Chapter 12
Shorebirds as Integrators and Indicators of Mudflat Ecology

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Contents

Abstract Shorebirds are major, but thus far under-acknowledged, players in mudflat food webs and associated physio-chemical processes. Mud is a critical habitat

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type for shorebirds, offering a multi-dimensional matrix of feeding opportunities through space and time. Shorebirds have evolved a spectrum of foraging modes with associated morphologies, and sensory and physiological adaptations which exploit these foraging opportunities. Although shorebirds are mud specialists and sentinels of mudflat ecosystem functioning, they have not yet been well integrated into the "mud club". In this chapter, we highlight the key roles shorebirds play in food webs, and in physical and chemical processes within mudflat ecosystems. We illustrate how shorebird distribution and behaviour provides a mirror of mudflat ecology because their foraging behaviour reflects the underlying ecological conditions, including temporal and spatial patterns in food/community structure in and across mud. In particular, shorebirds may be important indicators of essential fatty acid production by diatoms in epibenthic biofilm fields covering muddy intertidal flats, especially in estuaries. We conclude by highlighting the major challenges facing shorebirds today and call for a paradigm shift in shorebird conservation, based on recreating and restoring intertidal mud ecosystems.

1 Introduction

In this chapter, we will discuss the role of shorebirds, or waders (order Charadriifomes) in mudflat ecology. Exposed intertidal mudflats provide critical habitat for shorebirds for roosting, and more particularly, for foraging. Spectacular numbers of shorebirds congregate on mudflats at different stages in their annual cycles, with many mudflats and estuaries supporting >100,000 shorebirds annually (Fig. 12.1).

Mudflats are important feeding areas to shorebirds for various reasons. Mudflats tend to be productive, offering a wide diversity and high abundance of potential food. In addition, mudflats remain accessible in winter, even after interior wetlands at similar latitudes have become inaccessible, both due to the lower freezing point of sea water, and the relatively warmer ambient temperatures in coastal compared to inland areas (Warnock et al. 2002).

As has been repeatedly demonstrated in this book, while mudflats appear deceptively simple, uniform and barren from the shore, the realities of mud are physically, chemically and biologically complex. The biotic communities of mudflats populate a three-dimensional mosaic subjected to alternating periods of exposure and inundation by tides in addition to seasonal cycles (Whitlatch 1977; Martini and Wanless 2014). Tides limit shorebird distributions by making areas of mudflat inaccessible during flood and ebb tides every lunar day (24 h 50 min), and also shape shorebird distributions through their effects on the distribution of food (see Chaps. 5, 6 and 8). In this chapter, we will discuss the central role of shorebirds in mudflat ecosystems, including their role as primary consumers of intertidal epibenthic biofilms (Kuwae et al. 2008, 2012).

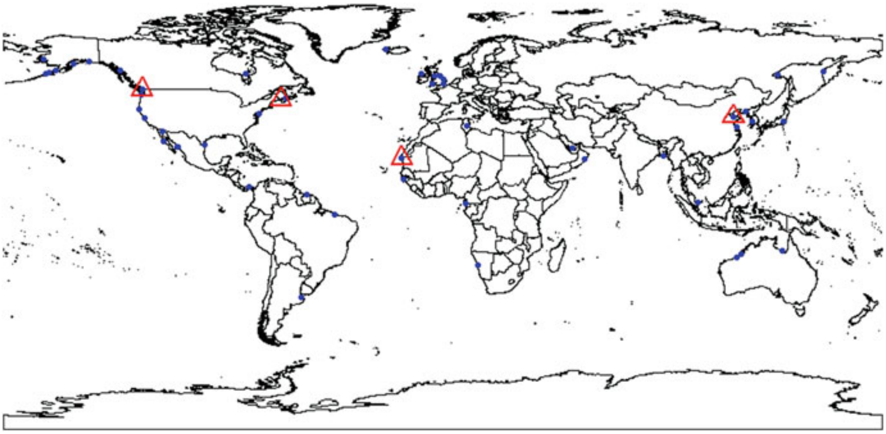

Fig. 12.1 Mudflats that annually host >100,000 shorebirds illustrated with solid blue circles. Data taken from summary Table in Butler et al. (2001). The four study areas highlighted as case studies are indicated with red open triangles. Map created in R v3.3.3 (R Development Core Team 2017) using the 'rworldxtra' library.

2 Shorebird Foraging Modes and Diets

Shorebirds that forage on intertidal mudflats face the challenges of locating and extracting food at sufficient rates, without ingesting excessive amounts of sediment within a tidal cycle. Several broad categories of foraging mode have been described, with individual species usually exhibiting more than one mode, depending on habitat, season and prey availability (van de Kam et al. 2004; Colwell 2010). Epifaunal prey visible on the surface are captured by *pecking* (Zweers and Gerritsen 1997), while prey suspended in shallow water are taken up the bill via *surface tension transport* (Rubega 1997) or *bill sweeping* (Moreira 1995; Barbosa and Moreno 1999). Shorebirds can capture buried prey by *probing* their bills into the sediment (Zweers and Gerritsen 1997). These modes each target a range of invertebrate taxa and sometimes the rhizomes of marine plants such as seagrasses (Robin et al. 2013). The fifth, most recently discovered foraging mode, *biofilm grazing*, targets an entirely distinct food source at the base of the food chain that was previously thought accessible only to invertebrates and fish (Kuwae et al. 2008, 2012).

2.1 Functional Morphology, Digestion and Physiology

For shorebirds, life on mudflats is associated with a suite of morphological and physiological adaptations. Shorebirds are characterized by having relatively long, slender legs compared to other birds (Johnsgard 1981; Barbosa and Moreno 1999), which allow them to wade while foraging without wetting their body feathers. In general, shorebird feet exhibit a similar arrangement of toes, with three forward facing digits and one backward facing digit, and many species exhibit partial or complete webbing between the toes (Johnsgard 1981). Both of these foot characteristics facilitate walking on mudflat surfaces but do not appear to be associated with particular foraging modes (Barbosa and Moreno 1999).

Other aspects of morphology (e.g., body size, eye size and placement, bill and tongue structure) and physiology (e.g., digestive organ size, enzyme activities) show clear associations with the specific foraging modes described in the previous section (Table 12.1). Shorebirds specialized in visual hunting of surface or shallowly buried prey (e.g., Charadriidae, see Fig. 12.2) tend to have short bills, and large, frontally positioned eyes with high visual acuity and a broad binocular field (Martin 2007). In comparison, shorebirds that forage on buried prey (e.g., Scolopacidae) cannot locate prey by sight. Their eyes are set higher in the skull, resulting in a narrow binocular field and maximizes their ability to detect approaching predators (Martin and Piersma 2009). Also, their bills are longer, more robust (Martin and Piersma 2009), and contain receptors (Herbst and Grandry corpuscules) that can detect changes in pressure, and are used to locate invertebrates within the sediment (Gerritsen and Meiboom 1986). Some probing foragers specialize on ‘soft’ food items, such as lugworms, while others may specialize on ‘hard’ food items, such as molluscs (van de Kam et al. 2004; Colwell 2010). Red knots, *Calidris canutus*, are particularly specialized in locating small hard objects in wet soft sediments by sensing the deviations from a spherical pressure field built up around a probing bill (Piersma et al. 1998; de Fouw et al. 2016). Molluscivoran shorebirds that swallow their prey whole, such as red knots, possess large, muscular digestive organs (e.g., the gizzard, a muscular stomach), effective in both crushing shells and processing large volumes of indigestible materials (Piersma et al. 1993; Battley and Piersma 2005b).

In contrast to the morphological adaptations for shorebirds foraging on invertebrates, epibenthic biofilm feeding depends primarily on tongue microstructure rather than bill macrostructure. Intertidal epibenthic biofilm is a thin, matrix-enclosed community of microphytobenthos (MPB), bacteria, and organic detritus bound together and adhered to the sediment surface by copious amounts of extracellular polymeric substances (EPS) (Stal 2003; Underwood and Paterson 2003, and see Chaps. 2, 3, 4, 5, 8 and 10). Diatoms within the biofilm afford easily digestible energy as well as a rich source of omega-3 fatty acids, particularly in their blooming phase (Duerksen et al. 2014; Stonik and Stonik 2015). Keratinized lateral spines coated in mucus along the edges and at the tip of the shorebird tongue are used to rapidly dab biofilm off the sediment surface, while backwardly-directed maxillary denticles on the tongue prevent biofilm boli from slipping forward out of the bill (Elner et al. 2005). Biofilm feeding appears most prevalent in “peeps” (Kuwae et al. 2008; Beninger et al. 2011; Quinn and Hamilton 2012; Jiménez et al. 2015), the smallest of the shorebirds, and in stints (Lourenço et al. 2017), but all shorebirds, including plovers, appear functionally able, and likely, to graze biofilm (Kuwae et al. 2012). Because biofilm is an easily digested food source (Duerksen et al. 2014; Stonik and Stonik 2015), large digestive organs are not a prerequisite (Kuwae et al. 2012). However, biofilm feeders likely require specific enzymes to process

Table 12.1 Overview of morphological and physiological adaptations associated with principle foraging modes, associated food types and representative shorebird species

Foraging mode	Body size	Search mode	Morphological adaptations	Physiological requirements	Diet	Representative shorebirds
Biofilm grazing	Small	Visual or gustatory	Short bill, spines on tongue	Enzymes for processing omega-3 fatty acids	Biofilm, diatoms, meiofaunal prey suspended in biofilm matrix	Peeps and stints
Pecking		Visual	Large, proximally placed eyes short bill		Epifaunal invertebrates, wide range of sizes	Plovers
Probing	Medium to large	Tactile	Long, robust bill with sensory pits	Large digestive organs	Infaunal invertebrates, large size	Medium to large sized sandpipers (red knots, curlews, whimbrels, etc)
STT		Visual	Needle shaped bill			Phalaropes, avocets

Where there are not specific adaptations required for effective use of a foraging mode, the cell is left blank. Surface tension transport (STT) requires little specialized morphological adaptation, and is therefore likely used opportunistically by a variety of shorebirds

Fig. 12.2 Ringed plovers (here capturing a polychaete) exhibit the typical morphology of visual foargers; large, frontally located eyes and short bills. Photo by Jan van de Kam.

Fig. 12.3 An avocet with prey enveloped in a water droplet at the tip of the bill. Photo by Jan van de Kam.

the omega-3 fatty acids that comprise a major component of diatomaceous biofilms (Duerksen et al. 2014; Stonik and Stonik 2015).

Although there has not been a detailed cataloguing of shorebird species that use surface tension transport to move small prey items up the bill, this foraging mode is commonly used in phalaropes and avocets (Rubega and Obst 1993; Rubega 1997) (see Fig. 12.3). Surface tension transport requires only the ability to modulate gape size, and a needle-shaped bill. The needle-shaped bill results in an increase in contact area and reduction in the free surface area of water drops in a proximal to distal direction along the bill, which facilitates the transport of droplets up the bill (Rubega and Obst 1993; Rubega 1997). As this bill shape is almost universal among shorebirds, surface tension transport is likely also widespread (Rubega 1997), and may represent an opportunistic foraging mode as opposed to a true specialization.

2.2 Flexible Foragers

The morphological and physiological adaptations required by the alternative foraging modes and diets do not constrain shorebirds to any single mode. Seasonal shifts in foraging mode and diet occur as a result of changes in the availability of alternative food types (Beukema et al. 1993) as well as fluxes in the demand for particular nutrients. Red knots (*Calidris canutus islandica*) are an excellent example of such foraging plasticity across their annual cycle. Red knots feed primarily on hard-shelled molluscs during the non-breeding season in the Dutch Wadden Sea in Northwestern Europe and, consequently, have large digestive organs including the gizzard, which process these prey (Battley and Piersma 2005a). However, during the breeding season in the Canadian High Arctic, they feed on superabundant arthropod prey, which are of higher digestive quality. Consequently, their gizzards atrophy, becoming a fraction of their winter gizzard mass (Vézina et al. 2012). On return to the non-breeding grounds in late summer, peaks in the availability of the common shrimp (*Crangon crangon*), a high quality food item, allow red knots to continue pecking for surface prey and to maintain relatively small digestive organs until autumn, when the availability of these prey types decline and knots resume feeding on low digestive quality bivalves (van Gils et al. 2005).

Western sandpipers (*Calidris mauri*) also exhibit a high degree of flexibility in the use of alternative foraging modes and diets (Elner and Seaman 2003). Females, the longer-billed sex, have a higher use of probing compared with males (Mathot and Elner 2004), and also winter in more southerly regions where buried prey are relatively more abundant (Mathot et al. 2007). Yet in both males and females, epibenthic biofilm grazing peaks during northward migration at stopovers such as the Fraser River Delta, British Columbia (Beninger et al. 2011) (see also Sect. 4 in Chap. 8). This peak in biofilm use coincides with a period in the annual cycle of migrant shorebirds when deposition of nutrient stores (both fat and protein) is critical for making long-distance flights between successive stopover sites (Piersma et al. 2005; Guglielmo 2010).

3 Shorebirds as Sentinels

Shorebirds depend on mudflats, and exhibit a suite of morphological and physiological adaptations which aid in efficiently locating and exploiting the foods mudflats have to offer [see above and review in van de Kam et al. (2016)]. Given their evolved relationship with mudflats, what, if anything, can careful observation of habitat use and foraging decisions by shorebirds teach us about mudflats? It turns out, quite a bit.

3.1 Shorebird Distributions

Shorebirds integrate information on multiple fitness-relevant parameters when selecting habitat, including the distribution and abundance of food, predators, and competitors (Piersma and Lindström 2004; Escudero et al. 2012). This occurs on 'contemporary' time scales, yet current shorebird distributions may also reflect competitive processes that have their origin in 'deep time' (Bom et al. 2018). With a solid understanding of their biology, the distribution of shorebirds can provide clues about the positioning of these factors (Piersma and Lindström 2004). For example, global patterns of shorebird distributions may provide a coarse proxy for global patterns of mudflat productivity (Butler et al. 2001). Mudflats require particular combinations of geological, physical and chemical conditions to form (see Chap. 2), and there are some seventy-nine intertidal mudflat areas worldwide with surface areas of over 5000 hectares (Deppe 1999). However, shorebirds are not found in equal densities across all available mudflats. Shorebirds are generally found in areas where species-specific food availability is highest, moderated by additional factors such as their own risk of predation by falcons (Zwarts and Wanink 1993; Ydenberg et al. 2002; van de Kam et al. 2004; Quaintenne et al. 2011; Piersma 2012).

Within sites, the behaviour and distribution of shorebirds also provide clues about local conditions (Folmer et al. 2012; Folmer and Piersma 2012). For example, the use of different zones in the intertidal reveals information about the distribution of food resources in general, and differences in the distributions of shorebirds known to specialize on different types of prey provide clues about differential distributions of prey types (Duijns et al. 2014, 2015; Bijleveld et al. 2016).

As mudflats are tidally-structured environments, shorebirds can only feed when the mudflats become exposed and accessible to foraging. Some shorebirds, such as dunlin (*Calidris alpina*) or redshank (*Tringa totanus*), will begin feeding almost the moment the upper intertidal area begins to be exposed, while other shorebirds, such as oystercatchers (*Haemotopus ostralegus*) and curlew (*Numenius arquata*), tend to wait longer on the falling tide before beginning feeding (van de Kam et al. 2004). Readers with some knowledge about shorebirds will realize that dunlin and redshank are small shorebirds, while curlew and oystercatcher are large, and as detailed above, smaller birds eat smaller prey. The timing of feeding of small shorebirds relative to large shorebirds on the falling tide reflects the spatial distribution of their preferred prey (van de Kam et al. 2004; Piersma et al. 2017), as well as limitations in their ability to access prey at different times based on their morphology (e.g., leg and bill length) and water depth. The larger prey preferred by oystercatchers and curlews occur mainly low in the intertidal zone, while the most important food for small shorebirds such as dunlin and redshank are found higher in the intertidal area.

The movement of shorebirds across the intertidal areas as they become exposed, also integrates information on the distribution of resources. However, food is not the only factor shaping foraging decisions. Shorebirds must also avoid predators. For many shorebirds, the upper intertidal area is the most dangerous during daytime

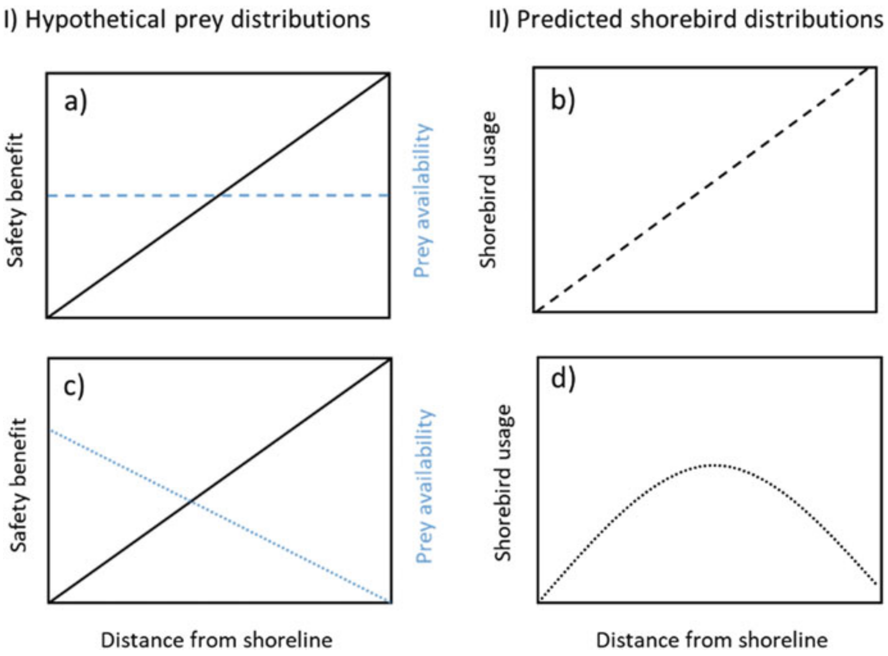

Fig. 12.4 Two hypothetical scenarios of food distribution along the intertidal (**a**, **c**) and the consequences for predicted shorebird distributions (**b**, **d**) if shorebirds are balancing food and safety. The first scenario (**a**), with a homogenous distribution of prey relative to the location in the intertidal predicts shorebird distributions to mirror the safety (**b**), while the second scenario, where prey abundance decreases with increasing distance from the shoreline (**c**), predicts a peak in shorebird use at intermediate distances from the shore (**d**).

foraging, because common shorebird predators, notably peregrine falcons (*Falco peregrinus*), sparrowhawks (*Accipiter nisus*) and merlin (*Falco columbarius*), have the greatest attack success when they are able to fly low over marsh vegetation, concealing their approach (Page and Whitacre 1975; Lazarus and Symonds 1992; Cresswell 1993; Dekker and Ydenberg 2004; Quinn and Cresswell 2004; van den Hout et al. 2014, 2017). If predation danger declines moving down the intertidal zones, we can predict how shorebirds should use the mudflat under different scenarios of resource distribution (Fig. 12.4). If appropriate-sized prey are distributed homogenously across the intertidal, then shorebirds would be expected to follow the tide as it moves out, because they can reduce predation danger without any reduction in food availability. Alternatively, if prey abundance is higher in the upper intertidal, for example because of differences in sediment characteristics or nutrient availability, then shorebirds would face a conflict between following the tide (minimizing predation risk), and remaining in the upper intertidal (maximizing intake rates), and they would be expected to show a peak intensity of mudflat use reflecting a compromise between avoiding predation and gaining energy (Pomeroy 2006; Fuller et al. 2013; but see also Jiménez et al. 2015).

Obtaining an overall estimate of mudflat use is challenging when intertidal areas are so vast as to make it impossible to perform simultaneous shorebird counts across the full intertidal zone. Nevertheless, just as distribution of shorebirds can be used to infer local resource conditions, the density of shorebird droppings can be used to infer the intensity of use of different zones in the intertidal area. Pomeroy (2006) found that shorebird droppings showed a peaked distribution in the mid-intertidal, consistent with the scenario where food abundance declined with distance from the upper intertidal. The invertebrate resource distribution was later confirmed to decline from the upper to lower intertidal, via benthos sampling (see Fig. 1 in Pomeroy 2006).

If the distribution and behaviour of shorebirds within- and across mudflats reflects current ecological conditions, then it follows that long-term changes in their distribution and/or behaviour may reflect long-term changes in ecological conditions. Given our knowledge of the factors driving variation in shorebird numbers, behaviour, morphology, and physiology, shorebirds may also serve as sentinels of changing conditions (Piersma 2003; Piersma and Lindström 2004; Kraan et al. 2009). We illustrate this notion with two examples.

3.2 Shorebirds as Indicators of Local Prey Changes

When shorebirds are highly specialized on particular prey resources at a site, changes in the availability of that resource may be mirrored by changes in the abundance of shorebirds at those sites. For example, the overexploitation of horseshoe crabs by humans resulted in catastrophic declines in the *rufa* subspecies of red knot (*Calidris canutus rufa*), which are highly dependent on lipid-rich horseshoe crab eggs while on stopover in Delaware Bay (USA) to refuel during their northward migration (Myers 1986; Baker et al. 2004; Niles et al. 2009). Similarly, declines in the abundance of shellfish in the UK and The Netherlands caused by local shellfisheries were associated with declines in molluscivore shorebirds (Piersma 2007; Kraan et al. 2009; Atkinson et al. 2010; van Roomen et al. 2012). At the same time, polychaete abundances increased, which was correlated with increases in the abundance of worm-eating waders (van Roomen et al. 2012).

In another example, the initiation of a baitworm harvesting industry in the Bay of Fundy, Canada, resulted in dramatic changes in foraging efficiency in semipalmated sandpipers, via its effects on non-target species in the community (Shepherd and Boates 1999). Areas of sediment that were disturbed by baitworm harvesting had 39% lower densities of *Corophium volutator* compared with undisturbed areas of sediment, and juvenile *C. volutator* were most strongly affected. This translated to a nearly 70% lower rate of capture of *C. volutator* by foraging semipalmated sandpipers, suggesting that the disturbance of sediment during baitworm harvesting may have additionally interfered with the use of visual and tactile cues (Shepherd and Boates 1999). Changes in the abundance and distribution of invertebrates, with concomitant shifts in shorebird abundances have also been documented in response to eutrophication (Alves et al. 2012) and the presence of pollutants (Furness 1993).

3.3 Shorebirds as Integrated Sentinels of Global Change

It is important to recognize that local changes in shorebird abundance or behaviour do not necessarily reflect changes in local conditions. Many shorebirds cover large areas of the globe over the course of their annual migratory cycle, and changing conditions at any one location could have cascading effects throughout their distribution. Perhaps the most striking example of shorebirds as integrated sentinels of global change comes from long-term studies of red knots at a major non-breeding site, the Banc d'Arguin, Mauritania.

The *canutus* subspecies of red knot (*Calidris canutus canutus*) has been studied intensively on the Banc d'Arguin for over 30 years. Red knots feed primarily on molluscs during the non-breeding season, which they consume whole and crush in their muscular gizzards (Battley and Piersma 2005a). On the Banc d'Arguin, the two principal molluscs making up their diet are *Dosinia isocardia* and *Loripes lucinalis* (see also Sect. 5.2). As part of a long-term research program aimed at monitoring the relative consumption of these two prey types, blood samples were collected over a period of 12 years and stable isotope analyses were used to infer diet. Unexpectedly, the analyses revealed that red knots were consuming rhizomes of the seagrass *Zostera noltii* and further that the relative contribution of seagrass to the diet was increasing across years (van Gils et al. 2016). More intriguingly, benthos sampling programs suggested that bivalve prey abundances were stable over the same time period. If local conditions on the Banc d'Arguin weren't driving the shift in diet, what was?

In fact, the changing diet of knots in Mauritania appears to be a cascading consequence of warming Arctic temperatures (van Gils et al. 2016). Red knots breed in the High Arctic. They arrive in early spring and must wait until after snowmelt to initiate their nests. Over the last 30 years, the date of snowmelt has advanced by an average of 0.5 days per year. Knots have simultaneously advanced the timing of their northward migration to the breeding grounds, but at only half the rate of the advancing snow melt (0.25 days per year on average) (van Gils et al. 2016). Consequently, knots are breeding later relative to snow melt dates, which may be contributing to a mismatch between the timing of chick hatching and the timing of invertebrate emergence (i.e., trophic mismatch). Such phenological mismatches have been proposed to result in decreased body size, due to organisms receiving suboptimal nutrition during their periods of most rapid growth. Indeed, knots have also decreased in body size, and more importantly, in bill length, over the last 30 years (van Gils et al. 2016).

The decrease in bill length may explain the diet shifts observed in Mauritania. Seagrass rhizomes are found very near the sediment surface, whereas *Dosinia* and *Loripes* are buried below the surface (Fig. 12.5). Thus, the bivalves are less

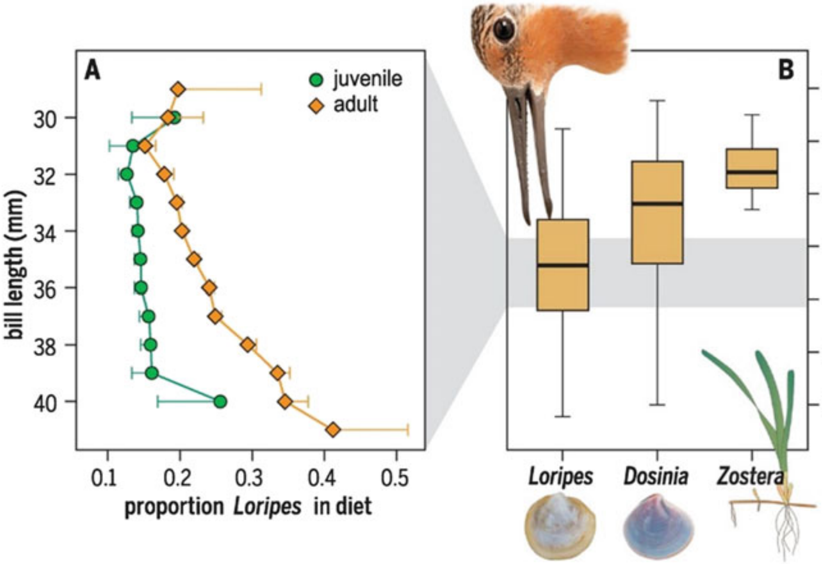

Fig. 12.5 Illustration of how decreasing bill length in red knots is associated with shifts in diets. (**a**) The proportion of *Loripes* in the diet is positively correlated with bill length. (**b**) The most accessible food to short-billed knots is *Zostera* seagrass. Figure reproduced with permission from van Gils et al. (2016).

accessible to shorter-billed birds, which may explain the recent increase in contribution of seagrass rhizomes to the overall diet of red knots in Mauritania.

4 Ecological Impacts of Shorebirds on Mudflats

Although shorebirds are major players in mudflat communities, and can contribute substantially to the understanding of intertidal mudflat ecology, to date, they have more typically been viewed as minor predators of low economic importance, compared to other players such as fish and invertebrates. Most shorebird research has been conducted with a strong ornithological focus, with only narrow connectivity to other intertidal mud-related disciplines in biology, ecology and oceanography. Yet shorebirds occupy a central place in mudflat trophic webs (Piersma 1987; Kuwae et al. 2012), and exert major predatory, physical and chemical impacts on mudflats.

The direct trophic links between shorebirds and primary producers, and between primary consumers and secondary consumers, reveals more complex trophic relationships than previously thought for shorebirds (Kuwae et al. 2012), and has provided new insights into community structure of mudflat ecosystems around the world. For example, direct competition between shorebirds and invertebrates for epibenthic biofilm could explain why small shorebirds are less abundant in the

African-Eurasian flyways, where they face high competition with other biofilm grazers (Bocher et al. 2007; Kuwae et al. 2012). In addition, complex food webs with greater trophic redundancy are generally more resilient, compared with relatively more simple food webs (Hooper et al. 2005). Further work identifying and modelling the links between food web complexity and ecosystem resilience should provide critical information for more effective management of shorebird habitats (Catry et al. 2016).

Does predation by shorebirds reduce prey populations? Observations on foraging rates of shorebirds, combined with shorebird densities, would suggest that they almost certainly must. However, detecting depletion of invertebrate prey by shorebirds is notoriously difficult (Sutherland et al. 2000; van der Meer et al. 2001; Colwell 2010). Estimating invertebrate abundances is itself challenging, given the heterogeneous nature of mudflats (both temporally and spatially), combined with the challenges of accurately identifying and enumerating samples (see Chaps. 5, 6, 8, and 15). In addition, rates of prey removal, though great, may not exceed rates of prey replacement (e.g., via reproduction) (e.g., Kalejta 1993).

Despite the technical complexities of detecting the predatory impacts of shorebirds, numerous studies have documented significant depletion of invertebrate prey by shorebirds, and in some cases, extreme depletion (reviewed in Colwell 2010). For example, shorebirds in the coastal wetlands of South Carolina during northward migration reduced both the density and biomass of invertebrates by approximately 50% (Weber and Haig 1997), and shorebirds at staging areas in Massachusetts during southward migration depleted prey by between 7 and 90%, depending on the year and prey type (Schneider and Harrington 1981).

Not surprisingly, evidence for prey depletion by shorebirds has more commonly been detected during migration, a period where increased energy demand couples with large numbers of shorebirds (sometimes in the hundreds of thousands) passing through a single site over a very punctuated time period. However, moderate levels of depletion of invertebrate prey by shorebirds has also been detected on the non-breeding grounds (e.g., Zwarts and Drent 1981; Zharikov and Skilleter 2003; Bijleveld et al. 2015). One example of extreme depletion of prey during the non-breeding season was that of an estimated depletion of *Hydrobia* and *Nereis* by approximately 90% in the Tees estuary, UK, where the intensity of prey depletion was likely exacerbated by port developments that significantly reduced the foraging areas available to shorebirds (Evans et al. 1979).

In addition to exerting strong effects on invertebrate numbers and biomass, predation by shorebirds has substantial physical and chemical impacts on mudflat ecosystems. Invertebrate grazers on epibenthic biofilm are recognized as important ecosystem engineers, altering the spatial-self organization of mudflats (Weerman et al. 2011, and see Chaps. 5, 6, 8, and 10). With grazing rates on epibenthic biofilm during migration at Roberts Bank in the Fraser River estuary, Canada, estimated at seven times body mass per day for an individual western sandpiper, and flock sizes in the tens to hundreds of thousands of shorebirds over a single tidal cycle, western sandpipers are estimated to be turning over 15 tonnes of sediment per day at this site (Elner et al. 2005; Kuwae et al. 2008). Thus, bioturbation resulting from biofilm grazing by large flocks of shorebirds has the potential to dramatically alter the physical structure of mudflat ecosystems.

Shorebirds can also have substantial chemical impacts on mudflats. For example, defaecation by shorebirds on mudflats can be a source of both organic and inorganic nutrients. Experiments have shown that defaecation by shorebirds can increase growth rates of diatomaceous biofilms by 20% (Jauffrais et al. 2015) and provide a route through which both nutrients and toxins move into and out of intertidal ecosystems (Saint-Béat et al. 2013; St. Clair et al. 2015). Comparisons of trophic webs and ecosystem functioning at the Brouage mudflats in the Marenne-Oleron Bay, France, at two different times of year highlight the critical role of shorebirds in nutrient cycling. Although the overall trophic links were similar both in winter (when shorebirds are present) and summer (when shorebirds are absent), the overall ecosystem functioning was enhanced when shorebirds were present, due to their positive impact on primary productivity via increased nutrient cycling (Saint-Béat et al. 2013).

5 Case Studies

Shorebirds are found in coastal and estuarine environments on every continent except Antarctica. Their distributions can be grouped very broadly into three Flyway systems; the Americas, the Asian-Australasian and the Africa-Eurasia flyways (Boere and Piersma 2012). Here, we present case studies of shorebird research from each of the three major flyway systems that illustrate their central role in mudflat ecosystems and highlight some current conservation concerns.

5.1 Discovering New Trophic Links in Mudflat Food Webs

The intertidal estuarine mudflats, marshes and open soil agricultural field habitats of the Fraser River Delta, in British Columbia, Canada, constitute what some refer to as Canada's most Important Bird Area (IBA) (Butler and Vermeer 1994) and a shorebird stop-over site of global significance (Drever et al. 2014). Roberts Bank, at the southern arm, has been termed the "ecological crucible" of the delta (Sutherland et al. 2013), supporting hundreds of thousands of western sandpipers during a three-week period in April–May, representing most of the global population (Butler et al. 1996; Drever et al. 2014). Despite its multiple conservation designations, the proximity of the Fraser River Delta to the downtown core of the City of Vancouver (30 km north of the delta), urbanization and other anthropogenic pressures have become increasingly intense over the past 40 years. Paradoxically, concerns about port development have resulted in Roberts Bank becoming one of the most intensively studied shorebird stopover sites in the world, which has shed new light on the role of shorebirds in mudflat trophic webs.

Fig. 12.6 Western Sandpiper feeding on epibenthic biofilm during breeding migration stopover on Roberts Bank (British Columbia, Canada). Photo Jason Puddifoot.

Although western sandpipers feed on intertidal mudflats throughout the Fraser River delta, Roberts Bank has the highest usage (Jardine et al. 2015). While invertebrate prey are abundant on Roberts Bank during northward migration (Mathot and Elner 2004), epibenthic biofilm is estimated to account for approximately 50% of the daily energy budget of western sandpipers on northward migration (Kuwae et al. 2008; Beninger et al. 2011; Jardine et al. 2015). Northward migration through the Fraser River Delta coincides with the diatomaceous biofilm blooms, which occur in spring (Admiraal and Peletier 1980; Sawai et al. 2016) (Fig. 12.6), suggesting that shorebirds may be specifically targeting biofilm.

Original studies of sandpiper feeding in the upper Bay of Fundy suggested a simple system with amphipods, *Corophium volutator*, comprising the single major prey (Hicklin and Smith 1979, 1984; Gratto et al. 1984; Barbeau et al. 2009) and shorebird density and foraging behaviour being directly related to *Corophium* availability (Wilson 1990; Wilson and Vogel 1997). A classic “ecological cascade” was then advocated, based on shorebird predation on *C. volutator* grazing on diatoms, and sediment cohesion properties controlled by mucopolysaccharides secreted by diatoms (Daborn et al. 1993). Initially, observations of diatoms in semipalmated sandpiper diet were dismissed as incidental intake resulting from a bill skimming behaviour that was assumed to be directed towards feeding on ostracods (MacDonald et al. 2012), though more recent studies have revealed that diatoms in biofilm are also targeted by sandpipers in the Bay of Fundy (Quinn and Hamilton 2012; Quinn et al. 2017).

While the finding that many shorebirds appear to rely heavily on epibenthic biofilm as a targeted food source adds increasing levels of complexity to system understanding, what is uncertain is whether the evolving picture of shorebird diets represents a more sophisticated knowledge base, or if shorebird diets themselves have altered in response to system changes over the past four decades (e.g., Shepherd et al. 1995). However, the bill and tongue structures associated with biofilm feeding (see Sect. 2.1) suggests that biofilm has long been an important, if unrecognized, component of shorebird diets.

5.2 Shorebirds Alter Mudflat Biogeochemistry and Benthic Communities

The Banc d'Arguin in Mauritania hosts the greatest number and densities of birds along the Africa-Eurasia flyway (Engelmoer et al. 1984; Campredon 2000). With more than two million shorebirds in winter (Altenburg et al. 1982), albeit with a steady decline of some shorebird species since the first counts in 1980 (Oudman et al. 2017), the Banc d'Arguin is by far the most important wintering site for migratory shorebirds using the East-Atlantic flyway in terms of numbers (e.g., Smit and Piersma 1989). The very large shorebird numbers on a rather small area of intertidal mudflats (approximately 500 km^2) results in very high predation pressure (Engelmoer et al. 1984; Wolff et al. 1993).

Although globally, high concentrations of shorebirds often coincide with regions of offshore productivity (Butler et al. 2001), this is not the case for the Banc d'Arguin. The food web of the Banc d'Arguin intertidal is mainly supported by local benthic primary production, a combination of seagrass and microphytobenthos, with much smaller contributions of phytoplankton, macrophytes and epiphytes (Wolff et al. 1993; Carlier et al. 2015; Catry et al. 2016). Seagrass meadows are recognized as one of the most productive of marine communities (Fenchel and Riedl 1970; Fisher and Hand 1984). Since a large portion of the plant material produced is eventually deposited as detritus, the abundance of organic material in the sediment is usually greater than the oxygen available for its degradation. Hemminga and Nieuwenhuize (1991) observed that seagrass leaves at Banc d'Arguin remain trapped in the seagrass beds and decompose *in situ*. Under such anaerobic conditions, decomposition is accomplished by the activity of sulphate-reducing bacteria, which can utilize inorganic compounds other than O_2 as electron acceptors (Fenchel and Riedl 1970). This results in hydrogen sulfide being the major inorganic constituent in the sediments of the Banc d'Arguin (van der Heide et al. 2012; van der Geest et al. 2014).

The hydrogen sulfide, in turn, is metabolized by the (currently) most common bivalve on the intertidal flats of Banc d'Arguin, *Loripes lucinalis* (Wijnsma et al. 1999; Honkoop et al. 2008; see Fig. 12.5). *Loripes* makes use of carbon metabolites produced by endosymbiotic chemoautotrophic bacteria (van der Geest et al. 2014), and carbon dioxide, oxygen and hydrogen sulfide are absorbed by the gill and transported to bacteriocytes harbouring the endocellular sulfur-oxidizing bacteria (Johnson et al. 1994; Le Pennec et al. 1995). The bacteria oxidize the H_2S and use some of the released energy to fix CO_2 in the Calvin cycle. Living close to the surface, *Loripes* is able to exploit sufficient sulfide, while at the same time being able to take up enough oxygen, including the oxygen that diffuses from the roots of seagrasses (Pregnall et al. 1984; van der Heide et al. 2012). The symbiotically-fixed carbon contributes two-thirds of their carbon consumption (Johnson et al. 1994).

In this ecological context, molluscivoran red knots have been shown to affect the biogeochemistry of the intertidal sediments and the functioning of the food web. Because of their dependence on bivalves, red knots reduce competition between the preferred prey species, i.e., the venerid *Dosinia isocardia* (van Gils et al. 2013; Ahmedou Salem et al. 2014; Oudman et al. 2016) and the co-occurring facultative mixotroph *Loripes lucinalis* (van Gils et al. 2012). *Dosinia* is a suspension feeder that only consumes suspended particulate organic matter. In areas where red knots were excluded, *Dosinia* was no longer selectively removed and became dominant over *Loripes*. Thus, without predation on *Dosinia*, stronger competition for suspended particulate organic matter forced *Loripes* to rely on energy produced by endosymbiotic bacteria (van Gils et al. 2012). This reduced sulfide concentrations and led to lower growth rates of *Loripes*. As sulfide is toxic to most organisms, predation by red knots detoxifies the sedimentary environment (van der Heide et al. 2012) and hence facilitates other benthic species.

5.3 Variable Effects of Anthropogenically-Disturbed Environments on Shorebirds

Spanning 20 degrees of latitude, the 18,000 km Yellow Sea coastline, which extends beyond China into the Koreas (Koh and Khim 2014; Wang et al. 2014), at least historically, constituted the largest continuous system of intertidal mudflats in the world (Healy et al. 2002). The Yellow Sea wetlands support 25% of the global total of waterbird species (Ma et al. 2014), but are nonetheless subject to intense anthropogenic disturbance (Fig. 12.7). China's coastal wetlands are heavily exploited for the polychaetes, bivalves, gastropods and crustaceans living in and on these mudflats (Melville et al. 2016; Yang et al. 2016). These benthic resources are impacted in other ways, since most inshore intertidal areas have forms of aquaculture (Li et al. 2011; Yang et al. 2016). Shellfish species of economic importance were introduced at intertidal mudflats where they did not occur previously (Guo 1999; Leung et al. 2008; Li et al. 2011; Tang et al. 2013), and some of these species are now regarded as invasive (Du et al. 2010). Young shellfish are routinely collected at one place and transported to another, and in this way benthic communities both at the mudflats of origin and destination are changed (Wang and Zhang 1995; H.-B. Peng et al. unpublished data).

Perhaps surprisingly, human impacts associated with Chinese mudflats and offshore areas are not always negative for shorebirds (Yang et al. 2016). On the mudflats on the Luannan coast in Bohai Bay, the small bivalve, *Potomocorbula laevis*, the staple food of staging red knots (Yang et al. 2013), appears to be benefiting from anthropogenic disturbances. Competition between settling juveniles and adults has been virtually eliminated by near-complete fishing away of the

Fig. 12.7 Flocks of red knots in Bohai Bay, Yellow Sea, China, an area subject to intense anthropogenic disturbance, including coastal developments (top panel) and fisheries (lower panel). Photos by Jan van de Kam.

population (for shrimp farming) in late summer and autumn, and an absence of predation on spat by epibenthic predators such as shrimps and crabs, due to persistent overfishing in recent decades, has resulted in increased numbers of

Potamocorbula, which now contribute 96% to the total numbers of 17 species. Thus, overfishing of competing marine mesopredators, in this case, might benefit staging shorebirds, at least in the short term.

The great importance of the Chinese mudflats for staging shorebirds, including red knots, during both northward and southward migration, has been established by multiple studies (Gill et al. 2008; Rogers et al. 2010; Battley et al. 2012; Iwamura et al. 2013). There is growing concern that habitat loss (Yang et al. 2011; MacKinnon et al. 2012; Ma et al. 2014; Murray et al. 2014, 2015; Wang et al. 2014; Piersma et al. 2016, 2017), in combination with overfishing, destructive harvesting of clams, and poisoning by pesticides for clearing unwanted organisms from mudflats seeded with spat reared elsewhere (Lin and Yuan 2005; Feng and Ma 2012; MacKinnon et al. 2012; Melville et al. 2016), are now negatively impacting the use by, and indeed the populations of, migrating shorebirds. The coastal wetlands in China are being filled in and reclaimed at accelerating rates, with the extent of the land claims increasing from 24,000 ha/year between 1950 and 2000 to 40,000 ha/year between 2006 and 2010. Over the past two decades, the length of seawall around the Yellow Sea has increased by a factor 3.4, reaching 11,000 km in 2010, prompting major conservation concerns (Ma et al. 2014).

Shorebird species that breed in the High Arctic and rely on the Yellow Sea mudflats to fuel their long-migration have shown the steepest population declines on their southern non-breeding areas (Amano et al. 2010; Wilson et al. 2011; Studds et al. 2017). A demographic study on red knots, great knots (*Calidris tenuirostris*) and bar-tailed godwits (*Limosa lapponica*) showed them to have identical patterns and rates of decline in survival, during the part of the annual cycle encompassing migration through the Yellow Sea area, a 'coincidence' that can only be explained by their shared use of the Yellow Sea intertidal mudflats (Piersma et al. 2016). Indeed, without exception, the evidence suggests that coastal shorebirds are currently limited by the shrinking coastal habitats in East Asia.

6 Conservation

As apparent from this and other chapters of this book, a paradigm shift is taking place over the ecological values of mud. Survival and recovery of the world's shorebird species demands a multidisciplinary scientific approach based on maintaining and restoring the ecological mechanisms supporting the productivity of mud. Conservation actions can no longer be left to ornithologists and habitat managers, however well-intentioned. We need to understand "mud" as a highly complex ecosystem driven by primary producers generating not only energy but also pulses of lipids. Shorebirds are but one indicator of compromised mud systems; commercial fisheries and people who rely on them are also victims, as are tens of thousands of undervalued invertebrate species.

6.1 Mud Is Not a "Wasteland"

Mud, the orphan habitat (Chap. 1), is one that few claim worthwhile for conservation. Generally, mud is regarded as a sticky, foul, pungent wasteland that serves no purpose, and can be developed with impunity. To the casual observer, unvegetated intertidal mud hosts sparse aquatic biodiversity compared to more charismatic habitat types, such as eel-grass and salt marsh (Beck et al. 2001). More perversely, while low productivity systems such as sandy beaches are prized for recreational and economic merits (Cooke et al. 2012), mud is frequently downgraded or altogether ignored in habitat classification schemes (Spurgeon 1999; Barbier et al. 2011). Yet, ironically, mud is not only productive but more ecologically critical to shorebirds than any other coastal habitat component.

As an essential medium to many species, the physical area of mud, and its functional integrity, require protection. In particular, conservation planning needs to incorporate the surrounding physical, chemical and biological processes supporting diatoms in epibenthic biofilm and their periodic production of essential fatty acids (Hixson et al. 2015; Colombo et al. 2016). A mudflat without a functional epibenthic biofilm community has limited value to shorebirds because all shorebirds that feed on mudflats rely on biofilm either as a direct food source (i.e., biofilm grazers; e.g. Kuwae et al. 2008, 2012; Lourenço et al. 2017; Quinn et al. 2017), or indirectly, as a primary food source for their invertebrate prey (Christianen et al. 2017). Thus, even for shorebirds that are not directly grazing biofilm, the epibenthic biofilm community is a critical component of habitat quality. As an example, mechanical dredging in the Dutch Wadden Sea is believed to have negatively impacted benthic diatom communities via sediment disturbance and increased turbidity, with the resultant decrease in benthic diatoms leading to catastrophic declines in *Macoma balthica* populations (Piersma et al. 2001; Compton et al. 2016), a major food source for wintering red knots.

Recognizing the broader conservation imperative of mud has the promise of not only maintaining entire species of migratory shorebirds but by re-creation and remediation of flats, saving others from extinction. Although shorebirds in themselves are important, the broader benefits of restoring mud translate into more sustainable coastal ecosystems and fisheries (Arts et al. 2009).

6.2 Threats to Mud

Intertidal estuarine mud is an irreplaceable habitat for shorebirds, but it is being subjected to global-scale replacement and degradation. The combined forces of global climate change (Struyf et al. 2004), sea level rise (Galbraith et al. 2002), invasive species (Ruiz et al. 1997, Chap. 11), coastal development (Ma et al. 2014), destructive fishing and overfishing (Piersma et al. 2001; Lotze et al. 2006, Chap. 13), and pollution (Kennish 2002), coupled with ignorance in scientific understanding of mud, pose species-level threats to shorebirds worldwide. For example, the major stopover sites along the collapsing Southeastern Asia Flyway have been subject to intensive coastal development (Ma et al. 2014; Piersma et al. 2017), with rates of loss of tidal flat ecosystems ranging between 0.5 and 1.8% per year (Murray and Fuller 2015). Reduced biofilm availability and resource quality to migrating shorebirds could be a contributing cause for these population declines (MacKinnon et al. 2012; Murray and Fuller 2015; Clemens et al. 2016; Piersma et al. 2016; Taylor et al. 2016). Similarly, predicted declines in lipid production at a global level as a consequence of climate change (Hixson and Arts 2016) will only exacerbate the cumulative effects of current factors, either directly reducing mud habitat availability or functioning.

6.3 Restoration and Recovery

We cannot conserve, much less restore, what we do not recognize or understand. Precipitous declines of shorebird populations over the last several decades underscore the need to elucidate supporting ecological mechanisms to better inform conservation strategies. Long distance migratory shorebirds are extreme athletes whose performance relies on an ability to use fatty acids as fuel (Weber 2009; Guglielmo 2010). Some shorebirds may be able to synthesize fatty acids endogenously. For example, the presumed-extinct Eskimo curlew (*Numenius borealis*) is believed to have fed primarily on lipid-poor berries prior to southward migration (Gill et al. 1998), though reports are largely anecdotal. However, most shorebirds are heavily reliant on dietary sources of fatty acids. For example, declines in access to lipid-rich horseshoe crab eggs has proven catastrophic for red knots migrating through Delaware Bay (Haramis et al. 2007). Interestingly, epibenthic biofilm also provides a rich source of polyunsaturated fatty acids (Twining et al. 2016; Quinn et al. 2017), and may therefore be a critical food for shorebirds that rely on dietary intake of fatty acids to fuel long-distance migration.

To date, epibenthic biofilm has not been explicitly considered when assessing general threats to shorebirds (Melville et al. 2016). However, realization of the importance of omega-3 fatty acids produced by phytoplankton, especially diatoms, to aquatic ecosystems is an emerging science, and there is already recognition that not all phytoplankton production is “equal” (Galloway and Winder 2015). The sources of these fatty acids on mudflats need to be identified, understood, restored and protected for effective shorebird conservation. Accordingly, we urge an international conservation initiative on mud. In doing so, conservationists will need to work in teams with engineers, oceanographers, marine chemists, diatomists, ecologists, physiologists and ornithologists, to re-create and/or conserve productive epibenthic biofilm over estuarine intertidal mudflats.

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