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Macroalgal Mats in a Eutrophic Estuary Obscure Visual Foraging Cues and Increase Variability in Prey Availability for Some Shorebirds

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Abstract Conservation of habitat for flagship species, such as birds, aids in the protection of biodiversity in critical ecosystems. Extensive mats of macroalgae stimulated by nutrient input to estuaries threaten critical successes in conservation made by legislation that reduces habitat destruction. Macroalgae can cover intertidal mudflats that are key foraging grounds for obligate visual foragers such as black-bellied plovers (*Pluvialis squatarola*), as well as foragers that routinely switch from visual to tactile foraging such as least sandpipers (*Calidris minutilla*), western sandpipers (*Calidris mauri*), and willets (*Tringa semipalmata*), and predominately tactile foragers such as marbled godwits (*Limosa fedoa*). We hypothesized that macroalgae would affect shorebirds directly by altering foraging behavior and indirectly by reducing prey availability. Mats reduced visual foraging (pecking) for sandpipers and marbled godwits and caused them to probe more often. Willets spent overall less time foraging than sandpipers and marbled godwits and did not alter their foraging strategy due to macroalgae. While foraging, black-bellied plovers, marbled godwits, and willets avoided macroalgae while sandpipers did not select between habitat types. This suggests macroalgae may have negative effects on plovers, marbled godwits, and willets by reducing foraging area but that sandpipers may utilize both macroalgae and bare sediments. Macroalgal mats indirectly influenced shorebirds by enhancing variability in prey availability across the mudflat landscape. By quantifying avoidance of or preference for mats, foraging behavior, and variation in prey availability, we showed that macroalgae have differential effects across shorebird foraging guilds.

Keywords Eutrophication · Forage · Generalist · Habitat · Macroalgal mat · Prey availability · Visual cues

Introduction

Estuaries support high biodiversity and are threatened by excess nutrient enrichment (e.g., Lotze et al. 2006) that stimulate macroalgal blooms. The resurgence of ecosystem-based conservation (Barbier et al. 2008; Frisk et al. 2011) emphasizes the protection and restoration of ecosystem function that can be disrupted by eutrophication. Anthropogenic nutrient enrichment interrupts a suite of ecosystem processes by increasing the frequency and severity of blooms of ephemeral macroalgae in estuarine habitats worldwide (e.g., Duffy et al. 2005; Morand and Merceron 2005). Some research has evaluated the effects of point sources of nutrient enrichment, such as sewage outfalls, on shorebird foraging (Alves et al. 2012). However, little work has investigated whether diffuse sources of nutrients, such as runoff from agriculture that stimulates macroalgae (Kennison and Fong 2014) reduce support for higher trophic consumers including shorebirds. Macroalgal mats can cover extensive sections of intertidal mudflats (Eyre and Ferguson 2002) that are essential foraging grounds for shorebirds (e.g., Castillo-Guerrero et al. 2009). Despite typically high abundances of benthic invertebrate prey on intertidal flats (Dit Durell et al. 2005), inter- and intraspecific

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competition between shorebirds can be high (Burger et al. 2007; Triplet et al. 1999). Macroalgal mats can influence the density, diversity, and community structure of key infaunal and epifaunal prey species by creating unfavorable conditions (Green et al. 2013); alternatively, mats may support a higher abundance of smaller-bodied prey (Brooks and Bell 2001), which may be available only to smaller shorebirds (Sutherland et al. 2000). These changes in prey density, location, and availability may alter shorebird use of sites (Goss-Custard et al. 1977; Spruzen et al. 2008). Moreover, Santos et al. (2009) found that detection of prey by shorebirds was related both to patch size and density of prey for dunlin (*Calidris alpina*) that tended to forage visually. Therefore, macroalgal mats may undermine conservation efforts by interrupting ecosystem function through changes in prey availability and the disruption of foraging behavior, and thus alter the competitive landscape for shorebirds.

Macroalgal mats may affect shorebird foraging behavior on mudflats by reducing prey intake due to visual or physical interference. When visually hunting, shorebirds peck at the sediment surface (Barbosa and Moreno 1999). When tactilely locating prey, they probe more deeply (Dominguez 2002). Differences in time spent pecking versus probing have been documented in response to physical differences in substrate (Lourenco et al. 2008; Mouritsen and Jensen 1992; Quammen 1982) and during nighttime obscuration of the sediment for visual foragers (Mouritsen 1994). Reductions in functional foraging habitat due to interference and visual obstruction may shift competitive advantages among bird species. For example, some species such as dunlin (*Calidris alpina*), ringed plover (*Charadrius hiaticula*), and black-bellied plover (*Pluvialis squatarola*) were less abundant on mudflats covered by macroalgal mats (Cabral et al. 1999; Murias et al. 1996) while other shorebird species did not alter their behavior due to mats (Murias et al. 1996). However, while pied avocets (*Recurvirostra avocetta*) completely avoided mats, Eurasian curlew (*Numenius arquata*) were indifferent to macroalgae (Murias et al. 1996). Shorebirds with longer bills may have access to both shallow and deeply burrowing prey (Alves et al. 2013; Durell and Le. V. Dit 2000), suggesting that these species would not avoid macroalgal mats and thus would have a competitive advantage over small billed birds with limited access; however, shorebirds with smaller bills may target smaller prey within mats. Macroalgal mats may disrupt specialized foraging behavior, such as sediment scything used by avocets (Johnson et al. 2003) or the pursuit of fish in shallow water utilized by reddish egrets (*Egretta rufescens*) and tricolored herons (*Egretta tricolor*). Thus, as habitat loss due to eutrophication continues, specialized foragers may be at a competitive disadvantage over generalist foragers (Durell and Le. V. Dit 2000). However, there is little understanding of how eutrophication alters competition among foraging shorebirds.

We hypothesized that all shorebirds with the ability to switch foraging strategies in sediments from visual to tactile (sandpipers, willets, and godwits) would decrease pecking and increase probing on mats due to obscured visual cues. Additionally, we hypothesized that small shorebirds may avoid macroalgal mats while foraging due to physical interference while birds with longer bills would not avoid macroalgal mats; alternatively, smaller birds may prey-switch to small invertebrates sheltering in mats. Finally, we expected a reduced density and diversity of infaunal shorebird prey in the sediments under macroalgae and a high density of small prey within mats.

Methods

Study Site

To evaluate the direct and indirect effects of macroalgal mats on shorebirds, we quantified behavior of five shorebird species and their prey availability over 2 years. We conducted our research at Mugu Lagoon (34° 11′ N, 119° 12′ W) (Fig. 1) which is located in California, USA along the Pacific Flyway and is an important stopover site for migrating shorebirds (Page and Shuford 2000). Prolonged macroalgal cover is typical of eutrophic lagoons in Mediterranean climates (van Hulzen et al. 2006), including Mugu Lagoon (Green 2011; Kennison 2008). At Mugu Lagoon, macroalgal mats can cover greater than 50 % of the benthos for as much as five consecutive months (Green 2011). Like most estuaries, Mugu Lagoon supports thousands of resident and migratory birds, including waders, waterfowl, raptors, as well as threatened and endangered shorebird species (Ambrose et al. 2006; Page et al. 1999). We chose four sites that comprised broad expanses of intertidal mudflat at least 50 m long (parallel to tide lines) and 50 m wide, or ~2,500 m^2 per site, for a total of 10,000 m^2. Sites were all within 1 km of each other but differed in distance to the estuarine mouth. Site 4 was closest to the mouth in the relatively well-flushed main basin. Sites 2 and 3 were connected to the main basin by wide and deep culverts and were on opposite sides (north vs. south, respectively) of the lagoon; Ambrose et al. (2006) showed that site 2 had higher percent sand than site 3 despite equivalent proximities to the mouth of the estuary. Site 1 was farthest from the mouth and presumably was the least vigorously flushed. However, when chosen, all sites had areas where large mats of macroalgae accumulated for many months (personal observation). We chose to pool data among sites to increase replication as not every target species of bird was found in sufficient number at each site for statistical analysis; thus, while site-to-site variability may influence shorebird foraging behavior, we were not able to determine site to site variability in this study.

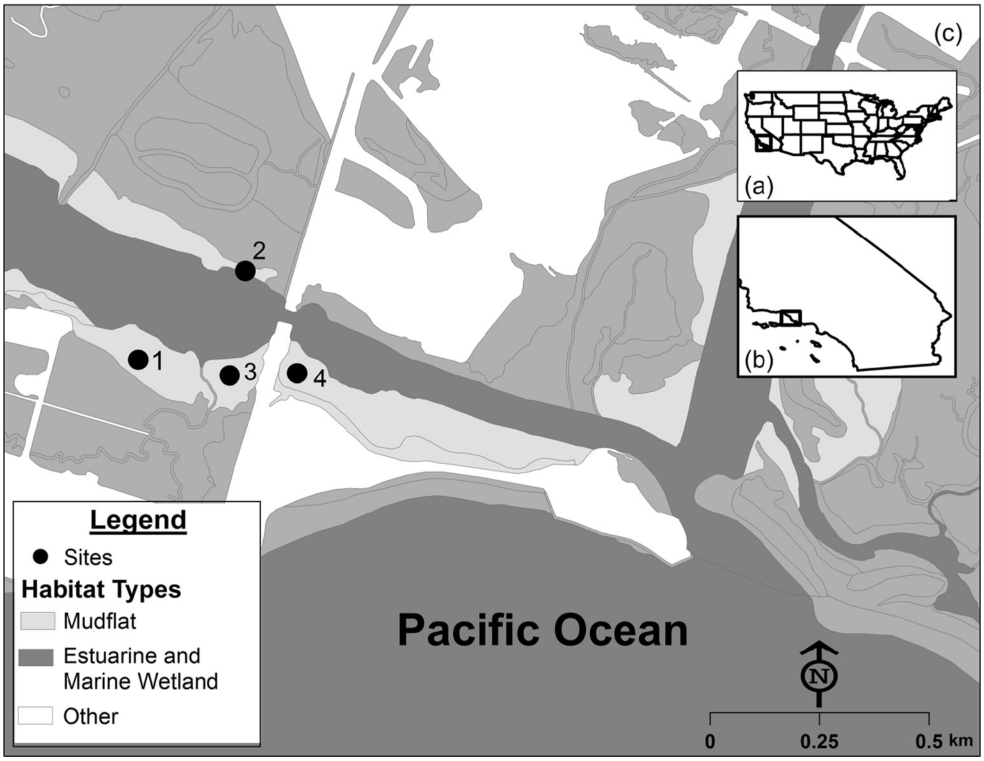

Fig. 1 Map of study area. Extent indicators show approximate locations. **a** USA, **b** Southern California, and **c** sites 1–4 at Mugu Lagoon

Description of Species

We selected five species on the basis of their abundance and foraging ecology. Black-bellied plovers (*Pluvialis squatarola*) have mean bill lengths of 3.1 cm (Lee and Hockey 2001), are obligate visual hunters (Hugie 2004), and often prey on annelids (Schneider and Harrington 1981). Their peak abundance occurs in fall and winter in California (Hubbard and Dugan 2003). In 2007 and 2008, black-bellied plovers had mean annual abundances of 270 and 237 across Mugu Lagoon (Ruane, unpublished data). Mean annual abundances for Western sandpipers (*Calidris mauri*) at Mugu Lagoon were 3,879 in 2007 and 4,958 in 2008 (Ruane, unpublished data). Western sandpipers have been documented to switch between visual and tactile foraging (Sutherland et al. 2000). Least sandpipers (*Calidris minutilla*) had lower abundances than western sandpipers across all of Mugu Lagoon totaling 1,258 in 2007 and 596 in 2008 (Ruane, unpublished data). Both least and western sandpipers vary slightly in their mean bill lengths (1.9 and 2.5 cm, respectively) but both consume benthic invertebrates, including oligochaetes and amphipods (Colwell and Landrum 1993; Safran et al. 1997). In addition, western sandpipers have been shown to consume copepods and biofilms (Kuwae et al. 2008; Sutherland et al. 2000). Both least and western sandpipers tend to achieve highest densities in fall in California (Long and Ralph 2001). We combined our observations of the two sandpipers found at Mugu Lagoon into one group, sandpipers (*Calidris* spp.). In 2009, we conducted tests to evaluate this decision (see Appendix A). Across Mugu Lagoon, willets (*Tringa semipalmata*) had abundances of 400 in 2007 and 490 in 2008 (Ruane, unpublished data). Willets have mean bill lengths of 5.4 cm (Hall and Fisher 1985) and are also capable of switching between visual and tactile foraging techniques (Rojas et al. 1999) as they feed on a wide range of crustaceans, annelids, and molluscs (Ramer et al. 1991; Stenzel et al. 1976). They tend to achieve highest abundances in fall and spring in California (Lafferty et al. 2013; Long and Ralph 2001). Across Mugu Lagoon, marbled godwits (*Limosa fedoa*) had abundances similar to willets with 586 found in 2007 and 530 in 2008 (Ruane, unpublished data). Marbled godwits are able to use both tactile and visual foraging techniques, though it is thought they rely mostly on tactile foraging (Castillo-Guerrero et al. 2009) and prey on annelids and molluscs (Ramer et al. 1991). Marbled godwits had the longest bills with mean bill lengths of 8.8 cm (Gibson and Kessel 1989) and tend to have highest densities in spring and fall in California (Lafferty et al. 2013).

Quantification of Behavior

We chose to quantify the foraging behavior of least and western sandpipers, willets, and marbled godwits due to their abundance and our observation that they foraged both on top of macroalgae and on bare sediment. Black-bellied plovers were not found in sufficient abundances to quantify behavior. We used focal observations and quantified foraging behavior as the percent of focal time each individual spent pecking (less than ½ bill length inserted into substrate), probing (greater than ½ bill length inserted into substrate), standing, walking, and other (usually grooming). We used an "out of site" category when birds were still visible but their behavior was temporarily obscured. Because we were interested in foraging behavior, we only present data on pecking and probing. Individual birds were randomly selected by scanning the flock from left to right and selecting the fourth bird from the left. To avoid pseudoreplication, fewer than 25 % of birds in any flock were observed. Shorebirds were observed foraging at low tide within the four sites on intertidal mudflats. Birds were observed for approximately 1–2 min (mean focal time 1.85± 0.26, mean±SD, range=0.86–2.01 min). This focal length was chosen because preliminary trials (Green, unpublished data) showed that it yielded sufficient data to evaluate differences in foraging behavior among substrates before the focal subject moved off the substrate. Bird behavior was dictated into a digital voice recorder. We used JWatcher™ 1.0 (Blumstein and Daniel 2007) to summarize each behavior as a percent of the total focal time and account for variable observation times. Focal observations were conducted from March–October in 2007 and 2008 since the species selected were all present during these times (Ruane, unpublished data). We used two-factor analysis of variance (ANOVA), with factors being macroalgal presence (±) and year (2007 and 2008). For sandpipers, we observed 40 on bare sediment and 31 on macroalgae in 2007and 30 and 34, respectively, in 2008. In 2007, we observed 29 willets on bare sediment and 27 on macroalgae and 42 and 39 in 2008. We observed 32 marbled godwits on bare sediment and 33 on macroalgae in 2007 while in 2008 sample sizes were 30 and 25, respectively. While site differences may affect shorebird foraging behavior, site was not included as a factor since not all species were observed foraging on bare sediment and macroalgae in the same site during the same year. Data did not meet the assumptions of ANOVA and were transformed. Some data were transformed to ranks but did not violate the assumptions regarding interactions in an ANOVA (Seaman et al. 1994).

Habitat Selection

To assess preference or avoidance of macroalgal mats by shorebirds we conducted scan samples on five separate low tide events in August 2008. From the same fixed position each sampling date, we observed black-bellied plovers, least and western sandpipers, marbled godwits, and willets as they foraged on mudflats during ebb tides. We documented the type of shorebird, if it was on or off a macroalgal mat, and if it was foraging. We quantified all birds of our target species that were estimated to be within one m along 300 m of the tide line. This area encompassed sites 1, 3, and 4 as well as regions of the mudflat beyond the site boundaries. Site 2 was not included due to the difficulty of observing shorebird habitat selection from our chosen position. Quantifying bird presence and foraging activity took less than 5 min. Immediately following each scan, the percent cover of macroalgae was quantified within one m of the same tide line by recording presence or absence of macroalgae every 10 m. We restricted our bird and macroalgal assessments to within 1 m of the tideline in order to keep the area surveyed constant among scans. Shorebird scans were conducted every 20 min from high to low tide. To assess selection of bare sediment or macroalgae while foraging and not foraging, we calculated the Ivlev electivity index for each species. Values below 0 suggest avoidance while values above 0 suggest selection.

$$\mathrm{Ei} = (\mathrm{oi} - \pi\mathrm{i})/(\mathrm{oi} + \pi\mathrm{i}) \tag{1}$$

oi Proportion of used units of category i
πi Proportion of available units of category i

For example, shorebird species A foraging on bare sediment:

> oi=for scan *X* (the number of birds of species A foraging on bare sediment)/(total number of bare sediment patches used by foraging and nonforaging birds of species A)
> πi=for scan *X* (the number of bare sediment patches) / (total number of patches)

It was likely the same birds were observed over many scans, therefore violating independence. Therefore, data could not be analyzed statistically but were averaged and summarized graphically.

Prey Availability

To assess differences in prey availability in sediments due to macroalgal mats, we quantified the density of infauna and site-attached epifauna in a subset of our sites for bird observations in 2007 and 2008. In 2007, we sampled infaunal and epifaunal prey availability under and away from mats within sites 1 and 2 because only these sites contained areas with and without macroalgal cover at the time of sampling. In each site, a 20-m long transect was haphazardly placed on top of mats and another 20-m transect was placed on bare sediment. Transects were separated by at least 50 m. In March 2007, five cores (5 cm in diameter, 10 cm in deep) were taken from randomly selected plots along each transect (n=20). This core depth was used to quantify prey available to all species in our study including marbled godwits, which have a mean bill length of approximately 9 cm (Gibson and Kessel 1989).

In 2008, site 2 was dropped from the study as it was very difficult to access and sites 3 and 4 were added, because they were more easily accessed and had appropriate macroalgal coverage in this year. Thus, site 1 was the only area to be measured in both 2007 and 2008. To increase replication, ten cores of sediment were taken from under macroalgal mats and ten from bare sediment in sites 1, 3, and 4 (n=60). Cores were taken in June 2008, 3 months later in the season than the March samples of 2007. To assess prey availability in mats from within each of the three sites evaluated in 2008, five samples of the mats (2 cm in diameter) were taken immediately above sediments that were collected for sediment macrofauna (n=15). Mats were cut to the benthos and placed in a bottle.

Since we were interested in macrofauna (infauna+small site-attached epifauna) as potential prey for shorebirds, all sediment cores and macroalgal mat samples were rinsed on site using 1.0-mm screens. While it is possible this choice of screen size may have resulted in our missing some key prey species such as meiofauna (invertebrates, <0.5 mm), which may be consumed by sandpipers (e.g., Sutherland et al. 2000), the high sand content of the sediments at these sites (Ambrose et al. 2006) made using 0.5 mm sieves prohibitively time consuming. However, Davis and Smith (2001) showed that least and western sandpipers prey on invertebrates greater than 4 mm on average and Kober and Bairlein (2009), who examined habitat selection and prey choice among shorebirds including marbled godwits, willets and sandpipers also utilized 1 mm sieves. Core contents were immediately preserved with 10 % buffered formalin then transferred to a solution of 70 % denatured ethyl alcohol and Rose Bengal. To limit error due to breakage during processing, only heads of worms and gastropods in their shells were counted (see Appendix B for detailed methods assessing community composition).

In the lab, invertebrates were separated from the macroalgal mat (when needed), identified to gross taxonomic category and quantified. A one-factor ANOVA (to test for site effects) was fitted on each faunal group found in the mats in 2008 (data for all but total macrofauna in Appendix B). Data were transformed as necessary to meet the assumptions of ANOVA. Rank-transformed data did not violate assumptions regarding interactions (Seaman et al. 1994) so we fitted ANOVA on the rank-transformed data.

Total sediment macrofauna did not meet the assumptions of normality or homoscedasticity, so we fitted a generalized linear model using a Poisson distribution. Effect sizes were reported as partial eta squared (η_p^2) (Cohen 1988). We interpreted variables with very small effect sizes (<0.1) as unimportant in explaining effects of substrate on behavior and prey availability.

Results

Focal analysis of shorebirds revealed a shift in foraging strategy from pecking while on bare sediment, to probing when foraging on macroalgal mats for two of our three bird taxa (Fig. 2; Table 1). Sandpipers spent 2.5 times more time pecking while foraging on bare sediment compared with when they foraged on top of macroalgae. Sandpipers spent approximately 90 % more time probing on macroalgal mats than on bare sediment. There were no differences between years. Marbled godwits showed the same shift in behavior as sandpipers. They spent nearly fourfold more time pecking on bare sediment compared with when they foraged on top of mats and more than doubled the percent of time probing while on top of macroalgal mats compared with when they foraged on bare sediments. Overall in 2007 marbled godwits spent a higher percent of time probing on macroalgae than in 2008; this difference resulted in a significant effect of year. Willets spent less time foraging than the other two species and did not alter their percent of time pecking when foraging on macroalgae or on bare sediment. However, they did spend a higher percent of time pecking in 2007 than in 2008, again resulting in an effect of year. Willets probed more on bare sediments in 2007 and more on macroalgae in 2008 resulting in an interaction between mat presence and year (Table 1).

Despite the relatively high percent macroalgal cover, 55±0.04 % (mean across all scans and dates±SE), shorebirds often did not show preferences for foraging on top of mats or away from them. However, when birds did selectively forage there were some species-specific patterns (Fig. 3). Obligate visual foraging black-bellied plovers showed slightly greater avoidance of macroalgae than bare sediment. Nonforaging plovers selected macroalgae and avoided bare sediment. By contrast, foraging sandpipers selected both bare sediments and macroalgae but favored bare sediments slightly. When sandpipers were not foraging, they avoided bare sediment slightly more than they avoided macroalgae. Marbled godwits avoided macroalgae more than bare sediment. Nonforaging godwits avoided bare sediments and selected macroalgae. Foraging willets showed slightly greater avoidance of macroalgae than bare sediment but tended to selected macroalgae slightly more often when not foraging.

Total macrofauna were less abundant under macroalgal mats but the effect varied by year. Total macrofaunal density was significantly affected by the presence of macroalgal mats in 2007 (Fig. 4), being approximately three times higher in bare sediment than under macroalgal mats (F=8.866, df=1, p=0.007, η_p^2=0.31). In 2008, differences in total macrofauna between substrates in site 1 but not sites 3 and 4 generated an interaction between mat presence and site (GLM, X^2=453984, p<0.0001 for significant interaction). In each year, there were taxon-specific responses to macroalgal presence (Appendix B).

Mat invertebrates were numerically dominated by small-bodied crustaceans, which had orders of magnitude higher densities than prey found in sediments. For example, copepods at site 1 were $3.64\times10^5\pm1.31$ (mean±SE m^{-2}) while spionid polychaetes collected from sediments at site 1 during the same survey had densities of $1.04\times10^4\pm0.2$ (mean±

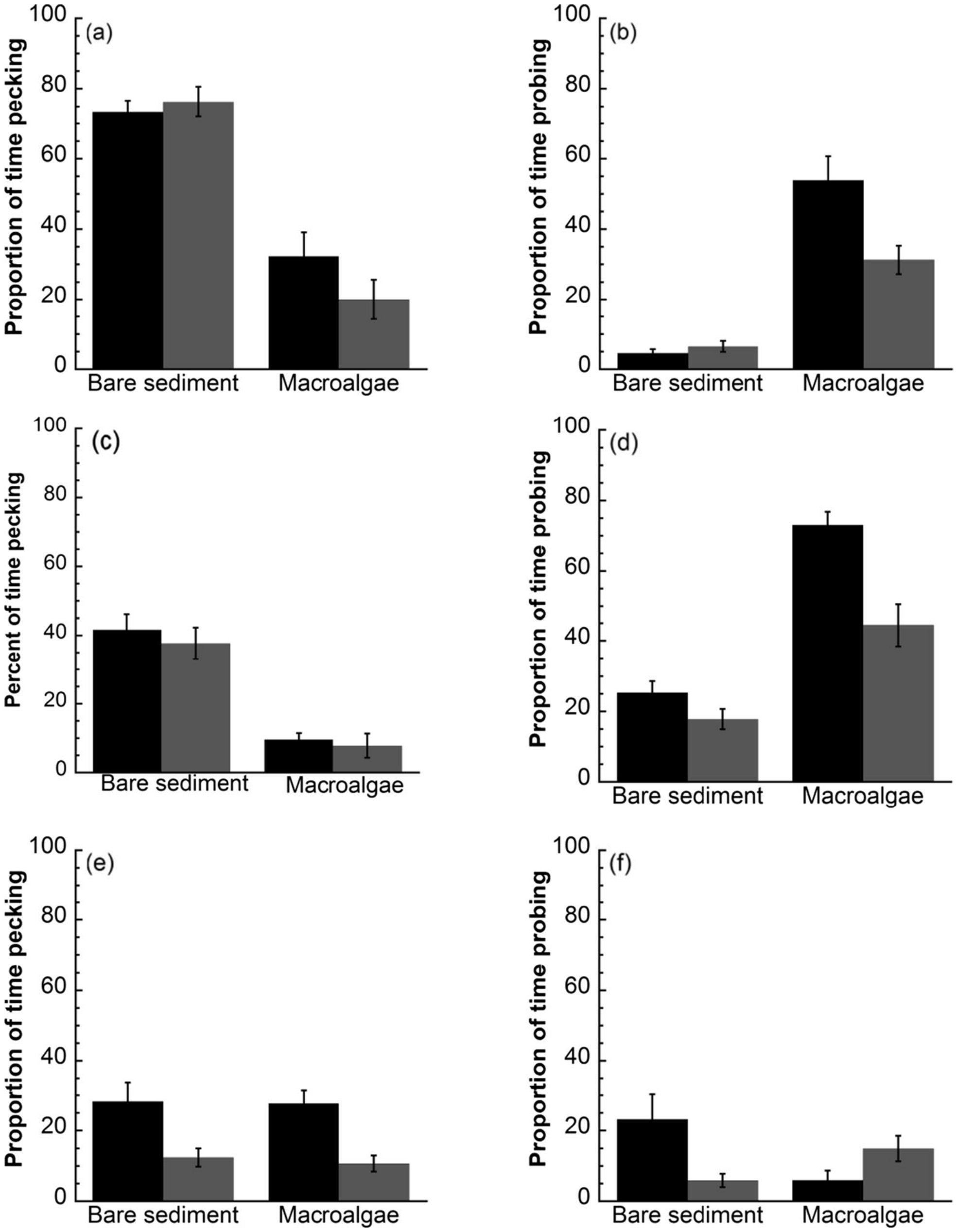

Fig. 2 Comparison of shorebird percent of time pecking (*left column*) or probing (*right column*) while foraging on bare sediment and macroalgae. *Top row*, sandpiper; *middle row*, marbled godwit; *bottom row*, willet; 2007 (*black*) and 2008 (*gray*). *Bars* are means (±SE)

SE m^{-2}). However, most taxa collected from mats showed no differences among sites (see Appendix B).

Discussion

Our work suggested that macroalgal mats obscured visual foraging cues for shorebirds. Higher probing efforts on top of mats showed that sandpipers and marbled godwits switched from visual to tactile foraging. Shifts from pecking to probing in shorebirds have only been demonstrated during nocturnal foraging (Lourenco et al. 2008; Rojas et al. 1999). However, our study was conducted in a highly eutrophic estuary where the abundance of macroalgae on sediments was greater than that of any other investigation evaluating the effects of macroalgae on shorebirds (Cabral et al. 1999; Murias et al. 1996). To our knowledge, no previous studies have demonstrated changes in shorebird foraging behavior due to physical obscuration. Increased probing could have energetic consequences (Nolet et al. 2002) for some species and therefore negative effects on population sustainability. On the other hand, obscuration by macroalgae could reduce competition for prey for small shorebirds if larger shorebird species switch from pecking invertebrates off the surface to probing for

Table 1 Two-factor analysis of variance testing if macroalgal presence influences the percent of time pecking and probing for sandpipers and godwits

Source	Peck				Probe			
	df	*F*	*P*	η_p^2	*df*	*F*	*P*	η_p^2
A. Sandpiper[a]								
Macroalgal presence	1	74.837	*<0.0001*	0.36	1	94.911	*<0.0001*	0.49
Year	1	0.018	0.892	0	1	0.692	0.407	0.01
Macroalgal presence[a] Year	1	1.401	0.239	0.01	1	0.469	0.495	0
Residual	131				98			
B. Marbled godwit								
Macroalgal presence	1	87.789	*<0.0001*	0.41	1	57.843	*<0.0001*	0.33
Year	1	2.299	0.132	0.02	1	19.404	*<0.0001*	0.14
Macroalgal presence[a] Year	1	0.016	0.901	0	1	3.389	0.068	0.03
Residual	116				116			
C. Willet								
Macroalgal presence	1	0.383	0.537	0	1	0.085	0.771	0
Year	1	14.318	*0.0003*	0.12	1	0.097	0.756	0
Macroalgal presence[a] Year	1	3.118	0.080	0.03	1	7.939	*0.006*	0.06
Residual	108				133			

[a] Transformed to ranks

subsurface prey. This could increase foraging opportunities for smaller shorebirds foraging on prey at the sediment surface or within mats.

Birds are the most widely used flagship species in the protection of biodiversity (Brooks et al. 2001) and our results suggested that some shorebird species may serve as indicators of functional habitat loss across the ecosystem due to their foraging microhabitat selectivity. For example, black-bellied plovers avoided mats more than they avoided bare sediments while foraging,

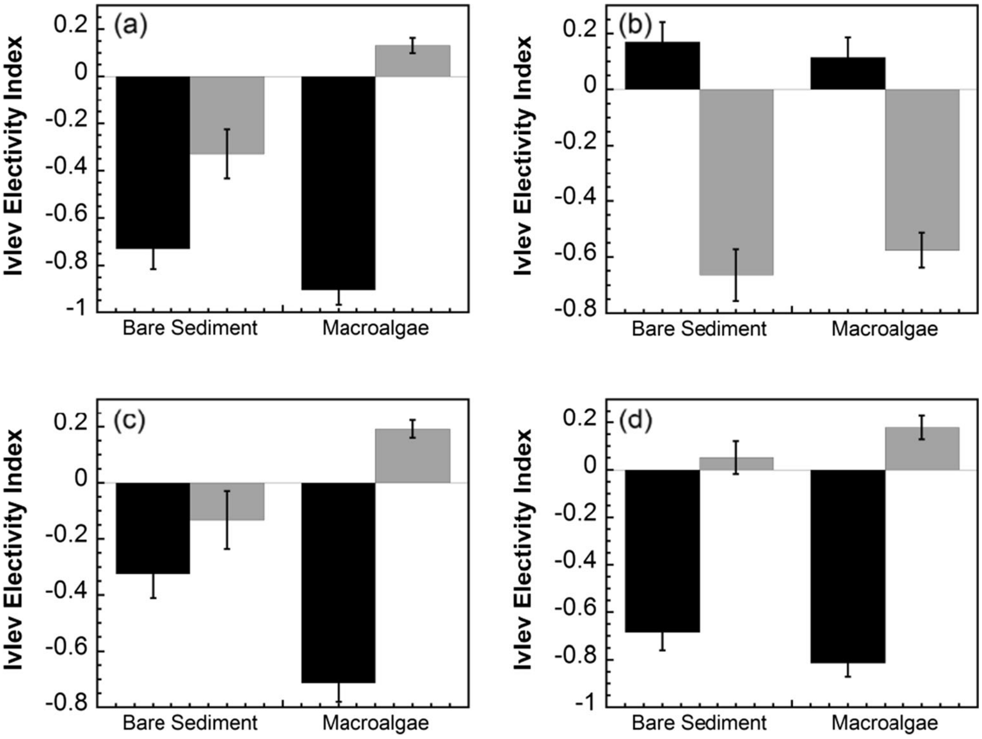

Fig. 3 Comparison of shorebird substrate selectivity while foraging and not foraging. **a** Black-bellied plover, **b** sandpiper, **c** marbled godwit, and **d** willet; foraging (*black*) and not foraging (*gray*). *Bars* are means (±SE)

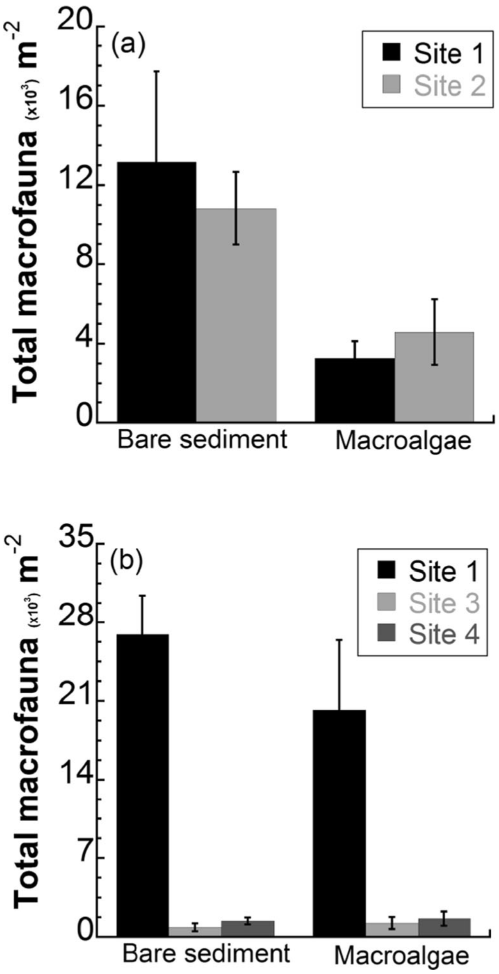

Fig. 4 Comparison of total macrofauna collected from bare sediments and sediments covered by macroalgal mats different sites; **a** 2007 and **b** 2008. *Bars* are means (±SE). Note scale change between panels

suggesting that areas covered by mats are not functioning equally as feeding habitat as bare sediments. This finding is supported by Cabral et al. (1999), who documented that ringed plovers (*Charadrius hiaticula*) and black-bellied plovers avoided foraging on top of mats. Similarly, we showed that marbled godwits and willets avoided macroalgae while foraging. In our study, willets were less selective than godwits, which supports Kober and Bairlein (2009) who found low habitat selectivity among willets. However, it is possible that our ability to detect selectivity was reduced because we were observing nonbreeding, migrating adults with high energy demands (Castillo-Guerrero et al. 2009). Moreover, our preference study was conducted in August when shorebird abundances were not at their peak, and this may have reduced competition for prey and increased the opportunity to select. While it is possible that either of these factors could have influenced habitat selectivity, this highlights the importance of understanding factors that alter prey detectability within sites used by nonbreeding shorebirds.

This study demonstrated that some shorebird species may not experience habitat loss through direct interference by macroalgal mats. We showed that mats enhanced site variability in prey availability in sediments while drift mats may ameliorate some variation in prey abundances among sites by serving as sources of colonizing macrofauna (Appendix B). The ability of marbled godwits and sandpipers to switch behavior and forage differently where mats were present suggested that these species may have some resilience to the widespread eutrophication of estuaries. In particular, sandpipers showed equivalent selection for macroalgae and bare sediment and readily switched from pecking on bare sediments to probing on mats. While on mats, sandpipers may have fed on copepods and ostracods that were often orders of magnitude more abundant in mats in our study (see Appendix B) compared with others (Arroyo et al. 2006) and were never found in sediments. However larger invertebrates such as oligochaetes contributed to higher biomass availability than copepods within mats (see Appendix B). Our data showed that both macroalgal mats and bare sediments had nearly three times higher prey biomass availability than sediments covered by macroalgal mats (see Appendix B). While Willets tended to avoid mats during foraging they demonstrated no changes in foraging method in response to macroalgae. This is likely due to their flexibility in prey choice (Maimone-Celorio and Mellink 2002) including the ability to eat *Pachygrapsus crassipes* and *Cerithidea californica* (Ramer et al. 1991; Sousa 1993), which do not appear to be negatively affected by macroalgae (Boyer and Fong 2005). Therefore, mats would not affect generalist foragers such as willets (Lowther et al. 2001). However, willets and marbled godwits do consume infauna (Gratto-Trevor 2000; Placyk and Harrington 2004) that our data showed can be negatively affected by macroalgae (see Appendix B). Therefore, willets and marbled godwits may show some minor dietary restrictions due to macroalgae, though their foraging behavior in this study did not reflect such limitations.

Our research contributes to a growing body of evidence that anthropogenic impacts result in a worldwide increase in generalist foragers. Green et al. (2014) demonstrated that macroalgal mats reduced macrofaunal functional diversity and enhanced generalist deposit feeders. As habitats continue to be drastically altered or destroyed, niches are homogenized and generalist foragers have the competitive advantage (Clavel et al. 2011). For example, Le Viol et al. (2012) reported that over two decades there was a major decline in specialist birds in favor of generalists in Europe, a finding which may be attributed to changes in land use. This trend toward generalist species is also occurring in marine ecosystems. Tewfik et al. (2005) showed that in a tropical seagrass community, proximity to development favored generalist foragers compared with a site with little anthropogenic influence. It must be noted however that while generalist and species with flexible foraging behavior may have higher success in eutrophic estuaries than visual foragers, they are still threatened by changes in land use. For example, in the Ballona wetlands located in Southern California, willet abundance has dropped 78 % since the 1950s (Cooper, personal communication), most likely due to changes in land use in and around the wetland. Thus species with flexible or generalist foraging abilities may have a short-term competitive advantage where eutrophication is severe. However, as macroalgal mats in estuaries increase and persist on foraging grounds for nearly half of the year (Green 2011), it is critical that we continue to evaluate whether macroalgal mats alter prey densities or the foraging behavior of species that depend on intertidal flats for survival.

Conclusions

Our work demonstrated that managing excessive macroalgal mats should be considered in conservation of shorebird habitat particularly in stopover sites along migration routes. Prey availability during the nonbreeding season is of critical importance (Castillo-Guerrero et al. 2009) as it likely influences long-term population dynamics of shorebirds and the effects of eutrophication on stopover sites warrants additional investigation. Moreover, more research is needed to determine if removal of visual cues by macroalgal mats negatively affect prey consumption by shorebirds and if there are energetic costs or benefits associated with increased probing efforts as eutrophication in estuaries increases worldwide. This study highlights the need to examine whether species with generalist foraging behavior and prey selectivity have a competitive advantage in eutrophic estuaries.

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