al. 2014; Redzuan and Underwood 2020, 2021; Ribeiro et al. 2013, 2020; Sahan et al.

**Table 12.1** Representative taxa of microphytobenthos found in European coastal sediment microbiomes, characterized by life form and habitat. Note that sediment type represents a continuum of sediment grain size and properties, and individual taxa may occur across this gradient

| Epipelon (clays and muds) (silts and silty sand) | Epipsammon (sand) | Tychoplankton (resuspended) |
|---|---|---|
| Diatoms (Stramenopiles, Bacillariophyceae) | | |
| *Navicula phyllepta, N. gregaria, N. perminuta, N. flanatica, N. Spartinetensis, N. salinarum N. peregrina, N. digitoradiata,, N. arenaria* | *Planothidium delicatulum Biremis lucens, Achnanthes* sp., *Nitzschia frustulum* | *Rhaphoneis minutissima, Rhaphoneis amphiceros* |
| *Gyrosigma limosum, G. fasciola, G. accuminatum Gyrosigma balticum* | *Amphora ovalis, A. salina. A.* c.f. *tenuissima* | *Cymatosira belgica Staurosira construens* |
| *Pleurosigma angulatum, Scolioneis tumida Hantzschia virgata, Tropidoneis vitrea* | *Opephora guenter-grassi* | *Thalassiosira* sp., *Actinoptychus senarius, Odontella aurita* |
| *Nitzschia* c.f. *panduriformis, Nitzschia sigma, Tryblionella apiculata* | *Dimeregramma minor* | *Opephora* sp. |
| *Cylindrotheca gracilis. C. signata, C. closterium* | *Catenula adhaerens* | |
| Euglenids (Stramenopiles, Euglenophyceae) | | |
| *Euglena deses, E. proxima* | | |
| Cyanobacteria | | |
| *Microcoleus chthonoplastes, Lyngbya aestuarii, spirulina* sp. | *Merismopedia glauca* | |
| *Oscillatoria limosa, O. princeps* | | |

Taken from: (Sabbe 1993; Underwood 1994; Underwood et al. 1998; Hamels et al. 1998; Bellinger et al. 2005; Forster et al. 2006; Ribeiro et al. 2013; Redzuan and Underwood 2020, 2021)

2007; Thornton et al. 2002; Underwood 1994; Underwood and Barnett 2006). The majority of the literature on benthic diatom diversity relies on microscopy-based identification and a morphology-based taxonomy, an approach which is time-consuming and requires a high level of expertise (Ribeiro et al. 2020). Where detailed studies have been conducted it is clear that deterministic (niche-based) factors rather than neutral factors determine the community composition of the abundant species (Plante et al. 2016, 2021; Thornton et al. 2002). Taxonomic composition of the dominant components in the microbiome is strongly influenced by sediment particle size (the balance of sands, silts, and clays) selecting for a range of highly motile biraphid epipelic (mud inhabiting), less motile mono- or biraphid epipsammic (attached to sand grains), or araphid, diatom taxa

(Table 12.1) (Hamels et al. 1998; Sabbe 1993; Underwood and Barnett 2006). The distribution of sediment types corresponds to gradients of physical energy, salinity, and water flow, with sands present in the more exposed marine sediments and clays and silts settling in the more sheltered, low-energy, upper reaches of estuaries, often exposed to a greater range of salinity conditions over tidal and seasonal cycles (Baas et al. 2019; Green and Coco 2014). These gradients are major factors that determine both alpha- and beta diversity in MPB microbiomes (Gong et al. 2015; Park et al. 2014; Plante et al. 2016, 2021; Ribeiro et al. 2013; Witkowski et al. 2000).

Salinity within an estuarine gradient and position on the shore, which relates to the degree of tidal exposure and period of subtidal disturbance, are important controls on diatom species distribution (Forster et al. 2006; Oppenheim 1991; Peletier 1996; Ribeiro et al. 2003, 2013; Sahan et al. 2007; Thornton et al. 2002; Underwood 1994; Underwood et al. 1998). These physical factors vary with seasonal changes in irradiance, thermal stress, and winter mixing and storminess and alter the species composition of estuarine benthic diatom communities (Oppenheim 1991; Underwood 1994, 2005). For example, species such as *Fallacia pygmaea* and *Navicula salinarum* are found in cold and warm months, respectively (Admiraal et al. 1984). Inorganic nutrient concentrations are a strong driver of dominant taxa. They correlate with microphytobenthic biomass and species composition on spatial and temporal scales (Thornton et al. 2002; Underwood et al. 1998).

Many patterns of species distribution in estuaries are based on correlative field surveys. Because of covarying gradients, especially of exposure at low tide, sediment type, salinity, and nutrient concentrations, it is not clear how much variability in community composition occurs in the absence of changes in nutrients (or by changes in other variables such as sediment particle size distribution) and over what time scales such variability operates. Experimental manipulations have shown that nutrients are a selective force in determining species composition (Sullivan 1999; Underwood et al. 1998; Underwood and Provot 2000). High concentrations of ammonium and sulfide (often due to sewage inputs or organic enrichment) can be inhibitory or selective for particularly resistant taxa (Admiraal 1984). Significant decrease in Chl *a* and changes in species composition in the Ems Dollard estuary occurred between 1979 and 1993 after the lowering of organic waste input from local potato starch industries onto adjacent mudflats (Peletier 1996). Small spatial scale (10–100 m) patterns in biomass and species composition were documented in the Colne Estuary (Thornton et al. 2002; Underwood et al. 1998), which have been experimentally demonstrated to relate to species-specific preferences (Underwood and Provot 2000) and tolerance to sulfide and anoxia (McKew et al. 2013).

High throughput sequencing (HTS) methodologies have been applied to the coastal benthic eukaryotic microbiome in the last decade. The results of these analyses have in general supported the conclusions of microscope-based approaches about patterns of richness, distribution of species, and correlation with environmental variables. However, HTS report higher operational taxonomic unit (OTU) richness than that recognized by morphological taxonomic approaches. Chen et al. (2017) found 6627 benthic microeukaryotic OTUs (18S rRNA gene, 97% sequence similarity cutoff) at Xiamen Island, China; Plante et al. (2021) identified 4411 different diatom OTUs (18S rRNA gene, sequence similarity threshold of 98%) in South Carolina sediments, while An et al. (2020) reported 9582 diatom OTU (*rbcL* gene, 98% similarity cut off) on Korean intertidal mudflats. Chen et al. (2017) found strong deterministic control of the abundant and conditionally rare taxa (total phosphorus, total nitrogen, salinity, phosphate, and total oxidized nitrogen for the dominant taxa) in benthic microbial eukaryote communities but rare species showed no spatial, environmental, or distance-decay pattern. Comparisons of the diatoms present on mudflat-salt marsh transitions on a number of barrier island sites in South Carolina, USA, revealed that 95% of all OTUs were rare, less than 0.1% of total sequence count and that a few key taxa (e.g., *Navicula* and *Gyrosigma* species) were dominant (Plante et al. 2021). Spatial effects (dispersal limitation) and spatially-structured environmental factors affected these dominant taxa that caused the significant differences in beta diversity between island sites. The presence of planktonic or tychoplankton taxa, e.g., *Thalassiosira* was also recorded in benthic samples (Plante et al. 2021). Within single geographical sites factors such as physical disturbance and sediment type (sands, muds) determined the dominance patterns of a few key taxa but with greater neutral or stochastic process elements influencing the composition of the different patches (Plante et al. 2016).

High throughput sequencing provides a much greater resolution of the richness of the eukaryotic members of the sediment microbiome than revealed by morphological microscopic approaches. This higher richness is due in part to a higher intensity of sampling (greater sample sizes) and because of multiple copies of target genes within single cells, which varies between taxa (Gong and Marchetti 2019). But it could also be caused by cryptic diversity within some groups of diatoms. Vanelslander et al. (2009) found that the common estuarine diatom morphospecies *Navicula phyllepta* was in fact two different species separated spatially along the salinity gradient of the Western Scheldt estuary. Clonal cultures of *Nitzschia inconspicua* isolated from across a range of freshwater, brackish, and marine habitats in the River Ebro were paraphyletic with six different genotypes and a range of different reproductive strategies and salinity tolerances (Rovira et al. 2015). Growth of two clonal cultures of *Cylindrotheca closterium*, isolated from the oligosaline and mesosaline regions of the Colne estuary, showed different growth optima to salinity and nitrogen gradients (Underwood and Provot 2000). Morphological approaches with their much lower sample sizes (usually 200–400 individuals) cannot sample as many rare taxa as HTS and cannot resolve cryptic diversity. Moreover, rare valves require greater identification skills and may just be reported as unidentified by the untrained eye. These factors hamper the understanding of community assembly processes for microphytobenthos. Comparison of morphological species lists from spatially-distant sites, especially when studied by different research teams, is difficult because of the judgment required for many morphological species. HTS data lends itself to larger spatial analyses (Clark et al. 2017) and avoids individuals' decisions on species attribution. However, ecological interpretation of HTS datasets also relies on accurate reference databases and consideration of the issues of numbers of copies of phylogenetically informative genes when translating to relative abundance (Gong and Marchetti 2019). There is a need for better taxonomic alignment in the libraries used to assign HTS DNA sequence data to coastal marine morphological species in order to minimize the risk of misidentification and to ensure that the latest taxonomic phylogenies are reported as is being done for freshwater diatoms (Pérez-Burillo et al. 2020). This is particular necessary in order to understand the role of the many rare taxa that HTS detects in coastal microbiomes. Are these OTUs representing cryptic diversity within recognized species complexes or are these new, unknown, species or false identifications made by the original sequence depositors? These challenges need addressing to understand the rules for community assembly in these coastal microbiomes.

Intertidal diatom-rich biofilms exhibit a positive relationship between assemblage biodiversity (species richness and Shannon diversity of abundant taxa) and net primary production (Forster et al. 2006). Experimental studies with cultured benthic diatoms show niche complementarity and transgressive over-yielding (increased biovolumes) for mixtures of up to eight species combinations but antagonistic interactions were present between some taxa (Koedooder et al. 2019; Vanelslander et al. 2009). Facilitation, possibly through mixotrophic growth on organic substrates produced by other diatoms, or by associated heterotrophic bacteria, was shown for *Cylindrotheca closterium*, which grew strongly in the spent media from *Navicula* cultures (Vanelslander et al. 2009). The nature of the competitive interactions between species is not well described. *Nitzschia* c.f. *pellucida* releases cyanogen bromide immediately after the onset of light. Cyanogen bromide is toxic to other diatom species that thrive in the immediate vicinity and cause their death (Vanelslander et al. 2012). There is generally a negative relationship between biofilm biomass and diatom diversity in mudflat biofilms with lower shore beach sediments exposed to a greater level of disturbance having a higher diversity and a more even species distribution than upper and mid tide sites that support high biomass (Forster et al. 2006; Hill-Spanik et al. 2019; Underwood 1994). At times, conditions can be favorable for the rapid growth of just a few taxa or even a single species may “bloom” resulting in a biofilm with low species diversity and high biomass (Forster et al. 2006; Underwood 1994; Underwood et al. 1998). These studies were conducted in high nutrient status estuaries with traditional microscopic assessments of composition. In lower nutrient environments a positive relationship between biofilm biomass and Shannon diversity (determined by HTS) has been found (Plante et al. 2021). When comparing biomass-diversity relationships between sediment types, epipsammic habitats can have both lower biomass and lower alpha-diversity than mudflat sites (Plante et al. 2016). This illustrates how more detailed studies on the causes and patterns of benthic diatom assemblage composition and functioning are needed.

### 12.2.2 Adaptations of Photoautotrophs to Living in Intertidal Sediments

The consequence of periods of tidal exposure for photosynthetic microorganisms living on intertidal sediments is that they can experience high incident radiation (including UVB) at varying times over the day and over a year (Laviale et al. 2015; Mouget et al. 2008; Waring et al. 2007). Additionally, sediment disturbance and mobilization by waves and tidal flows mixes cells out of the photic zone of the sediment surface (De Jonge and van Beusekom 1995; Redzuan and Underwood 2020; Savelli et al. 2019). Autotrophic microphytobenthos has adapted to these environmental pressures of high irradiation and sediment disturbance in various ways. Motility is a key adaptation for MPB taxa living in mud and silty sediments allowing them to (re)position at locations with a favorable light climate within the sediment. Motile MPB is primarily composed of pennate diatoms (motile taxa found on mud are termed epipelon) and euglenophytes, as well as some taxa of filamentous cyanobacteria (Underwood and Kromkamp 1999). Upon tidal exposure the populations of phototrophic organisms undergo mass vertical migration, which brings cells to the surface (Consalvey et al. 2004; Jesus et al. 2009) in order to be able to photosynthesize. This vertical migration has been recognized for over a century (Perkins 1960) and is a macroscale feature visible to the naked eye as a color change of the sediment and is even detectable by remote sensing (Méléder et al. 2020; Savelli et al. 2020).

The motility of MPB exhibits a number of features of ecological relevance. There is an underlying endogenous rhythm of motility, which is maintained for a number of days in the absence of light or tidal stimuli. This rhythmicity is detectable in terms of changing cell density at the sediment surface, intensity of photosynthetic pigments, and rate of photosynthesis and carbohydrate production (Coelho et al. 2011; Haro et al. 2019; Perkins 1960; Round and Palmer 1966; Serôdio et al. 1997; Smith and Underwood 1998). These patterns of rhythmicity are evidence for a circadian rhythm and circadian rhythm regulator genes such as *kaiA, kaiB*, *kaiC*, and peroxiredoxin (*prx*) are expressed by cyanobacteria and diatoms in microbial mats (Hörnlein et al. 2018). Circadian rhythms of activity have also been found in the expression patterns of conserved gene transcripts for photosynthesis (PSI and PSII) and $CO_2$ fixation (RuBisCO) of cyanobacteria and diatoms in intertidal cyanobacterial mats (Hörnlein et al. 2018). Circadian rhythms can be entrained by external stimuli. MPB shows entrainment of rhythmicity by tidal exposure cycles as well as by day-night light cycles (Haro et al. 2019; Hörnlein et al. 2018; Perkins 1960; Serôdio et al. 1997). Haro et al. (2019) found that endogenous rhythms of migration and net community primary production were lost after exposure to continuous light for 3 days but were reset by re-imposition of an alternating light regime. Although easily demonstrated and reported quite some time ago (Perkins 1960; Round and Palmer 1966) the mechanism by which MPB maintains its endogenous vertical migration rhythms in synchrony with the progressive daily movement of the tidal exposure window (Happey-Wood and Jones 1988) is not yet resolved.

Taxon-specific differences are present within the mass movement of the whole community during tidal emersion-immersion cycles. Some taxa only appear at the sediment surface for short periods of the exposure period (e.g., Round and Palmer 1966; Round 1979; Underwood et al. 2005) or have a specific movement in response to light stimuli (*Gyrosigma balticum*, Jönnson et al. (1994)). Barranguet et al. (1998)

proposed that cells of different species micro-migrated into and out of the surface photic zone of the biofilm during illumination thus avoiding photo-inhibition while maintaining an overall high assemblage photosynthesis. Single cell imaging of intact biofilms provided evidence for this (Oxborough et al. 2000; Underwood et al. 2005), correlating time and light intensity with the species present at the sediment surface during tidal exposure.

Microphytobenthos shows strong behavioral responses to light intensity with populations migrating down into sediment to avoid high light (Perkins et al. 2002, 2010; Prins et al. 2020; Underwood 2002). MPB can also detect spectral composition with high and low intensities of blue and red light generating different patterns of surface-active biomass and photo-acclimation in diatom-rich mudflat biofilms (Prins et al. 2020). Benthic diatoms can also sense UVB radiation and will move away from the surface even when PAR light intensities are constant (Waring et al. 2007). Benthic diatoms respond to light through a combination of positive and negative phototaxis (directional movement) and photokinesis (changing speed) (Cohn et al. 2016). There are differences in response between diatom species. *Navicula perminuta* exhibits positive phototaxis at low levels of blue light and negative phototaxis at high intensities as well as a photokinetic response to red light. However, under the same conditions *Cylindrotheca closterium* only displayed photokinetic responses to red light and no blue light response (McLachlan et al. 2009). *Craticula cuspidata*, *Stauroneis phoenicenteron*, and *Pinnularia viridis* have different positive and negative photophobic (changing direction of movement) responses to red, green, and blue light (Cohn et al. 2016). Light sensing appears to take place at the apices of the cell valves and is therefore not necessarily directly associated with the chloroplast (Cohn et al. 2016; McLachlan et al. 2012). High intensity blue light at the apex of *N. perminuta* causes an increase in intracellular calcium concentration along the line of the raphe in the cell wall followed by a reversal of the direction of movement (McLachlan et al. 2012). Diatoms possess genes that code for phytochromes, cryptochromes, aureochromes, and other light receptor proteins for harvesting red/far red and blue light (Blommaert et al. 2020; König et al. 2017; Mann et al. 2020). Benthic diatoms in sediment experience a gradient of the light spectrum with red light most rapidly attenuated and blue light penetrating deepest (Lassen et al. 1992). Differential motility behavior modulated by spectral quality would allow cells to position themselves in a favorable light climate within the narrow photic zone of intertidal sediments.

Benthic diatoms are photo-physiologically flexible and are able to use rapid photochemical and non-photochemical quenching (NPQ), the xanthophyll cycle (XC), and longer-term acclimation of Chl *a* and other photopigments in order to maintain high rates of primary production in a rapidly varying light climate over tidal emersion and during the year (Barnett et al. 2015; Juneau et al. 2015; Prins et al. 2020; Underwood et al. 2005; Waring et al. 2010). The ability to dissipate light energy through NPQ and XC is particularly important for non-motile species that cannot migrate away from damaging light conditions. Experimental work has demonstrated differences in the ability of diatom species to induce high levels of NPQ and XC (Barnett et al. 2015; Blommaert et al. 2018). Epipsammic diatoms, which are found attached to sand grains, have high capacity for non-photochemical quenching (NPQ), while epipelic diatoms have lower potential NPQ, and non-motile tychoplankton, which live under low light conditions in frequently-mixed and resuspended sediments, also possess a low capacity for NPQ (Barnett et al. 2015; Blommaert et al. 2018).

### 12.2.3 Distribution of MPB Biomass in Coastal Sediments

The biomass of MPB present at any location and time is a consequence of the physical and environmental conditions of the preceding period. MPB shows rapid growth responses and can increase their biomass over a period of a few days when conditions are conducive to growth (Nedwell et al. 2016). Nutrients, light availability, and sediment type are major controls of biomass (Cibic et al. 2019; Underwood and Kromkamp 1999), while grazing and desiccation (McKew et al. 2011; Savelli et al. 2018), physical disturbance by waves, wind, and tides (de Jonge and van Beusekom 1995; Redzuan and Underwood 2020, 2021; Savelli et al. 2018), and macrofauna (birds) (Booty et al. 2020) may have local impacts.

Combined, these environmental factors produce general patterns of higher biomass on upper intertidal flats and in sheltered regions of estuaries (Daggers et al. 2020; Underwood and Kromkamp 1999). Seasonal patterns are variable between locations. In temperate zones biomass may peak at any time throughout the year, though summer peaks are common. However, summer declines have also been reported as the result of grazing or temperature stress (Daggers et al. 2020; Nedwell et al. 2016; Park et al. 2014; Savelli et al. 2018; Underwood and Paterson 2003). This seasonal variability reflects in part the spatial patchiness of MPB, which occurs on a range of scales from cm to km (Redzuan and Underwood 2021; Spilmont et al. 2011; Taylor et al. 2013; Weerman et al. 2012). Only a few long-term (>3 years) data sets of MPB biomass exist, and these indicate that sediment type, exposure or tidal position, windiness, and, to a lesser extent, air temperature are the main drivers of biomass. De Jonge et al. (2012) found similar inter-annual patterns of biomass at different stations in the Ems estuary (Netherlands) and a long-term positive relationship between biomass and annual air temperatures with higher Chl *a* content during the 1990s during the monitoring period from 1976 to 1999. Van der Wal et al. (2010) used remote sensing data to determine MPB biomass on mudflats in the southern North Sea over the period 2001 to 2009 and found broad synchrony in the patterns of occurrence and biomass between estuaries, although stronger relationships were present within regional data sets (e.g., within Dutch estuaries). Weather and summer temperatures strongly influenced MPB biomass in the Loire estuary (France) from 1993 to 1998 and from 2006 to 2010 (Benyoucef et al. 2014).

### 12.2.4 Interactions between Photoautotrophs and Chemoheterotrophs and the Turnover of Organic Carbon in Coastal Microbiomes

Photosynthetic activity by MPB produces oxygen and a variety of labile carbon compounds. MPB, particularly diatoms, produces extracellular polymeric substances (EPS) as well as low molecular weight labile carbon compounds (Bellinger et al. 2005, 2009; Underwood and Paterson 2003). EPS molecules are important in creating a biofilm matrix that increases sediment stability (Baas et al. 2019; Hope et al. 2020) and provide protection from desiccation and salinity stress (Steele et al. 2014). The production of these molecules is variable and is moderated by environmental factors (e.g., light and nutrients, Staats et al. 2000; Underwood and Paterson 2003) and rhythms of vertical migration (Hanlon et al. 2006; Perkins et al. 2001; Smith and Underwood 1998). These environmental factors drive a distinct seasonality in the balance of labile and recalcitrant exudates produced over a year (Moerdijk-Poortvliet et al. 2018a, b). There is evidence from freshwater studies that EPS production and biofilm formation by diatoms is enhanced by the presence of certain bacterial taxa (Bruckner et al. 2008, 2011; Grossart et al. 2005). These interactions appear to be species-specific. Bacterial-diatom interactions have negative effects on estuarine diatom biomass in cultures with a single diatom species but are neutral in co-cultures of different diatom species (Koedooder et al. 2019). Different benthic diatom taxa promoted the growth of assemblages of sediment bacteria. For example, *Seminavis robusta* cultures supported the Alphaproteobacteria *Thalassospira* sp., *Roseobacter* sp., and *Kordiimonadaceae* sp. and the Bacteroidetes *Mangrovimonas* sp. and *Owenweeksia* sp., while monocultures of the diatoms *Cylindrotheca closterium* and *Navicula phyllepta* had different bacterial assemblage profiles (Koedooder et al. 2019). There is evidence of antagonistic interactions between the bacterial assemblage associated with a certain diatom species with other benthic diatom taxa (Stock et al. 2019). This suggests that different diatom species may have their own associated bacterial microbiome.

Microphytobenthos-derived dissolved organic carbon compounds contribute 30 to 50% of the total organic matter in the sediments (Bellinger et al. 2009) and represent the key source of labile organic carbon (Nedwell et al. 2016). The importance of this carbon source varies in different intertidal habitats (sandy to muddy; temperate to tropical) (Cook et al. 2007; Oakes et al. 2010, 2012). MPB-fixed carbon has a characteristic $\delta^{13}$C signal that can be tracked through food webs (Christianen et al. 2017). EPS $^{13}$C-carbon has been tracked into the phospholipid fatty acids (PLFA) and RNA of various bacterial groups (Bellinger et al. 2009; Gihring et al. 2009; Middelburg et al. 2000; Taylor et al. 2013). Major utilizers of diatom EPS in aerobic sediments are Alphaproteobacteria, Gammaproteobacteria, and Bacteriodetes, and in anaerobic conditions Deltaproteobacteria (Bohórquez et al. 2017; McKew et al. 2013; Miyatake et al. 2014; Taylor et al. 2013). A subset of Alphaproteobacteria and Gammaproteobacterial taxa was adapted to utilize diatom EPS before it became available to the rest of the bacterial assemblage (Taylor et al. 2013). Different bacterial groups (for example, Sphingobacteria and *Tenacibaculum* (Bacteroidetes), two classes of Verrucomicrobia (Verrucomicrobiae and Opitutae)) grow preferentially on labile and refractory diatom EPS (Bohórquez et al. 2017; Underwood et al. 2019). Turnover rates of these different DOC fractions vary under aerobic and anaerobic conditions. Anaerobic conditions lead to preferential breakdown of refractory compounds and enhance the growth of Firmicutes (Clostridia, Lachnospiraceae, Peptostreptococcaceae, Ruminococcaceae, and other unclassified Clostridiales) and sulfate-reducing Deltaproteobacteria (Desulfobacteraceae and Desulfobulbaceae) (McKew et al. 2013). There are close linkages between photoautotrophic and chemoheterotrophic microorganisms present in the coastal sediment microbiome and evidence of antagonistic, synergistic, and mutualistic interactions. Hörnlein et al. (2018) proposed the *Choirmaster-Choir* theory. This theory predicts that the rhythmic release of photosynthate and other metabolites is controlled by the circadian clock of the photoautotrophic members of the microbiome (cyanobacteria, diatoms) and dictates the genetic clocks of other microbes either directly or in association with external Zeitgebers such as light and temperature, which results in a synchronized activity during a 24-h cycle. This idea remains to be further explored.

## 12.3 Nitrogen Cycling in the Marine Coastal Microbiome

The dominant heterotrophic bacteria found in aerobic coastal sediments are Actinobacteria, Alphaproteobacteria, Gammaproteobacteria, Chloroflexi, Verrumicrobiae, and Bacteriodetes (Bohórquez et al. 2017; McKew et al. 2013; Yao et al. 2019; Yi et al. 2020). The relative abundance of the different groups is strongly influenced by sediment characteristics particularly by sediment grain size, organic content, pH, and nitrogen and phosphorous availability (Yao et al. 2019; Yi et al. 2020). In estuarine environments, salinity and freshwater inputs influence taxonomic composition, with Actinobacteria and Betaproteobacteria more abundant in lower salinity zones or during periods of higher rainfall. For example, Actinobacteria, Chloroflexi, and Verrucomicrobia showed significant differences between rainfall seasons in the Yangtze estuary (Yi et al. 2020). However, overall salinity-related changes in assemblages appear to be more pronounced in estuarine bacterioplankton assemblages (Gołębiewski et al. 2017; Osterholz et al. 2018) than in estuarine benthic assemblages where organic matter and sediment properties are most influential (McKew et al. 2013; Yao et al. 2019; Yi et al. 2020). Marine coastal sediment microbiomes exhibit profound depth profiles of the distribution of taxonomic groups of bacteria reflecting the gradient of electron acceptors (Böer et al. 2009; Webster et al. 2010; Wilms et al. 2006). In muds with high organic carbon content, high rates of bacterial activity, and limited diffusion of oxygen, the anaerobic zone can be as near as a few millimeters below the surface and sometimes even reaches the surface. In the anaerobic zone the processing of organic carbon is largely driven by sulfate reduction and nitrogen cycling with Delta- and

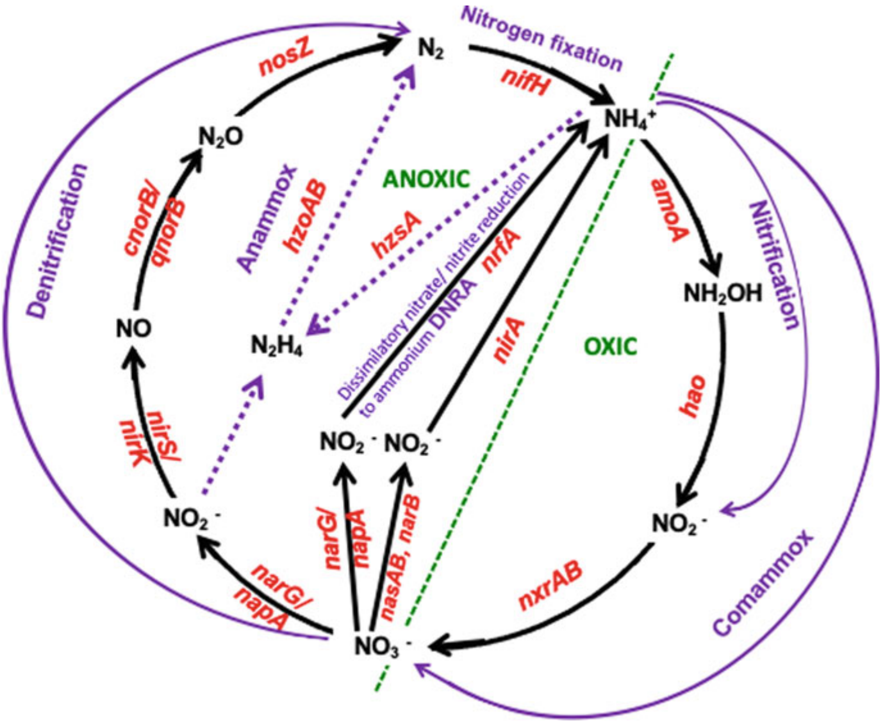

**Fig. 12.1** The nitrogen cycle in coastal sediments indicating transformations (purple), functional genes (red), and oxic/anoxic zones (green)

Epsilonproteobacteria, including sulfate-reducing bacteria, e.g. Desulfomonadales, as well as Archaea as prominent players (McKew et al. 2013; Nedwell et al. 2016; Webster et al. 2010).

The nitrogen (N) cycle (Fig. 12.1) is mediated by metabolically diverse groups of microorganisms. The location of the different processes in the sediment is determined by sediment redox state. Microbial-driven N transformations are especially crucial in coastal systems, which often receive high anthropogenic N inputs (e.g., via fluvial discharges) resulting in organic matter breakdown and oxygen depletion (Nedwell et al. 2016). Characterizing N cycle communities in the environment by traditional microbiological methods has been problematic due to the difficulties in obtaining pure cultures of the responsible microorganisms. However, molecular methods and HTS techniques have enabled researchers to uncover the functional nitrogen-cycle microbiome of these ecosystems.

### 12.3.1 Nitrogen Cycling in Aerobic Coastal Sediments: Nitrification and Aerobic Ammonia Oxidation and Comammox

Autotrophic ammonia oxidation is the rate-limiting step in nitrification and important in the N cycle (Fig. 12.1). During nitrification, aerobic ammonia-oxidizing bacteria (AOB) and archaea (AOA) oxidize ammonium by ammonia monooxygenase (encoded by *amoA*) (McTavish et al. 1993). With AOB, the second step is the dehydrogenation of hydroxylamine to nitrite by hydroxylamine oxidoreductase (encoded by *hao*) (Arp et al. 2002). However, AOA genome data does not appear to contain *hao* gene homologs, and an alternative mechanism has been proposed (Hallam et al. 2006). Nitrite is oxidized to nitrate by nitrite-oxidizing bacteria (NOB) (e.g., *Nitrospira*). Previously, based on 16S rRNA gene sequencing autotrophic ammonia oxidation was thought to be restricted to two monophyletic lineages of aerobic ammonia-oxidizing bacteria (AOB) (Head et al. 1993). The first lineage belongs to the Betaproteobacteria (Beta-AOB) (e.g., *Nitrosomonas, Nitrosospira*) and the second lineage belongs to the Gammaproteobacteria (Gamma-AOB) (e.g., *Nitrosococcus* sp.) (Head et al. 1993). However, metagenome libraries from seawater (Venter et al. 2004) and soil (Treusch et al. 2005) revealed putative genes involved in ammonia oxidation from uncultured Thaumarchaeota. AOA *amoA* gene sequences form five clusters four with cultured representatives (*Nitrosocaldus*, *Nitrososphaera*, *Nitrosopumilus*, *Nitrosotalea*) and the fifth is known as "*Nitrososphaera* sister" cluster (Pester et al. 2011).

Aerobic ammonia oxidizers are found in most environments (Table 12.1) (Francis et al. 2005; Jiang et al. 2009; Phillips et al. 1999; Stehr et al. 1995; Whitby et al. 1999, 2001). In some ecosystems AOA outnumber AOB often by a factor of 10 to 1000 (Beman et al. 2008; Wuchter et al. 2006). This is the case, for example, in North Sea coastal sediments (Lipsewers et al. 2014) and coastal waters (Smith et al. 2014a), suggesting a greater contribution of AOA to nitrification in these systems (Jiang et al. 2009). However, in some coastal and estuarine sediments AOB are more abundant than AOA (Caffrey et al. 2007). In a hypernutrified temperate estuary (Colne, U.K.) with gradients of salinity and ammonia concentration, benthic AOB (notably *Nitrosomonas* spp.) were significantly more abundant (by 100-fold) than AOA, suggesting that AOB were the main contributors to nitrification (Li et al. 2015a). Seasonal differences in nitrification in coastal sediments have been observed with the highest rates often in the summer (Li et al. 2015a). However, in North Sea coastal sediments, AOA 16S rRNA gene transcriptional activity was higher in the winter despite the lower abundance of these organisms (Lipsewers et al. 2014, 2017). In contrast, higher AOA abundances were found in the winter in the North Sea water column, which was attributed to ammonia availability and the lack of competition for ammonia with phytoplankton (Pitcher et al. 2011; Wuchter et al. 2006). Differences in spatial distribution between *Nitrosospira* and *Nitrosomonas* have also been found. For example, in freshwater lake sediments, *N. europaea* was present in littoral sediments whilst *N. eutropha* was found in profundal sediments, whilst members of *Nitrosospira* were ubiquitous (Whitby et al. 1999, 2001); and in the water column of the Mediterranean Sea, where different members of the betaproteobacterial ammonia oxidizers were associated with particulate material and planktonic samples (Phillips et al. 1999).

The oxidation of ammonia via nitrite to nitrate was originally considered to be a two-step process catalyzed by two functionally distinct groups of chemolithoautotrophs (ammonia oxidizers and nitrite oxidizers). However, a nitrifying bacterium belonging to *Nitrospira* was discovered and sequencing of its genome revealed that it has all the genes necessary for the oxidation of ammonia and nitrite (Daims et al. 2016). The discovery of the complete oxidation of ammonia to nitrate in one organism (comammox) (Fig. 12.1) has changed the paradigm that this process requires two distinct functional groups of microbes and raises questions about the role of comammox *Nitrospira* in N-cycling.

Comammox organisms belong as far as known to the *Nitrospira* lineage II (Daims et al. 2016; Koch et al. 2019). Based on *amoA* gene sequences from metagenomes comammox bacteria comprise two clades, A and B (Daims et al. 2016; Palomo et al. 2018; Van Kessel et al. 2015). Putative comammox (clade A) *amoA* gene sequences were previously misidentified as "unusual" methanotroph *pmoA* genes relating to *Crenothrix* in the Gammaproteobacteria (Stoecker et al. 2006) or presumed to belong to a methanotroph from Alphaproteobacteria (clade B, *amoA*) (Radajewski et al. 2002). Clade A is further delineated in two groups: clades A.1 and A.2 (Xia et al. 2018). Since comammox bacteria do not form a monophyletic group within the *Nitrospira,* lineage II comammox and canonical nitrite-oxidizing *Nitrospira* cannot be distinguished by 16S rRNA-based methods (Pjevac et al. 2017). Comammox bacteria have been found in various habitats (Table 12.2) with high proportions in estuarine and coastal environments (Xia et al. 2018). In the open ocean, however, comammox *amoA* genes were either rarely detected (Daims et al. 2016) or absent (Xia et al. 2018).

### 12.3.2 Environmental Factors Influencing Nitrification and Ammonia Oxidation

Although AOA and AOB coexist there is evidence of niche differentiation linked to various environmental factors (e.g., temperature, ammonium concentration, oxygen, pH, salinity, light, macrofaunal activity) (Caffrey et al. 2007; Cao et al. 2011; Dang et al. 2010; Erguder et al. 2009; Scarlett et al. 2021; Stehr et al. 1995). Ammonium concentration and availability are major factors for niche partitioning of AOA versus AOB with lower concentrations generally favoring AOA (Clark et al. 2020; Martens-Habbena et al. 2009). In some coastal sediments low phosphate availability selects for AOA over AOB (Lipsewers et al. 2014). In subsurface sediments *Nitrosomonas* dominated and was linked to nitrite concentration (Cao et al. 2012). In estuarine sediments, decreased dissolved oxygen altered AOB *amoA* expression but not AOA (Abell et al. 2010). Phytoplankton may also outcompete nitrifiers for substrates in surface waters (Smith et al. 2014b). In estuarine sediments benthic microalgae have a high demand for ammonium (Thornton et al. 1999) and can outcompete AOB, reducing the rates of nitrification (Risgaard-Petersen 2003).

**Table 12.2** Representative N-cycle microorganisms found in various coastal marine and estuarine environments

| N-cycle microorganisms | Environment | Reference |
|---|---|---|
| **Aerobic ammonia oxidizing bacteria (AOB)** | | |
| *N. europaea*, *N. communis*, *N. oligotropha* (cluster 6a), *N. marina* (cluster 6b), *Nitrosospira* spp. (clusters 13–15) | Coastal environments (Jiaozhou Bay) | Dang et al. (2010) |
| *Nitrosomonas* spp. | Hypernutrified estuary (Bahía del Tóbari) | Beman and Francis (2006) |
| *Nitrosomonas* spp.<br>*Nitrosospira* spp. | Estuarine (brackish) (Westerschelde estuary)<br>Estuarine (marine) (Westerschelde estuary) | Sahan and Muyzer (2008) |
| Estuarine/marine *Nitrosospira*-like cluster and *Nitrosomonas*-like cluster | Estuarine sediments (Elkhorn Slough) | Wankel et al. (2010) |
| *Nitrosospira* spp., *Nitrosomonas* spp. (*N. marina*, *N. oligotropha*, *N. ureae*, *N. eutropha*) | Wetland sediments of subtropical coastal mangroves | Wang et al. (2013) |
| *Nitrosospira* sp. and *Nitrosolobus multiformis* | Coastal sediments (North Sea) | Lipsewers et al. (2014) |
| **Aerobic ammonia oxidizing archaea (AOA)** | | |
| *Nitrosopumilus maritimus, Nitrososphaera gargensis* | Wetland sediments of subtropical coastal mangroves | Wang et al. (2013) |
| *Nitrosopumilus maritimus* | Mangrove sediments, South China Sea sediments | Li et al. (2011b); Cao et al. (2012) |
| *Nitrosopumilus* subclusters 12 and 16 (stable marine cluster), *Nitrosopumilus* subcluster 4.1 (estuarine cluster) | Marine coastal sediments (North Sea) | Lipsewers et al. (2014) |
| *Nitrosopumilus maritimus*, *Nitrosphaera gargensis* | Subtropical macrotidal estuarine sediments | Abell et al. (2010) |
| **Comammox** | | |
| Clade A.1 (e.g., *Cand.* Nitrospira nitrificans, *Cand.* Nitrospira nitrosa, clade A.2, clade B | Various sediments (tidal flat, saltmarsh, coastal), coastal waters | Xia et al. (2018) |
| **Anammox** | | |
| *Scalindua* spp., *Kuenenia* spp. | Wetland sediments of subtropical coastal mangroves | Wang et al. (2013) |
| Uncultured Planctomycetes, *Cand.* Scalindua spp., *Cand.* Brocadia spp., *Cand.* Kuenenia spp. | Anoxic basin on Black Sea | Kuypers et al. (2003) |

(continued)

**Table 12.2** (continued)

| N-cycle microorganisms | Environment | Reference |
|---|---|---|
| **Denitrification** | | |
| *Anaeormyxobacter delahogens* 2CP-C, *Thermus thermophilus* strain HB8, *Geobacter metallireducans*, *Rhodoferax ferrireducans*, *Halomonas halodenitrificans*, *Rhodobacter sphaeroides*, *Cupriavidus necator*, *Hahella chejuensis*, *Shewanella* spp., *vibrio* spp., *Saccharophagus degradans*, *Rhodopseudomonas palustris*, *Magnetospirillum magneticum* AMB1, *helicobacter hepaticus* ATCC51449, *pseudomonas* spp. | Hypernutrified estuarine sediments | Smith et al. (2007) |
| *Alcaligenes* spp. *(A. faecalis, A. xylosoxidans) pseudomonas* spp. *(P. Stutzeri)*, *Bradyrhizobium japonicum*, *Blastobacter denitrificans* | Sediments within the oxygen-deficient zone, Pacific coast | Liu et al. (2003) |
| **Dissimilatory nitrate reduction to ammonium (DNRA)** | | |
| *Shewanella frigidimarina, Chlorobium phaeobacteroides* | Hypernutrified estuarine sediments | Smith et al. (2007) |
| **Nitrogen fixation** | | |
| *Azotobacter* spp., *Azospirillum* spp., *campylobacter* spp., *Beggiatoa* spp., *Enterobacter* spp., *Klebsiella* spp., *vibrio* spp., *Desulfobacter* spp., *Desulfovibrio* spp., *clostridium* spp. cyanobacteria including unicellular and non-heterocystous species, (Chromatiaceae, Chlorobiaceae, Chloroflexaceae, Rhodospirillaceae), archaea (e.g. *Methanococcus* spp., *Methanosarcina* spp.) | Marine/ seagrass sediment, estuarine sediment, salt marsh sediment, *Spartina* roots, *Zostera* roots, beach sediment, intertidal sediments, seawater | Herbert (1999) |

Differential sensitivity to pollutants between AOB and AOA in coastal environments has also been found with higher Beta-AOB diversity in polluted sites whilst AOA were unaffected (Cao et al. 2011). Agriculturally-impacted estuarine sediments were dominated by AOA and *Nitrosomonas* spp. *amoA* sequences, whilst *Nitrosospira* spp. dominated less impacted sites (Wankel et al. 2010). Distinct clusters of *Nitrosomonas* and *Nitrosospira* lineages have been found in eutrophic coastal sediments subjected to inputs from nearby wastewater treatment plants and polluted rivers (Dang et al. 2010). Silver nanoparticles inhibited AOB-driven nitrification but not AOA in a temperate eutrophic estuary (Beddow et al. 2017). Addition of titanium nanoparticles resulted in increased ammonium fluxes from sediments into overlying water, which could be due to lower rates of ammonia oxidation and nitrification, as well as a decrease of net MPB primary productivity (Passarelli et al. 2020). Beta-AOB *N. europaea* and *N. communis* lineages also thrive in heavy metal-polluted environments and in environments with high ammonium concentrations (Dang et al. 2010; Stein et al. 2007). In estuaries, *Nitrosospira*-like lineages appear to be better adapted than *Nitrosomonas* (Cao et al. 2011) and Beta-AOB (particularly the *N. oligotropha* lineage) and could be used as bioindicators of pollution in coastal systems (Dang et al. 2010).

Comammox bacteria are functionally versatile and adaptative to many environments (Hu and He 2017). Comammox bacteria exhibit niche partitioning influenced by various environmental factors (Shi et al. 2020) and differences in abundance among clades have been found (Xia et al. 2018). Co-occurrences of comammox with canonical ammonia oxidizers indicate a potential functional differentiation between these groups (Bartelme et al. 2017; Palomo et al. 2018; Pjevac et al. 2017) and may depend on whether the main activity of comammox in an environment is ammonia oxidation or nitrite oxidation (Xia et al. 2018). Comammox bacteria may outnumber AOB (Xia et al. 2018) and can functionally outcompete other canonical nitrifiers in highly oligotrophic systems (Hu and He 2017). However, which factors drive niche specialization between comammox and canonical ammonia oxidizers currently remains unknown.

### 12.3.3 Nitrogen Cycling in Anaerobic Coastal Sediments: Anammox, Denitrification, and Dissimilatory Reduction of Nitrate to Ammonium

Anaerobic ammonia oxidation (anammox) involves the conversion of ammonium and nitrite to $N_2$ in the absence of oxygen (Fig. 12.1). Some anammox bacteria are facultative chemoorganotrophs that can also metabolize organic compounds, notably formate, acetate, and propionate (Kartal et al. 2007; Strous et al. 2006), allowing anammox bacteria to adopt a “disguised” denitrifying lifestyle (Kartal et al. 2007). Anammox bacteria form a monophyletic order of the Brocadiales within the Planctomycetes (Jetten et al. 2010), and consist of five candidate genera: *Candidatus* Kuenenia (Strous et al. 2006); *Candidatus* Brocadia (Oshiki et al. 2011; Strous et al. 1999); *Candidatus* Anammoxoglobus (Kartal et al. 2007); *Candidatus* Jettenia (Quan et al. 2008), and *Candidatus* Scalindua (Schmid et al. 2003).

Anammox bacteria are found in virtually any anoxic environment that contains fixed N (Table 12.2). Although anammox is responsible for a large proportion of $N_2$ production in marine sediments, in eutrophic coastal sediments, and saline tidal marsh sediments, anammox is not important relative to denitrification (Koop-Jakobsen and Giblin 2010; Thamdrup and Dalsgaard 2002). Although anammox bacteria have been found in coastal and estuarine sediments (Li et al. 2011a; Tal et al. 2005; Trimmer et al. 2003) and coastal mangrove wetlands (Cao et al. 2011; Li et al. 2011a), greater anammox bacterial diversity occurs in the Oxygen Minimum Zones (OMZs) of oceans (Woebken et al. 2009). Anammox bacteria are abundant and active in oxygenated upper sediments and bioturbated marine coastal sediments in the North Sea (Lipsewers et al. 2014). High anammox bacterial abundances have also been found in surface sediments of hypernutrified estuarine tidal flats (Zhang et al. 2013). In some environments anammox bacteria are scarce like suboxic and anoxic aquatic systems where low anammox bacterial diversity was found and comprised mostly of *Scalindua* (Penton et al. 2006).

Denitrification is fundamental in the N cycle releasing nitric oxide (NO), nitrous oxide ($N_2O$), and dinitrogen gas ($N_2$) to the atmosphere (Fig. 12.1). As denitrifying bacteria belong to different phylogenetic groups the 16S rRNA gene is not very useful for analyzing denitrifier communities. Instead, functional genes involved in denitrification have been targeted, e.g., *napA*, *narG* (nitrate reductase), *nirS*, *nirK* (nitrite reductases), and *nosZ* (nitrous oxide reductase) (Nogales et al. 2002) (Fig. 12.1). Denitrifiers are facultative organoheterotrophic anaerobes that constitute a phylogenetically diverse group spanning >50 different genera (Jones and Hallin 2010; Zumft 1997). Most denitrifiers belong to the alpha-, beta-, gamma-, and epsilon-Proteobacteria (Braker and Conrad 2011). The most frequently isolated denitrifying bacteria belong to the Pseudomonads (Herbert 1999). Denitrification has also been found among Firmicutes, Actinomycetes, Bacteroidetes, Aquificaceae, and Archaea (Braker and Conrad 2011). Denitrification is also widespread among Foraminifera, *Gromiida* (Piña-Ochoa et al. 2010; Risgaard-Petersen et al. 2006), and fungi (Braker and Conrad 2011).

Denitrification is widely distributed in the environment (Table 12.2). In the ocean however, denitrification is geographically restricted to a few oceanic regions (e.g., OMZs and hemipelagic sediments) (Jayakumar et al. 2009) and distinct *nirS* and *nirK* populations have been found within the oxygen-deficient zone in marine sediments (Liu et al. 2003). In eutrophic estuaries, denitrification can mediate the lowering of N load and contribute to eutrophication control (Nogales et al. 2002). Indeed, in coastal and estuarine sediments denitrification can remove >50% of inorganic N inputs from terrestrial systems (Nedwell et al. 2016; Rivera-Monroy et al. 2010; Seitzinger 1988). In coastal and estuarine sediments denitrification rates are generally higher than in shallower waters (Herbert 1999).

In addition to denitrification, microbial nitrate reduction may also take place via alternative pathways. Dissimilatory nitrate reduction to ammonium (DNRA) (Fig. 12.1) is particularly important in organic-rich sediments (King and Nedwell 1987; Laverman et al. 2006) and tends to retain bioavailable N in aquatic ecosystems. DNRA is common in bacteria (e.g., Proteobacteria, Firmicutes, Verrucomicrobia, Planctomycetes, Acidobacteria, Chloroflexi, *Beggiatoa*, *Thioploca*, and *Chlorobia*) (Papaspyrou et al. 2014; Preisler et al. 2007), and also occurs in eukaryotes (e.g., diatoms, fungi) (Pajares and Ramos 2019). Anammox bacteria may also perform DNRA in the presence of small organic compounds (Kartal et al. 2007) or ammonium might be released from fermentative reactions (Herbert 1999; Lam et al. 2009). DNRA is commonly found in environments low in oxygen, such as OMZs (Lam et al. 2009) and sediments with steep oxygen gradients (Kamp et al. 2011). DNRA has also been found in the Namibian inner-shelf bottom waters (Kartal et al. 2007) and deep-sea sediments (Pajares and Ramos 2019).

### 12.3.4 Environmental Factors Influencing the Anaerobic Nitrogen Cycling Biome

Anammox is controlled by several environmental factors including salinity (Sonthiphand et al. 2014), temperature (Qian et al. 2018), organic matter content (Trimmer and Engström 2011), and inorganic N availability (Trimmer et al. 2005). Interactions between AOA, AOB, and anammox bacteria have been shown where nitrifiers supply nitrite to anammox (Lam et al. 2007, 2009). In mangrove sediments, positive correlations occur with AOA diversity and abundance and anammox *hzo* gene abundances (Li et al. 2011a, b; Li and Gu 2013), suggesting that complex interactions exist between anammox bacteria and ammonia oxidizers. Sulfide may also inhibit anammox bacteria (Dalsgaard et al. 2003; Jensen et al. 2008).

Nitrogen removal via denitrification may cause a decrease in N availability, which in coastal environments can severely impact primary producers and levels of eutrophication (Herbert 1999; Seitzinger 1988). Numerous environmental factors (e.g., N availability and concentration, temperature, oxygen concentration, water depth, organic matter quality and quantity, bioturbation) affect denitrifier distribution and abundance (Braker et al. 2000; Dang et al. 2009; Liu et al. 2003; Prokopenko et al. 2011; Zhang et al. 2014). Denitrification rates also show distinct seasonal patterns driven largely by temperature, nitrate, and availability of organic carbon (Kaplan et al. 1977). Denitrification rates decrease in the spring (in estuarine sediments) (Jørgensen and Sorensen 1988) and in the summer (in subtropical macrotidal estuarine sediments) where *nirS*:*nirK* ratios are negatively correlated with temperature (Abell et al. 2010). Nitrate concentration and oxygen have an impact on denitrifying communities (Liu et al. 2003) and nitrate availability drives *nirS* communities whilst *nirK* communities respond to other parameters (Jones and Hallin 2010). To date, the ecological function of these denitrifying communities and the factors that determine the composition of *nirS*/*nirK* communities remains unknown (Jones and Hallin 2010). Sulfide also decreases denitrification rates (Porubsky et al. 2009). Yet, paradoxically in sulfidic sediments some microorganisms use sulfide as an electron donor for denitrification (Bowles et al. 2012). Bioturbated sediments from large burrowing macrofauna also increase coupled nitrification-denitrification (Laverock et al. 2011; Papaspyrou et al. 2014).

Seasonal and spatial differences in DNRA have been found with increased rates in the summer throughout sediment depths compared to other times when activity was restricted to deeper sediments (Jørgensen 1989). In intertidal and subtidal environments DNRA may change on a daily basis due to the growth and photosynthetic activity of benthic microalgae. Photosynthetically evolved oxygen diffuses into the surface of the sediment during daylight which inhibits DNRA (Herbert 1999). MPB photosynthesis can decrease the rate of denitrification of nitrate that diffuses into the sediment from the water column (Dw) but stimulates the rate of coupled nitrification-denitrification (Dong et al. 2000; Risgaard-Petersen 2003). In estuaries, high *nrfA* gene abundances (encoding cytochrome c nitrite reductase) have been found and change along gradients of salinity and nitrate (Papaspyrou et al. 2014).

### 12.3.5 Nitrogen Fixation in Coastal Sediments

Biological nitrogen fixation involves specialized groups of autotrophic and heterotrophic bacteria and archaea that possess molybdenum (Mo)–Fe protein (dinitrogenase) (encoded by *nifDK*) and Fe protein (dinitrogenase reductase) (encoded by *nifH*) (Fig. 12.1). Oxygen exposure deactivates nitrogenase and oxygenic phototrophs must separate dinitrogen fixation from oxygenic photosynthesis either spatially (e.g., in heterocysts) or temporally (Berman-Frank et al. 2003).

Nitrogen-fixing organisms (diazotrophs) are a diverse group of bacteria and archaea that include members of the Chromatiaceae, Chlorobiaceae, Chloroflexaceae, Rhodospirillaceae, and chemoautotrophic bacteria and archaea (Bergman et al. 1997; Capone 1988; Raymond et al. 2004). Marine diazotrophs mainly include non-heterocystous, heterocystous, symbiotic, and unicellular cyanobacteria (e.g., Ca. Atelocyanobacterium thalassa [UCYN-A]; *Crocosphaera watsonii* [UCYN-B] and *Cyanothece* [UCYN-C]) (Capone 1988; Martinez-Perez et al. 2016; Pajares and Ramos 2019). Other marine diazotrophs include heterotrophic bacteria (e.g., *Klebsiella*), anoxygenic phototrophic bacteria (e.g., *Chlorobium, Chromatium*), strict anaerobic chemotrophs (e.g., *Clostridium, Desulfovibrio*), methanogenic Euryarchaeota and Planctomycetes (Pajares and Ramos 2019). Nitrogen-fixing eukaryotes are not known and it seems that these organisms solved the problem by entering in symbiosis with nitrogen-fixing bacteria (Kuypers et al. 2018).

The main factors that affect marine diazotroph distribution are oxygen, light, temperature, inorganic N, phosphorus, iron, and organic matter (Pajares and Ramos 2019). In estuaries and coastal regions, UCYN-A are highly abundant (Moreira-Coello et al. 2019), along with heterotrophic bacteria (Pajares and Ramos 2019). Several factors influence nitrogen fixation activity in benthic sediments including carbon availability, temperature, light, pH, oxygen, inorganic N, salinity, and trace metal availability (Herbert 1999). Organic carbon availability is generally the main factor limiting the nitrogen fixation in unvegetated sediments (Herbert 1999). In unvegetated shallow coastal lagoons and intertidal sediments where light is not limiting, dense communities of benthic nitrogen-fixing cyanobacteria may occur (Herbert 1999; Stal 2016; Stal et al. 2019). In tropical coastal marine lagoons sediment nitrogen fixation contributes 11% of the annual N input (Hanson and Gundersen 1977) and high rates occur in temperate sediments, mudflats, and salt marshes, especially in organically rich sediments (Nedwell and Aziz 1980; Herbert 1999). Cyanobacterial mats (both temperate and tropical) exhibit high nitrogen fixation rates linked to dark-light cycles and are under the control of circadian clocks (Herbert 1999; Hörnlein et al. 2018; Stal 2016; Stal et al. 2019). High nitrogen fixation rates have been found in salt marsh sediments which has been attributed to organic compounds excreted from plant roots coupled to plant photosynthetic activity (Moriarty and O'Donohue 1993; Whiting et al. 1986) whilst rates in bare marine sediments were low (Herbert 1999).

## 12.4 Archaea in Marine Sediment Microbiomes

### 12.4.1 An Array of Coastal Archaea: Marine Group III (Putative Pontarchaea), Asgard Archaea, Marine Benthic Group D, and Woesarchaeota

Archaea are an important component in the surface sediments of intertidal communities with an abundance of one to two orders of magnitude lower than bacteria (Li et al. 2012; McKew et al. 2011; Wang et al. 2020). Deeper in the sediment, e.g., in the sulfate-methane transition zone, they can be in equal abundance (Li et al. 2012; Wang et al. 2020). Until the 1990s the domain Archaea was divided into Euryarchaeota and Crenarchaeota but this view is rapidly changing (see Baker et al. 2020). Methanogens were the only Archaea in coastal environments that were well known. Advances in sequencing technology unveiled the uncultured archaeal diversity in coastal settings. Evidence for the presence of Archaea in non-extreme environments such as the open ocean was thanks to the pioneering work of Norman Pace, Ed DeLong, Jed Fuhrman and colleagues (DeLong 1992; Fuhrman et al. 1992; Pace 1997). Archaea were described from Colne Point salt marsh in Essex, U.K. by Munson et al. (1997) who detected 16S rRNA gene sequences of methanogens, haloarchaea, and an archaeal lineage that was distinct from any known taxon. Subsequently, this unknown archaeal taxon was detected elsewhere, e.g., from the deep sea (Fuhrman and Davis 1997) and continental shelf samples (Vetriani et al. 1998). It became known as Marine Group III (MG-III) Euryarchaeota with a proposed phylum-level reassignment to Pontarchaea (Li et al. 2015b). Further surveys, using fosmid clones and metagenome assembled genomes (MAGs), revealed the distribution and putative functions of MG-III. For example, Haro-Moreno et al. (2017) showed that MG-III phylotypes living in the photic zone probably have a photoheterotrophic lifestyle, which they based on the presence of photolyase and rhodopsin genes as well as of genes for peptide and lipid uptake and degradation. It remains to be seen whether the coastal MG-III found by Munson et al. (1997) are similar to epipelagic or bathypelagic phylotypes (Haro-Moreno et al. 2017).

Kim et al. (2005) found MG-III Euryarchaeota in tidal flat sediments from Ganghwa Island, Korea, together with many sequences that were considered to be Crenarchaeota, which had not been detected in the Colne Estuary salt marshes by Munson et al. (1997). This phylogenetic lineage was referred to as Marine Benthic Group B (MBG-B) by Vetriani et al. (1998), a sister group of the Deep-Sea Archaeal Group (DSAG), which have been reclassified as members of the Asgard Archaea. Specifically, MBG-B are now known as Thorarchaeota (Seitz et al. 2016) and DSAG as Lokiarchaeota (Spang et al. 2015). Phylogenomic analysis places Eukaryotes within the archaea most closely related to the Asgard archaea, which possess a range of eukaryote features. The classification of the Asgard archaea has contributed to redefining the tree of life from three domains into one with two domains (Williams et al. 2020). Thorarchaeota (MBG-B) have been found in a number of different estuaries (Fig. 12.2; Zou et al. 2020a), including the Colne, Essex, U.K. (Webster

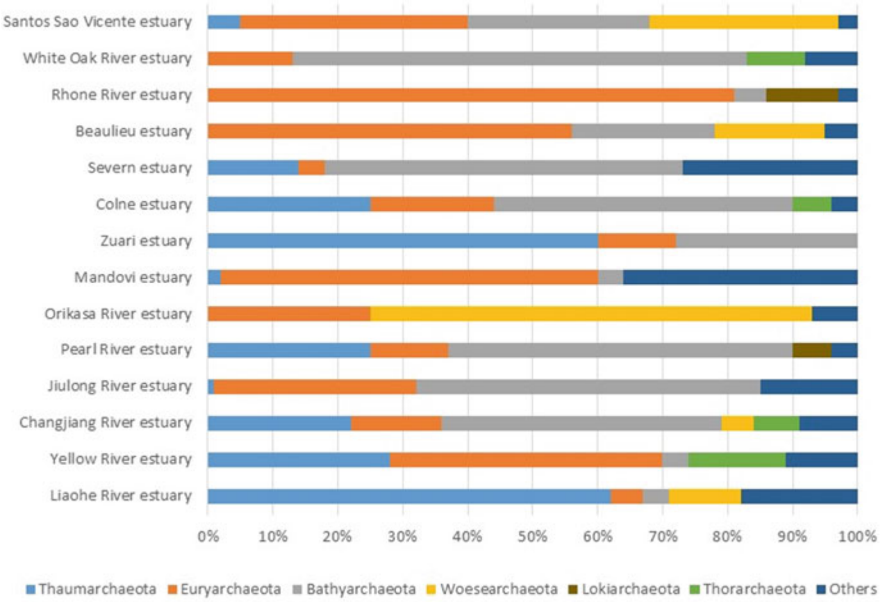

**Fig. 12.2** Relative abundance of archaeal taxa in estuarine sediments, based on 16S rRNA gene clone libraries. This figure is produced from data collated by Zou et al. (2020a). Refer to Zou et al. (2020a) for details of the source papers and the primers pairs used

et al. 2015). Thorarchaeota from White Oak River estuary, North Carolina, USA, have the genetic capacity for protein degradation with the formation of acetate as well as for the reduction of elemental sulfur and thiosulfate and therefore this group of organisms may play an important role in carbon and sulfur cycling in estuarine sediments (Seitz et al. 2016). Lokiarchaeota in Namibian shelf sediments anaerobically consume necromass and extracellular polymeric substances from diatoms and also fixed $CO_2$ via the $H_2$-dependent Wood–Ljungdahl pathway (Orsi et al. 2019). This archaeal mixotrophic activity was more rapid than that of bacteria emphasizing that archaea should not be overlooked in sediment biogeochemical processes (Orsi et al. 2019).

Another archaeal group that is commonly found in estuaries is the Marine Benthic Group D or MBG-D (also called DHVE1), which has been variously called Thermoprofundales or Izemarchaea (Baker et al. 2020; Zhou et al. 2019). MBG-D were the second most abundant archaea in the Pearl River Estuary, China, after the Bathyarchaeota (Wang et al. 2020; see also Zou et al. 2020b) and were also detected in sediments along the Colne Estuary, U.K. (Webster et al. 2015). MBG-D seem to be heterotrophic with the capacity for degrading proteins (Lloyd et al. 2013). In addition, the potential for mixotrophic growth was revealed upon the reconstruction of MBG-D genomes from a mangrove sediment (Zhou et al. 2019).

Woesearchaeota, formerly known as DHVEG-6 (Liu et al. 2018a, b), are globally distributed in many environments including estuaries where they are usually a minor component of the microbial community but occasionally reach a high abundance (Fig. 12.2; Zou et al. 2020a). In *Zostera marina* seagrass beds and nearby bare sediment in Rongcheng Bay, Yellow Sea, China, Woesearchaeota (42% of Archaea) were the most abundant archaea followed by Bathyarchaeota (21%) and Thaumarchaeota (17%) with specific subclades of Woesearchaeota and Bathyarchaeota enriched in the vegetated areas (Zheng et al. 2019).

### 12.4.2 Bathyarchaeota (Miscellaneous Crenarchaeota Group) and Thaumarchaeota Are Generally the Most Abundant Archaea in Marine Sediments

There are two other even more widely distributed and abundant examples of novel archaeal taxa in estuarine environments. The Marine Group I, which together with species from terrestrial environments belongs to the Thaumarchaeota, consists predominantly of ammonia-oxidizing Archaea, which are discussed in Sect. 12.3.1. The Marine Group I are abundant in estuarine sediments (Fig. 12.2) and dominated in a large-scale study of eastern Chinese marginal seas (Liu et al. 2020). The Miscellaneous Crenarchaeota Group (MCG), now known as Bathyarchaeota, is one of the most abundant phyla on Earth and generally the most abundant archaea in estuarine sediments (Fig. 12.2; Li et al. 2012). Bathyarchaeota have an anaerobic organoheterotrophic lifestyle (Seyler et al. 2014), probably degrading proteins (Lloyd et al. 2013), carbohydrates (Lazar et al. 2016), aromatic (Dong et al. 2019; Meng et al. 2014), and aliphatic (Dong et al. 2019) compounds, as well as a variety of other organic matter (Seyler et al. 2014). The aforementioned taxonomic groups and the Bathyarchaeota are phyla and hence comprise a variety of different microorganisms with an array of genetic and functional capacities, which will likely reflect their ecological distribution in estuarine sediments. Bathyarchaeota, for example, comprise 25 subclades (Zhou et al. 2018). Lazar et al. (2014) propose that the Bathy-6 in contrast to other lineages prefers suboxic sediment with minimal free sulfide. Bathy-6 also has the genetic capacity to take up and catabolize a wide range of carbohydrates and proteins (Lazar et al. 2016) and may be able to carry out dissimilatory nitrite reduction to ammonium (DNRA) (Lazar et al. 2016). By performing diverse enrichments from estuarine sediments Yu et al. (2018) showed that subclade Bathy-8 grew on lignin as an energy source. Then, by using lipid stable-isotope probing, these authors demonstrated that lignin-degrading cultures used bicarbonate as a carbon source. This organoautotrophic growth on an abundant biopolymer may partially explain its dominance particularly in estuarine sediments that receive input from plant debris (Yu et al. 2018).

Thus, a variety of different archaea contribute to the turnover of organic matter in coastal sediments while some of them may be autotrophic at the same time. There is a need to better understand the contribution of archaea to benthic cycling of carbon, sulfur, and nitrogen as well as their interactions with other organisms. Obtaining enriched or pure cultures, as was done for Lokiarchaeota (Imachi et al. 2020), will be necessary in order to understand the ecophysiology of archaea in coastal sediments.

### 12.4.3 Archaea Drive the Methane Cycle in Coastal Sediments

Strictly anaerobic methane-producing archaea perform the final step in the anaerobic degradation of organic matter. Much is known about methanogens, primarily because many strains from different classes have been isolated and studied in detail. All characterized methanogens belong to the phylum Euryarchaeota and include: Methanobacteriales, Methanococcales, Methanomicrobiales, Methanosarcinales, Methanopyrales, Methanocellales, and Methanomassiliicoccales (Lyu and Liu 2018) and the class Methanonatronarchaeia (Sorokin et al. 2017, 2018). The first-described methanogens use the major products of microbial fermentation either hydrogen plus $CO_2$ (hydrogenotrophic) or acetate (acetoclastic) (Thauer et al. 2008). Fermentation and methanogenesis occur when energetically favorable electron acceptors such as oxygen, nitrate, and sulfate have been depleted such as is the case in deeper coastal sediments (Wilms et al. 2006, 2007). However, methanogenesis also occurs near the surface of coastal sediments, where sulfate reducers outcompete methanogens for hydrogen and acetate. Here, methanogens coexist with sulfate-reducing bacteria by using non-competitive methylated substrates, such as methylamine (e.g., Oremland et al. 1982). Methylamines, methyl sulfides, and other methylated compounds are common in marine and hypersaline environments as breakdown products of osmolytes (McGenity and Sorokin 2018) and also as components of lipid polar head groups, e.g., choline (Jameson et al. 2018). Methylotrophic methanogenesis could be distinguished into two mechanisms: (1) hydrogen-independent carried out by several representatives of the Methanosarcinales, and (2) hydrogen-dependent carried out by several other groups (Feldewert et al. 2020). Hydrogen-dependent methylotrophic methanogens also appear to compete with $H_2$-utilizing sulfate-reducing bacteria as long as the partial pressure of hydrogen is low and there is a supply of suitable $C_1$-compounds owing to their superior affinity for hydrogen (Feldewert et al. 2020).

A summary of the numerous investigations on coastal/estuarine methanogenesis is beyond the scope of this chapter. For a discussion of methanogenesis in the Colne Estuary, see Nedwell et al. (2016). The Colne Estuary, U.K., is typical for many global estuaries as methane production occurs along the length of the estuary together with sulfate reduction but at a rate almost two orders of magnitude lower than sulfate reduction (Nedwell et al. 2004). In the Colne Estuary a change from acetoclastic and hydrogenotrophic taxa to methylotrophic (*Methanococcoides*) and versatile (*Methanosarcina*) taxa from the head to the mouth was observed (Webster et al. 2015). The salinity (and, hence, sulfate) gradient that characterizes estuaries, together with proximity to land and sea, are major reasons why these environments have a higher diversity of methanogens than other ecosystems (Wen et al. 2017). For example, *Methanoregula* is typically freshwater while *Methanococcoides* is typically marine but both are common in estuaries (Wen et al. 2017). An investigation on methanogens and methanogenesis in mangrove sediments showed that the dominant taxa were Methanomicrobiales and Methanosarcinales together with putative hydrogen-dependent methyl-reducing methanogens *Candidatus* Methanofastidiosa and Methanomassiliicoccales, the latter exhibiting the highest activity (Zhang et al.

2020). Thus, even for a well-known archaeal process much has to be learned about the diversity of the responsible microbes.

It came as a surprise that methylotrophic methanogenesis may be a property of non-euryarchaeal candidate phyla within the archaea such as Verstraetearchaeota (Vanwonterghem et al. 2016) and Bathyarchaeota (Evans et al. 2015). This was based on the possession of *mcr* genes coding for methyl coenzyme M reductase (Mcr) complex, which catalyzes the terminal step of methanogenesis. Subsequently, *mcr* in *Candidatus* Syntrophoarchaeum was proposed to code for an enzyme involved in short-chain alkane oxidation and its sequence was similar to the *mcr* sequences from Verstraetearchaeota and Bathyarchaeota (Evans et al. 2019). Thus, it is supposed that these archaea are not methanogens but oxidize short-chain alkanes.

Consumption of short-chain alkanes may not be a common process in estuaries because propane and butane are not present in large amounts. However, anaerobic oxidation of methane produced by methanogens occurs ubiquitously especially in the sulfate-methane transition zone (SMTZ) (Boetius et al. 2000; Hoehler et al. 1994) and is a near-quantitative sink for the methane produced (Egger et al. 2018). This process is carried out by polyphyletic groups of uncultured archaea, which are related to methanogenic Euryarchaeota and referred to as ANME (anaerobic methane oxidizers) (Evans et al. 2019; Knittel et al. 2018). The original mechanistic explanation for anaerobic oxidation of methane was that it occurs as a syntrophic process in which the ANME methanotrophs convert methane to hydrogen, which is consumed by associated bacteria most typically in marine sediments by sulfate-reducing bacteria (Boetius et al. 2000). However, the precise mechanism of anaerobic oxidation of methane is debated in terms of: 1) the main interacting bacterial species and their terminal electron acceptors (e.g., sulfate, Fe III, Mn IV, and nitrate), 2) the internal metabolic processes in the ANME methanotrophs, which genetically resemble methanogens, and 3) the energetics and mode of exchange e.g., metabolite transfer or direct interspecies electron exchange (McGlynn 2017).

In estuaries, which overall are a methane source, more methane reaches the atmosphere as salinity decreases due to a combination of greater methane production and less effective anaerobic removal where sulfate reduction is lower (Dean et al. 2018). However, there remains much to be learned about the sources and sinks of methane in coastal environments and particularly in estuaries. For example, in a brackish Baltic Sea estuary, anaerobic oxidation of methane was identified as an important process presumably coupled to iron III and manganese IV reduction (Myllykangas et al. 2020).

### 12.4.4 Haloarchaea Are Consistently Present and Locally Abundant in Coastal Sediments

Extremely halophilic Euryarchaeota belonging to the Halobacteria (more commonly referred to as haloarchaea) dominate in coastal environments where seawater evaporates to create hypersaline conditions such as in sabkhas, hypersaline lagoons, as well as artificial salt pans (McGenity and Oren 2012). However, Munson et al.

(1997) reported that haloarchaea were abundant in a temperate salt marsh. This observation led Purdy et al. (2004) to culture haloarchaea from creek or saltmarsh pan sediments, aerobically, over a range of salinities, with either glucose or glycerol as carbon and energy sources, and with antibiotics to inhibit growth of bacteria and eukarya. They isolated three taxa of haloarchaea one of which had strains that grew slowly at seawater salinity and optimally with 10% NaCl, a property that is unusual for haloarchaea (Purdy et al. 2004). Subsequently, haloarchaea have been found in coastal environments across the globe sometimes locally at high abundance. This is particularly true for members of *Haladaptatus*, which are likely to contribute to carbon cycling during periods of desiccation.

## 12.5 The Coastal Fungal Microbiome

Fungi are a ubiquitous component of all ecosystems. They support the decomposition of lignocellulosic compounds (Bani et al. 2019; Francioli et al. 2020), provide industry-relevant bioactive products (Overy et al. 2019), and in vegetated habitats (e.g., coastal marshes) produce mycorrhizal networks that facilitate nutrient uptake by plants (Smith and Read 2008). In addition, through the differential accumulation of fungal pathogens, they can promote plant biodiversity and productivity (Mommer et al. 2018).

Within coastal marshes, mycorrhizal associations sustain specific interactions between plants and fungi that are beneficial to survival and growth. For example, the arbuscular mycorrhizal (AM) fungi (Phylum: Glomeromycota), which are obligate plant-root endosymbionts of most terrestrial plant species, decrease salt stress, and increase water uptake in plants growing in coastal marshes (Evelin et al. 2009). They may also decrease the impacts of localized hypoxia experienced by plant roots during tidal inundation. AM fungi play similar roles in plant nutrient acquisition (P and N uptake in exchange for plant-derived C) in coastal marshes as they do in most terrestrial habitats (Fitter 2005). The rewards to a given plant species of this symbiosis depend both on the identification of the AM fungal species present and on the soil/sediment nutrient levels (Hoeksema et al. 2010). Thus, these interactions influence plant competition dynamics at the ecosystem scale (van der Heijden 2002). In salt marshes the interaction between nutrient levels and AM fungi can influence plant zonation via changing the competitive ability of different plant species (Daleo et al. 2008), although this is less extensively studied than for terrestrial habitats. For example, in the presence of AM fungi and at low nutrient concentrations *Spartina densiflora* has a competitive advantage over *S. alterniflora* but this is reversed by increased nutrient concentrations and/or suppression of AM fungi (Daleo et al. 2008). Other fungal phyla (e.g., Basidiomycota and Ascomycota) comprise species that provide the primary route for the decomposition of vascular plant litter and the remineralization of carbon in salt marshes, although bacteria may supersede fugal decomposers under more saline conditions (Cortes-Tolalpa et al. 2018). Some specificity in fungal decomposer communities appears to be present with different fungal species decomposing different plants and being present at different geographic locations (Calado et al. 2019; Cortes-Tolalpa et al. 2018; Lyons et al. 2010). Decomposition activity shows limited spatial variability on marshes (Buchan et al. 2003) and is largely uninfluenced by changes in salinity (Connolly et al. 2014), although which fungal decomposers are present may be affected by salinity (see below). However, decomposition rates vary seasonally (Buchan et al. 2003) and related microbial activity varies across diel cycles (Kuehn et al. 2004). Invasive (non-native) plant species affect bacteria-to-fungal ratios in marshes (Zhang et al. 2018), potentially altering decomposition rates via the introduction of novel substrates. This link between decomposition and substrate type means that there is also a certain degree of top-down control on fungal saprotrophs, where the modification of the physical structure of aboveground vegetation by animal grazers can alter both recalcitrant autochthonous input and the capacity to trap less-recalcitrant allochthonous inputs of plant material (Mueller et al. 2017).

Fungal biodiversity within coastal marshes is regulated by the identity and abundance of the plant species present, tidal inundation and salinity, alongside environmental gradients in physiochemistry that covary with salinity (Alzarhani et al. 2019; Mohamed and Martiny 2011). Across three marshes of different salinity (27–33, 15–25, and 0–10 ppt) fungal species richness was predominantly influenced by the presence of plant species and less influenced by salinity and other environmental gradients (Mohamed and Martiny 2011). This most likely reflects increased heterogeneity in the microhabitats that fungi occupy and differential patterns of co-occurrence (and or host specificity) across fungi and plant species. In contrast, the community composition of fungi from the same marshes was primarily determined by the underlying salinity gradient and not by the identity of plant species present, reflecting levels of halotolerance across fungal species limiting their occurrences to marshes within their salinity tolerances (Mohamed and Martiny 2011). However, larger-scale studies examining multiple marshes ($n = 3$) in high- and low-salinity environments (33–43 and 3.3–5.9 ppt) have shown contrasting results; with abiotic factors primarily determined the patterns of fungal richness while the interaction between abiotic and biotic factors determined community composition (Alzarhani et al. 2019). Moreover, the relationship between abiotic variables and fungal species richness was not generalizable across marshes and the relative influence of abiotic and biotic factors on community composition also varied. Subsequently, statistical models relating fungal biodiversity to the abiotic and/or biotic factors on a particular salt marsh performed poorly at predicting fungal biodiversity on other marshes despite the similarities between these environments (Alzarhani et al. 2019). These context-dependencies can be attributed, among other things, to differences in the functional groups of fungi present in salt marshes where certain abiotic or biotic variables were more strongly related to specific functional groups than over others (Alzarhani et al. 2019).

In coastal marine and aquatic estuarine environments adjacent to salt marshes much less is known about the diversity and functionality of fungi. Typically, estuaries support more diverse fungal communities than coastal marine environments, which in turn are more diverse than oceanic environments (Jeffries et al. 2016). This gradient of fungal diversity reflects the flow of terrestrial matter into estuarine systems and the role of the critical transition zone between freshwater and marine systems that determines benthic biodiversity (Levin et al. 2001). Fungal turnover is highest in estuarine environments when compared to other marine systems because terrestrial, freshwater, and non-halotolerant species give way to halotolerant fungi found in near-shore environments (Burgaud et al. 2013). In coastal environments that experience extreme salt stress (e.g., hypersaline lagoons) fewer fungal species are present (e.g., *Trimmatostroma* spp., *Emericella* spp., and *Phaeotheca* spp.) and in general there are only a few known halophilic fungal species (Gostinčar et al. 2010). In the absence of terrestrial plant species with which to interact, the major functional role of fungi in these environments is the decomposition of lignocellulosic compounds and recycling of vascular plant litter (Newell 1996), alongside those that are pathogens. This also includes lignin degraders (Bucher et al. 2004), which contribute to the primary decomposition of woody debris in estuarine environments (Poole and Price 1972; Tsui and Hyde 2004). The primarily saprophytic role fungi play in estuary environments has led to them being dominated by Basidiomycota and Ascomycota (Burgaud et al. 2013; Wang et al. 2019), but with a reduction in terrestrial subsidies in coastal waters, many species of Chytridiomycota become abundant (Jeffries et al. 2016; Sun et al. 2014). Generalizing these patterns of presence of fungal phyla is problematic as the dominance of species from different phyla changes with geographic locations. For example, in the Baltic Sea, low-salinity areas (< 8 ppt) contain fungal communities compositionally similar to those in local freshwaters, but higher-salinity areas (> 8 ppt) contain fungal communities similar to those in marine systems (Rojas-Jimenez et al. 2019). However, in these locations Basidiomycota and Ascomycota dominate in the marine environment and Chytridiomycota in freshwaters (Rojas-Jimenez et al. 2019). It is also worth noting that DNA sequences from Glomeromycota (AM fungi) have been detected during surveys in near-shore fungal communities, which if they originate from spores suggests a previously underexplored dispersal route (Lacerda et al. 2020). Given the important role of fungi in degrading complex organic material close species–species interactions and biogeochemical coupling between the fungal and algal, bacterial, and archaeal constituents are expected in coastal sediment biomes. These questions are currently unanswered.

## 12.6 Impacts of Oil Pollution on Coastal Microbiomes

An estimated 1.3 million tons of oil enters the marine environment each year (National Research Council 2003). This includes oil from natural seeps and spills associated with the extraction and transportation of petroleum (e.g., tanker, pipeline, and coastal facility spills). The largest offshore oil spill in history was The Deepwater Horizon spill resulting from the Macondo well blowout that resulted in the release of 134 million gallons of crude oil into the Gulf of Mexico. Despite the deposition of large quantities of oil in deep water systems, or being biodegraded, chemically dispersed, or burned in situ, large quantities of oil still reached coastal ecosystems and contaminated 2100 km of coastline. This pollution caused serious negative effects on marine life and coastal saltmarsh, seagrass, and reef systems (Beyer et al. 2016). Many coastal environments are particularly vulnerable to oil spills because many oil refineries are situated at the coast or at large estuaries. The majority of the 20 largest oil tanker spills to date also occurred close to the coast when tanker vessels ran aground (ITOPF 2019). Oil spills have major effects on coastal ecosystems such as mass mortality of invertebrates, birds and mammals. For example, the Prestige oil spill caused a decrease of 66% of total species richness on Spanish Galician beaches (de La Huz et al. 2005) and the Exxon Valdez spill on the Alaskan coast caused major sea otter (Monson et al. 2000) and seabird (Piatt and Ford 1996) mortalities. Oil can also have toxic effects on microorganisms because the accumulation of hydrocarbon molecules in the membrane can result in loss of membrane integrity and impaired cellular homeostasis (Sikkema et al. 1995). This can have major impacts on key microbial ecosystem services such as coastal nitrogen cycling (Horel et al. 2014; Zhao et al. 2020). For example, some ammonia-oxidizing bacteria and archaea are, respectively, 100 and 1000 times more sensitive to hydrocarbon toxicity than model heterotrophs (Urakawa et al. 2019). Whilst large oil spills are thankfully rare, coastal ecosystems are threatened continually with chronic oil and hydrocarbon pollution from rivers and land runoff (National Research Council 2003) and intensive industrial and recreational activities around coasts particularly near estuaries and harbors (Duran et al. 2015; McGenity 2014; Nogales and Bosch 2019).

Crude oil contains a complex mix of hydrocarbons that includes saturated aliphatic hydrocarbons such as cycloalkanes, linear *n*-alkanes (ranging from short chains to long chains with over 40 carbon atoms), and branched alkanes such as pristine and phytane (Weisman 1998). There are also many aromatic hydrocarbons such as the monoaromatic BTEX compounds (benzene, toluene, ethylbenzene, and xylene) and polyaromatic hydrocarbons that include a wide range of both parent and methylated 2- to 5-ring compounds such as naphthalenes, phenanthrenes, pyrenes, and perylenes. In addition to these two main classes of hydrocarbons there is a variety of large and highly recalcitrant asphaltene and resin compounds. Whilst certain processes remove some components of oil from the environment (e.g., evaporation of the lighter fractions, chemical- or photo-oxidation), unless oil is physically removed, the primary loss route will be via natural biodegradation by hydrocarbon-degrading microbes that utilize hydrocarbons as their carbon and energy source (Harayama et al. 1999; Head et al. 2006; McGenity et al. 2012). Because of the complexity of oil, its biodegradation requires a diverse consortium of species that can degrade different hydrocarbons. There is niche partitioning between the different species in the consortium in the utilization of different hydrocarbon substrates (Head et al. 2006; McGenity et al. 2012; McKew et al. 2007).

### 12.6.1 Diversity of Hydrocarbon-Degrading Microbes in Coastal Sediments

High concentrations of hydrocarbons can dramatically alter the composition of coastal microbial communities leading to large decreases in species richness and diversity coupled with the selection for specialist hydrocarbon-degrading bacteria (Head et al. 2006; McGenity et al. 2012). In estuarine and coastal sediments hydrocarbons are particularly used by Alpha- and Gammaproteobacteria (Chronoupolou et al. 2013; Coulon et al. 2012; Greer 2010). The selection for specific bacterial species may be influenced by numerous factors including the concentration or type of oil and/or its degree of weathering (Head et al. 2006) or environmental conditions such as temperature or the concentration of key nutrients such as nitrogen and phosphorus (Coulon et al. 2007). However, many common patterns are observed globally, such as an increase in the relative abundance of obligate hydrocarbonoclastic bacteria (OHCB; Yakimov et al. 2007) in oxygenated oil-contaminated marine sediments. The OHCB include key genera such as *Alcanivorax*, *Thalassolituus*, *Oleiphilus*, *Oleispira*, and *Oleibacter*, which typically degrade alkanes as well as *Cycloclasticus,* which degrade a wide range of PAHs. The name "OHCB" is a slightly misleading because these organisms are not truly "obligate." For example, in pure culture *Alcanivorax* degrades some other compounds (Radwan et al. 2019) and also some polyesters (Zadjelovic et al. 2020). However, there is still very limited evidence that the OHCB are competitive for non-hydrocarbon substrates in the environment and their lifestyle is often restricted to the use of hydrocarbons or their fatty acid or alcohol derivatives. The OHCB are often in low abundance in marine environments when hydrocarbons are absent but respond quickly and grow rapidly in response to oil pollution. Their streamlined genomes are specifically geared toward a hydrocarbon-degrading lifestyle (Kube et al. 2013; Schneiker et al. 2006; Yakimov et al. 2007) and their marine distribution is truly global (Yakimov et al. 2007). In muddy and sandy coastal sediments, OHCB such as *Alcanivorax, Oleibacter, Cycloclasticus*, and *Marinobacter hydrocarbonoclasticus* tend to increase in abundance and often dominate the bacterial community after the addition of crude oil (Chronoupolou et al. 2013; Coulon et al. 2012; Kostka et al. 2011; Thomas et al. 2020).

*Alcanivorax borkumensis* (Yakimov et al. 1998), a specialist *n*-alkane and branched alkane degrader, was first isolated from North Sea sediments and was the first OHCB to have its genome sequenced (Schneiker et al. 2006). Since its discovery 14 named species and a large diversity of unclassified *Alcanivorax* have been recorded in the NCBI database, including species isolated from deep sea sediments such as *A. dieselolei* (Liu and Shao 2005), *A. pacificus* (Lai et al. 2011), and *A. mobilis* (Yang et al. 2018), or from intertidal sediments such as *A. jadensis* (Fernandez-Martinez et al. 2003) and *A. gelatiniphagus* (Kyoung Kwon et al. 2015). *Alcanivorax* is often dominant in oil-contaminated intertidal sediments globally, including in the Gulf of Mexico, in the Atlantic Galician coast, and in Mediterranean beaches following the Deepwater Horizon (Newton et al. 2013; Rodriguez-R et al.

2015), Prestige (Acosta-González et al. 2015), and Agia Zoni (Thomas et al. 2020) oil spills, respectively.

Another key alkane degrader in intertidal sediments is *Thalassolituus*, the type strain of which was isolated from harbor seawater/sediment samples in Milazzo, Italy (Yakimov et al. 2004). *Thalassolituus* is a highly competitive *n*-alkane degrader in estuarine environments and mudflats (McKew et al. 2007; Sanni et al. 2015) but is also found globally including deep water environments such as the oil plume from the DWH oil spill in the Gulf of Mexico (Camilli et al. 2010). *Oleibacter* related to the type strain *O. marinus* 201 (Teramoto et al. 2011) or a variety of unclassified strains is important in coastal fine-grained (Chronoupolou et al. 2013; Coulon et al. 2012; Sanni et al. 2015) and sandy (Thomas et al. 2020) sediment communities. However, like *Alcanivorax* and *Thalassolituus, Oleibacter* species are not specific to oil-degrading communities within coastal sediments as they (along with many other oil-degrading bacteria) are also found in a variety of marine environments, including for example seawater at 10,400 m in the Challenger Deep at the southern end of the Mariana Trench (Liu et al. 2019). This suggests that it is the availability of hydrocarbon that selects for oil degraders rather than the specific environmental conditions themselves. Low temperature often results in the selection for *Oleispira*. Bacteria closely related to the psychrophilic alkane-degrading *Oleispira antarctica* (Gregson et al. 2020; Kube et al. 2013; Yakimov et al. 2003) are important in oil-contaminated temperate coastal microbial communities at winter temperatures (4 °C) (Coulon et al. 2007), as well as in cold environments such as deep arctic sediments (Dong et al. 2015) and sea-ice (Gerdes et al. 2005).

*Cycloclasticus* often plays the primary role in PAH degradation in coastal environments (Chronoupolou et al. 2013; Coulon et al. 2012; Duran and Cravo-Laureau 2016; Kasai et al. 2002; McKew et al. 2007; Sanni et al. 2015; Thomas et al. 2020). This genus comprises a wide variety of PAH-degrading species, including *C. pugetii* (Dyksterhouse et al. 1995), *C. oligotrophus* (Wang et al. 1996), *C. spirillensus* (Chung and King 2001), and *C. zancles* (Messina et al. 2016). There is a bivalve- and sponge symbiont lineage that can also degrade short-chain alkanes (Rubin-Blum et al. 2017).

In addition to these specialist hydrocarbon-degrading genera there are many other species from more nutritionally versatile genera that degrade hydrocarbons and many are regularly found in oil-polluted coastal sediments. There are too many to consider here but they include, for example, species from genera such as *Marinobacter* (particularly *Marinobacter hydrocarbonoclasticus* (Gauthier et al. 1992)), *Alteromonas*, *Erythrobacter, Idiomarina, Microbacterium, Psuedomonas, Pseudoalteromonas, Rhodococcus, Roseovarius, Shewanella, Sphingomonas, Vibrio*, and *Xanthomonas* (e.g. see Prince et al. (2018) for a review of all hydrocarbon degraders, Goñi-Urriza and Duran (2018) for the role of bacteria in hydrocarbon degradation in coastal microbial mats, Greer (2010) for a review of bacterial diversity in hydrocarbon-polluted estuaries and sediments, and Supplementary Table 12.1 in Thomas et al. (2020) for many such observations in sandy coastal sediments).

Whilst aerobic biodegradation of hydrocarbons dominates in sediments, those that become buried in anoxic sediments can remain there for decades (Reddy et al. 2002) as anaerobic biodegradation of hydrocarbons is slow in comparison with aerobic biodegradation. Aerobic hydrocarbon degraders rely on oxygen not only for respiration; oxygen is also required for the primary step of hydrocarbon degradation catalyzed by oxygenase enzyme systems (Wang and Shao 2013; Wang et al. 2018). Consequently, anaerobic bacteria must employ alternative pathways of biodegradation in the absence of oxygen. Due to the abundance of sulfate in coastal sediments many of the known anaerobic hydrocarbon oxidizers in coastal sediments are sulfate-reducing bacteria related to *Desulfosarcina*, *Desulfococcus*, *Desulfonema*, *Desulfobacula*, *Desulfotomaculum*, *Desulfotignum*, and *Geobacter* (McGenity 2014; Païssé et al. 2008; Rabus et al. 2016). Also, marine sediments are subjected to oscillations in oxygen concentration as the result of the tides, burrowing, and oxygenic phototrophic activity, which can encourage the growth of certain phylotypes of *Alcanivorax* (Terrisse et al. 2017).

The relative abundance of genera with potential hydrocarbon-degrading abilities can be used to estimate hydrocarbon exposure in an environment using the Ecological Index of Hydrocarbon Exposure (Lozada et al. 2014), which is based on microbial composition determined by 16S rRNA gene sequencing, as the numbers of hydrocarbon-degrading bacteria typically correlate with the concentration of hydrocarbons in sediments (Thomas et al. 2020).

### 12.6.2 Association of Hydrocarbon-Degrading Bacteria with Photoautotrophs

Many hydrocarbon-degrading bacteria in intertidal sediments have close association with photoautotrophs. Hydrocarbons can alter the composition of phototrophic communities considerably, for example, by inhibiting enzyme activities and photosynthesis (Megharaj et al. 2000). This toxicity may favor hydrocarbon-resistant species. For example, cyanobacteria belonging to *Phormidium, Planktotrix*, and *Oscillatoria* have shown varying degrees of tolerance to oil pollution (Van Bleijswijk and Muyzer 2004). In sediment mesocosms with oil-polluted fine-sediments that were dominated with the hydrocarbonoclastic bacteria *Alcanivorax*, *Cycloclasticus*, and *Oleibacter,* there was also an increased abundance of MPB, primarily due to a ten-fold increase in the abundance of cyanobacteria (Chronoupolou et al. 2013; Coulon et al. 2012). This increase was attributed to a lower grazing pressure and/or nitrogen depletion, which encouraged the growth of diazotrophic cyanobacteria. Some microalgae coexist with hydrocarbon-degrading bacteria (Amin et al. 2009; Chernikova et al. 2020; Gutierrez et al. 2013) and diatom-OHCB floating biofilms have been seen in mudflat sediments after an experimental oil spill (Coulon et al. 2012). There are numerous hypothesized ways that phototrophs enhance hydrocarbon degradation including direct degradation (although evidence for this is limited), supplying key resources (e.g., oxygen, N, Fe) to hydrocarbon-degrading bacteria, or assisting in immobilizing hydrocarbon-degrading bacteria within EPS. Phototrophs in turn can benefit from higher $CO_2$ concentrations from hydrocarbon-degrading bacterial respiration (e.g., see reviews by Abed 2019; Ardelean 2014; McGenity 2014; McGenity et al. 2012).

### 12.6.3 Mechanisms of Oil Biodegradation

Generally, the bioavailability and rate of degradation of hydrocarbons decreases with increasing carbon number. Saturated hydrocarbons are often degraded at higher rates than light aromatics. The high-molecular-weight aromatics and polar compounds are degraded at low rates (Leahy and Colwell 1990). Most hydrocarbon-degrading bacteria will typically degrade a small range of either aliphatic or aromatic compounds, although some bacteria may possess pathways for catabolism of both aliphatic and PAH compounds such as some *Pseudomonas* (Whyte et al. 1997), *Rhodococcus* (Andreoni et al. 2000), or *Colwellia* (Mason et al. 2014) strains. Uptake via transport systems lowers the substrate concentration around the cell driving diffusive flux of hydrophobic hydrocarbons toward the cell (Harms et al. 2010), whilst the production of extracellular or cell-bound surface-active compounds (e.g., glucolipid biosurfactant produced by *Alcanivorax* (Yakimov et al. 1998)) increases bioavailability by decreasing the interfacial tension between water and oil (Marchant and Banat 2012). Aerobic hydrocarbon-degrading bacteria are equipped with a wide array of genes that code for monooxygenase enzyme systems to activate hydrocarbons such as the two integral-membrane non--heme iron alkane monooxygenase systems AlkB1 and AlkB2 and three heme-containing P450 cytochromes employed by *Alcanivorax* (Gregson et al. 2019; Schneiker et al. 2006; Yakimov et al. 1998) that convert medium-chain *n*-alkanes or branched alkanes to a primary alcohol that can be further degraded by an array of alcohol- and aldehyde dehydrogenases. Long-chain alkanes can be biodegraded with AlmA flavin-binding monooxygenases (Wang and Shao 2014) or similar sub-terminal Baeyer-Villiger monooxygenases in *Thalassolituus oleivorans* (Gregson et al. 2018). Dioxygenase systems are typically employed by aerobic PAH-degraders such as the PhnA1, PhnA2, PhnA3, and PhnA4 proteins (alpha and beta subunits of an iron-sulfur protein, a ferredoxin and a ferredoxin reductase, respectively) that make up a PAH dioxygenase system in *Cycloclaticus* strain A5 (Kasai et al. 2003).

Fine-grained intertidal sediments such as mudflats are typically anoxic below 1–2 mm. This prevents the activation of hydrocarbons using oxygenase enzymes. The exact mechanisms of the anaerobic activation of hydrocarbons are less well understood but may include direct carboxylation, methylation followed by addition to fumarate, or even utilization of nitrite to activate alkanes (McGenity et al. 2012; Meckenstock and Mouttaki 2011; Rabus et al. 2016; Widdel and Musat 2010; Zedelius et al. 2011).

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