

Macroalgal fouling on the intertidal mole crab *Emerita analoga* facilitates bird predation

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Abstract In this work, we studied the effects of predation by birds on the intertidal mole crab *Emerita analoga* fouled by macroalgae in a sandy beach of central Peru (11° S). The epibiosis affected mostly the larger animals, especially adult females. Epibiosis prevalence for the entire intertidal population was relatively low (1–2%), however, within the size range affected by epibiosis in the intertidal zone (18–23 mm in carapace length), 20–38% of the animals were fouled. Focal observations of birds showed that fouled animals are preferred over those non-fouled of the same size class and hence the same sex, being consumed at a higher rate than their proportion in the intertidal (Chesson's alpha index of prey selection >0.96), and estimations of mortality rates indicated that more than 35% of the intertidal fouled animals are removed everyday by birds. The effect of epibiosis may be mainly attributed to a higher burrowing time or an increased visual attractive effect of the algae, which make fouled animals more conspicuous to predatory birds, or because of fouling enhances profitability of the animals.

The results show that epibiosis has negative effects on *E. analoga* through increasing predation by birds, which in turn restricts the distribution and abundance of fouled *E. analoga* in the intertidal zone.

Keywords *Emerita analoga* · Epibiosis · Indirect interactions · Peru · Predation · Sandy beach

Introduction

Indirect interactions may be an important cause of variation in populations and communities (e.g., Menge 1995). Indirect interactions occur via two basic ways (Wootton 1993): (1) due to linked direct interactions between species pairs (i.e., interaction chain) and (2) when a third species change how a pair of other species interact (i.e., interaction modification). By modifying the body surface properties of an organisms through tactile, visual, or chemical cues, epibionts can attract or repel predators, modulating in this way consumer–prey interactions (e.g., Wahl and Hay 1995; Wahl et al. 1997; Laudien and Wahl 2004).

Many hypotheses concerning sandy beach communities have developed over the past two decades, putting sandy beach studies into an increasing theoretical framework (e.g., Defeo and McLachlan 2005). Main generalizations concern the increase in species richness and abundance from reflective to dissipative beaches (e.g., McLachlan and Dorvlo 2005) and the increasing importance of biological factors (e.g., competition) in controlling community structure and population dynamics in dissipative beaches (e.g., Defeo et al. 1997, Dugan et al. 2004), whereas at reflective beaches, populations are physically controlled (Defeo et al. 1997, Defeo and McLachlan 2005). Despite these advances, the importance of other forces such as

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predation, parasitism, or epibiosis is still poorly studied (Defeo and McLachlan 2005; but see Takahashi et al. 1999, Manning and Lindquist 2003).

In protected to moderately exposed sandy beaches within and outside the Ancón Bay (central Peru: 11° 46' S, 77° 11' W), an epibiotic association between green macroalgae (*Enteromorpha* spp.) and the mole crab *Emerita analoga* (Crustacea, Anomura, Hippidae; Fig. 1) was recently described (Firstater et al. 2009). *Emerita analoga* is a widespread and abundant decapod inhabiting sandy beaches of the temperate west coast of America (Efford 1969; Contreras et al. 1999; L pez et al. 2001) and is a characteristic species of the swash zone (Contreras et al. 1999), frequently dominating in abundance and biomass the intertidal macrofauna of sandy beaches (e.g., Dugan et al. 2000). Given its abundance, *E. analoga* often plays an important role in the secondary production of sandy beaches (e.g., Alvitres et al. 1998), being consumed by several predatory birds that use the intertidal zone for feeding (e.g., Blokpoel et al. 1992; Hubbard and Dugan 2003). The association between green macroalgae and *E. analoga* has a seasonal pattern, being fouled animals present only during summer and absent during winter, possibly because macroalgae growth is enhanced in warmer water conditions (Firstater et al. 2009). Furthermore, the association was found in one of the most productive marine systems (Tarazona et al. 2003), and it is likely that nutrients play an important role on its development (Valiela et al. 1997; Firstater et al. 2009). Epibionts attach to the anterior part of the carapace and first appendages, forming a dense, floss-shape mat, usually one to twofolds the surface of the animal (Firstater et al. 2009; Fig. 1a). Epibiosis affects mainly the larger individuals of the population, with neutral effects on demographic and life history parameters of *E. analoga*, but with a positive effect on their body condition (Firstater et al. 2009). Fouled animals have longer burrowing times than those non-fouled, and when animals are buried into the sediment, the mat of attached macroalgae remains always above the sediment surface (Firstater et al. 2009; Fig. 1b). The negative effect on burrowing ability is attributed only to the epibiosis, since burrowing time is reversible when macroalgae is experimentally removed (Firstater et al. 2009). The reduced burrowing ability of fouled *E. analoga*, and the potential visual attractive effect of the macroalgae, suggests that the epibiosis might increase the predation risk by birds and hence its mortality rate.

In this work, we evaluate the importance of predation by birds on intertidal *E. analoga* fouled by macroalgae in a sandy beach close to the Anc n Bay. In particular, we (1) investigated the epibiosis prevalence by macroalgae on the intertidal population of *E. analoga*, (2) calculated and compared predation rates by birds on fouled and

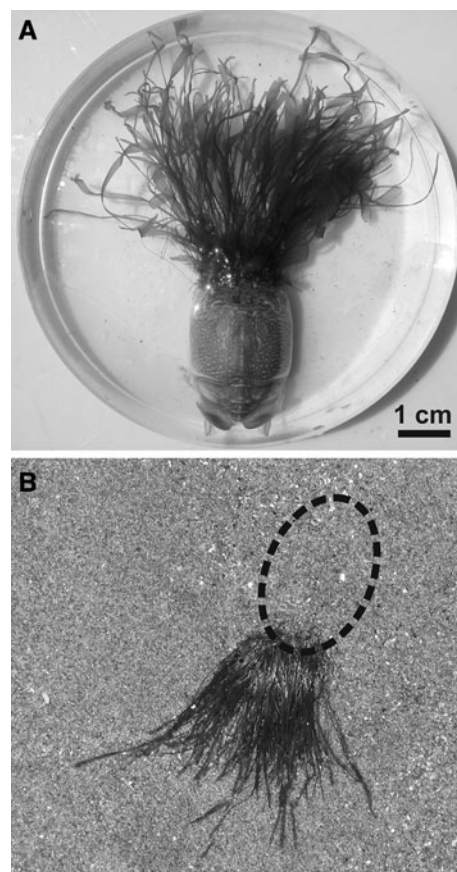


Fig. 1 **a** Green macroalgae epibiont attached to the anterior part of the carapace of *Emerita analoga*; **b** floss-like mat of green macroalgae epibiont in the sediment surface, indicating the presence of a buried *Emerita analoga* (dashed line)

non-fouled animals, and (3) estimated mortality rates due to predation of *E. analoga* with and without epibiosis.

Methods

Study site

The study was conducted during austral summer months in a beach (Playa Huaquillo, ~200 m long) located south of the Anc n Bay (central Peru: 11° 46' S, 77° 11' W). The beach is delimited by rocky cliffs and rock outcrops and is exposed to a moderate wave action. Its morphodynamic state corresponds to an Intermediate Type I beach (*sensu* Short and Wright 1983), with a mean grain size of 0.25 mm and a mean slope of 2.75% (Firstater et al. 2009). Tides have a mixed semidiurnal regime and average amplitude of 0.54 m (Direcci n de Hidrograf a y Navegaci n 2006). The area is characterized by high nutrient input due to upwelling and probably due to organic loads of anthropogenic origin, and with low oxygen concentration

due to stagnation (Tarazona et al. 2003; Firstater et al. 2009).

Emerita analoga density and epibiosis prevalence

We conducted three samplings of *E. analoga* density: one in December 2005, the other in February 2006, and the last in April 2007. Samplings were performed at three different intertidal levels: the uppermost was performed on moist but unsaturated sand ~2 m above the effluent line (thereafter “retention zone”, *sensu* Salvat 1964), the other ~2 m below the effluent line (thereafter “upper swash zone”), and the lowermost in the lower limit of the swash zone (thereafter “lower swash zone”). No samplings were conducted in the dry sand zone, as previous surveys indicated that no animals were present there. Our observations suggested that fouled and non-fouled animals are more abundant in the shallow subtidal zone; thus, in April 2007, we also sampled that zone (between 0.5 and 1 m depth). All samplings were done along ten equally spaced transects perpendicular to the shoreline. One sampling unit was collected along each transect and at each shore level with a core of 0.025 m² and 0.15 m depth. The collected material was sieved through a 1-mm mesh, and *E. analoga* individuals were placed in numbered plastic bags. In the laboratory, all individuals were sexed (under a dissecting microscope); separated into juveniles, males, females without eggs, and ovigerous females, discriminating in each case the fouled animals; and measuring them to the nearest 0.01 mm (carapace length [CL]; from the tip of the rostrum to the distal scoop). Megalopae were not included in this analysis. Densities of fouled and non-fouled *E. analoga* were compared among levels of the shore and sampling dates with factorial ANOVAs (Zar 1999). Size distributions were compared among shore levels at each sampling date with Kolmogorov–Smirnov two-sample test (Zar 1999). Mean sizes of fouled and non-fouled *E. analoga* were compared among sexes, levels of the shore, and sampling dates with factorial ANOVAs (Zar 1999). For ANOVA’s, data were log transformed to meet parametric assumptions (Zar 1999). When interactions between factors were significant, multiple comparisons Tukey test was used (Zar 1999).

Birds abundance and predation on *Emerita analoga*

Quantification of predation rates by birds was performed weekly from November 2005 to March 2006 by periods of two consecutive days. Most observations started at mid-morning (~9:00) and ended at the early afternoon (~16:00), and complementary observations were conducted at daybreak (~6:00) and before sunset (~18:00) to

account for possible variations in foraging behavior. Bird species present were identified using Clements and Shany’s (2001) field guide. To quantify predation rates, focal observations were conducted at a distance of no more than 50 m from the birds with binoculars (16 × 50), and data was saved into a portable tape recorder. Each bird was observed during periods of 5–10 min, completing a total of 29 h of focal observations. The following categories of behavior were recorded: (1) peck: striking at the substrate with the bill, (2) prey capture: prey captured from the substrate, and (3) swallow: swallowing action after the capture of a prey. Handling time is the time elapsing from the capture of a prey until it is swallowed. The following categories of prey items were identified: (1) *E. analoga* without epibiosis, (2) *E. analoga* with macroalgae epibiont, and (3) other items. Because assumptions for parametric tests were not met, predation rates and handling times on *E. analoga* with and without epibiosis were compared for each bird species with the non-parametric Kolmogorov–Smirnov two-sample test (Zar 1999). To evaluate preference for fouled or non-fouled *E. analoga*, the Chesson’s alpha index (Chesson 1978) was used. The index measures an invariant degree of preference on the part of the predator (Pearre 1982). The index is:

$$\text{Chesson's alpha} = (r_i/p_i) / \sum_i (r_i/p_i)$$

where r_i and p_i are the proportion of prey item i in the diet and the environment, respectively. Therefore, this index indicates the preference of a consumer for a food type relative to the other food types present. In our case with two food types (i.e., fouled and non-fouled *E. analoga*), values >0.5 indicate preference for that prey.

To calculate the daily mean number of birds foraging in the beach along a day, we recorded the total number of individuals feeding or resting twice at each sampling day. The daily mean number of birds was the average of both censuses. In all possible cases, we identified the beach zone (i.e., lower and upper swash, retention and dry zones) where birds fed or rested.

Mortality of *Emerita analoga* caused by birds

Only mortality caused by *Larus modestus* was calculated, given that the other bird species occurred at too low numbers to include them into the analysis. In this study, mortality was defined as the fraction of fouled and non-fouled *E. analoga* consumed that were present in the intertidal area and thus accessible to predation by birds; thus, this value does not represent the mortality rates for the entire population of *E. analoga*, since subtidal animals were not included. Mortality was calculated as follows:

$$M_{f,nf} = (Np \times B \times F_{f,nf}) / (Ne_{f,nf})$$

where M is the mortality rate; Np is the daily mean number of predators present in the beach and B is the fraction of predators that were actively foraging, both Np and B were obtained from the bird censuses; F is the predation rate, estimated from the focal observations; Ne is the number of intertidal *E. analoga*, and f and nf indicate the fouled and non-fouled *E. analoga*, respectively. Ne was estimated from the core samplings of December 2005 and February 2006 (i.e., within the period in which we made bird observations). Total abundance of *E. analoga* was estimated separately for each sampling date and only for the swash zone (no animals were found in the retention zone, see Results). For this, the average density obtained with the core samplings ($N = 20$; 10 sampling units at each the upper and lower swash zones) was multiplied by the total area of the swash zone. The area of the swash zones was estimated by multiplying the width of the zone by the length of the beach. The width of the swash zone was measured with three parallel transects established between the effluent line and the lowest tide mark, indicated by bore collapse. We chose to use the two values of total abundance estimations (i.e., one for each sampling date), instead of each value obtained in each sampling unit, as these yielded zero animals in some instances, disabling the calculation of mortality. Because we wanted to estimate daily mortalities, we calculated daily predation rates by considering that birds forage during sunlight hours (i.e., on average 12 h during the study season; Dirección de Hidrografía y Navegación 2006). Our observations indicated that the larger animals were fouled (see Results). Thus, given that prey size may influence the preference by birds (e.g., Goss-Custard 1977), but we were unable to account for this during focal observations, to avoid size as a confounding factor, we also evaluated mortality by considering that all animals consumed were within the size range of fouled animals or larger (i.e., by only including these animals in the calculation of Ne_f).

To compare proportions of fouled and non-fouled *E. analoga* consumed, the distribution of all of the possible mortality values of fouled *E. analoga* was generated by multiplying each value of $Np \times B$ (i.e., the number of birds actively foraging) by each value of F_f and dividing it by each of both December 2005 and February 2006 values of Ne_f ; in an analogous way, the distribution of all of the possible mortality values of non-fouled *E. analoga* was generated by multiplying each value of $Np \times B$ by each value of F_{nf} and dividing it by each of both December 2005 and February 2006 values of Ne_{nf} . This yielded distributions of 13 152 values of mortality. For both distributions, standard normal confidence limits (Manly 1998) were

constructed to evaluate significant differences in the percentage of fouled and non-fouled *E. analoga* consumed.

Results

Emerita analoga density and epibiosis prevalence

Density of *E. analoga* was higher in the lower than in the upper swash zone in all sampling dates (two-way ANOVA, $F_{1,54} = 22.53$, $P < 0.001$; Fig. 2), and mole crabs were never found in the retention zone. The sampling of April 07 revealed that the density of *E. analoga* in the subtidal zone was not different from that of the lower swash zone, and at both levels, the densities were higher than in the upper swash zone (one-way ANOVA, $F_{2,27} = 13.26$, $P < 0.001$; Tukey HSD test, $P < 0.005$ for the significant differences; Fig. 2). Size distributions of *E. analoga* differed between the upper and lower swash levels at all sampling dates and between the lower swash and subtidal zone in the sampling of April 07 (K–S two-sample test, $P < 0.05$ in all of the cases; Fig. 3); although there were no differences between the subtidal and upper swash zone (K–S two-sample test, $P > 0.05$; sampling of April 07; Fig. 3). These differences, however, were not consistent along sampling dates: in Dec 05, the differences may be attributed to a larger proportion of mid-sized animals in the lower swash zone; in Feb 06, these differences can be explained by the presence of more animals of the larger size classes in the lower swash zone and smaller animals in the upper swash zone; in April 07, large-size animals were present in the lower zones (i.e.,

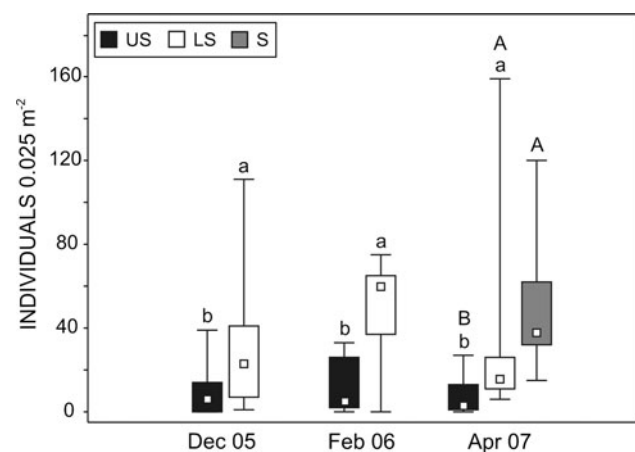


Fig. 2 Densities of *Emerita analoga* (individuals 0.025 m^{-2}) in the upper swash (US), lower swash (LS), and subtidal (S) zones in the three sampling dates. Different *lowercase letters* indicate differences between the *upper* and *lower* swash zone after two-way ANOVA; different *uppercase letters* indicate differences among the three shore levels in April 07 after one-way ANOVA. Here and thereafter, *vertical lines* represent 0.01 and 0.99 percentiles, *box limits* are the 0.25 and 0.75 percentiles, and *symbols within boxes* are the median

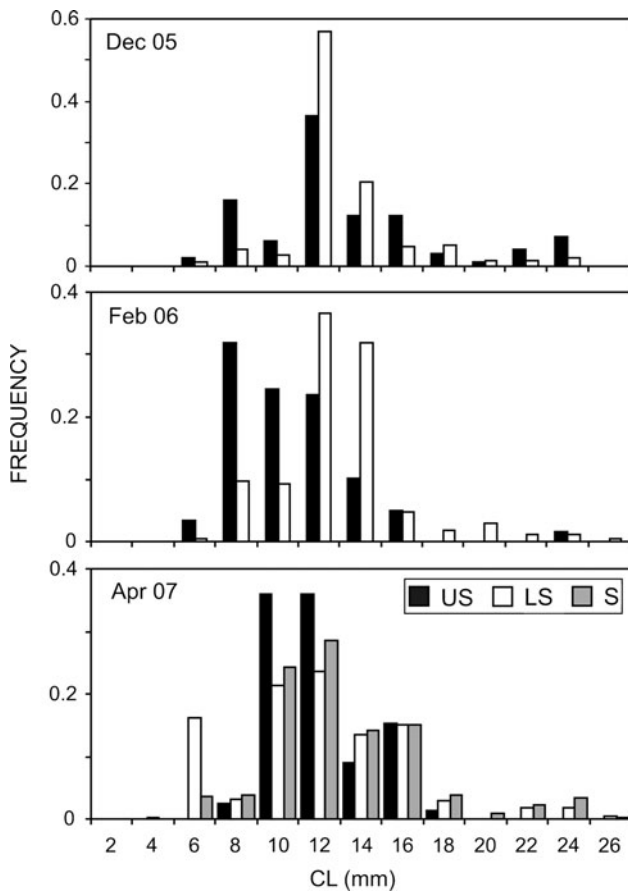


Fig. 3 Size frequency distributions of *Emerita analoga* in the intertidal levels sampled in (a) December 05, (b) February 06, and (c) April 07

subtidal and lower swash zones), but also a high number of recruits were found in the lower swash zone (Fig. 3).

Fouled animals were only found in the subtidal and the lower swash zone (Fig. 4). Epibiosis prevalence in the lower swash zone was 1.12, 2.57, and 1.33% in Dec 05, Feb 06, and April 07, respectively; for the whole intertidal zone (i.e., lower and upper swash zones pooled), epibiosis prevalence was 0.88, 2.12, and 1.11% in Dec 05, Feb 06, and April 07, respectively. In the subtidal zone (April 07), epibiosis prevalence was 8.07%. Despite the low overall prevalence in the intertidal and subtidal zone, epibiosis affected mainly the larger animals. Only females were found fouled in the lower swash zone (Fig. 4). Within the size range affected at this level of the shore (18–23 mm CL; see Fig. 4), between 20 and 38% of the animals were fouled. In non-ovigerous and ovigerous females, epibiosis prevalence was 2.8–5.8 and 17.6–66.7%, respectively. Fouled females of the lower swash zone were larger than those non-fouled (both ovigerous and non-ovigerous grouped given the low number of fouled females found; two-way ANOVA, $F_{1,222} = 31.0, P < 0.0001$; Fig. 4), and those sampled in December 2005 were larger than those

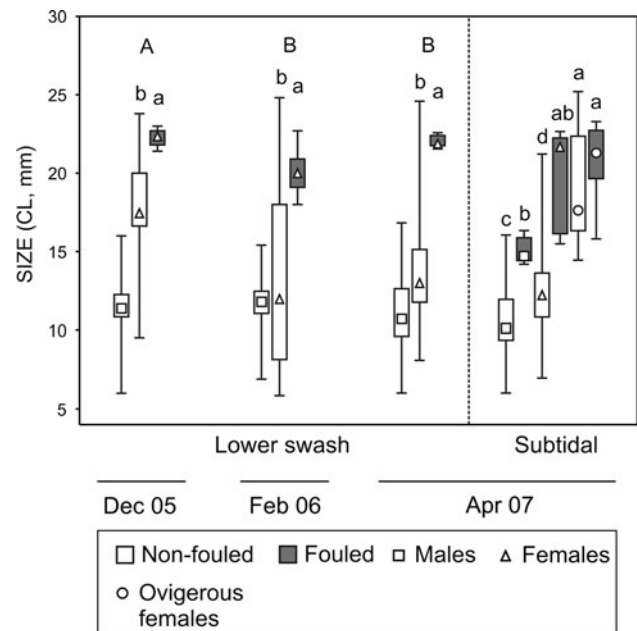


Fig. 4 Size (CL, mm) of fouled and non-fouled *Emerita analoga* in the lower swash (only females) and subtidal zones (both males and females). Ovigerous and non-ovigerous females were pooled for the analysis in the lower swash zone, given the low numbers of fouled non-ovigerous females found. Males from the lower swash zone were included in the figure but were not compared. Different lowercase letters indicate size differences between fouled and non-fouled females. Different uppercase letters indicate size differences among sampling dates. Different analyses were conducted for the lower swash and subtidal zones

from February 2006 and April 2007 (two-way ANOVA, $F_{2,222} = 3.96, P < 0.05$; Tukey HSD test, $P < 0.001$ for the significant contrasts; Fig. 4). In the subtidal zone (sampling from April 07), both males and females were found fouled (Fig. 4), and 33% of the animals within the size range affected were fouled. In males, non-ovigerous, and ovigerous females of the subtidal, epibiosis prevalence was 4.9, 5.3, and 85.7%, respectively. There, a significant sex \times epibiosis interaction was found (Table 1), since fouled males and fouled females were larger than non-fouled males and non-fouled females, respectively; but fouled and non-fouled ovigerous females were not different. Furthermore, there were no size differences among fouled non-ovigerous females and both fouled and non-fouled ovigerous females (Fig. 4; Table 1).

Birds abundances and predation on *Emerita analoga*

Bird species present in the beach were the gray gull *Larus modestus*, the Franklin’s gull *Larus pipixcan*, the band-tailed gull *Larus belcheri*, the black oystercatcher *Haematopus ater*, the common oystercatcher *Haematopus palliatus*, and the whimbrel *Numenius phaeopus* (Table 2). All of these species were observed capturing and eating

Table 1 Results of the two-way ANOVA for the differences in size between fouled and non-fouled animals for the subtidal zone

Effect	SS	d.f.	MS	F	P
Sex	0.85	2	0.43	56.32	0.0000
Epibiosis	0.45	1	0.45	59.49	0.0000
Sex × Epibiosis	0.12	2	0.06	7.78	0.0005
Error	3.40	450	0.01		

E. analoga with variable intensity, but they also fed on stranded remains and little unidentified items.

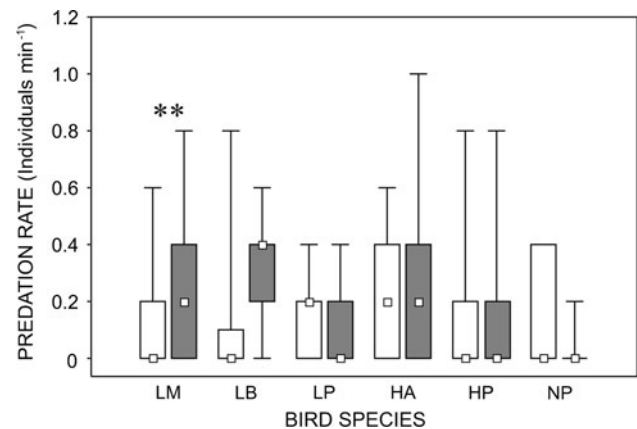
Larus modestus was the most abundant bird species along the sampling dates and was the only bird species present in the beach in all of the days of observation (Table 2). Focal observations of 274 *L. modestus* were performed for a total of 1354 min (Table 2). On average, 39% of *L. modestus* individuals observed in a day were feeding, while the other 61% were resting. *L. modestus* fed mainly along the swash zone (98% of the observations), employing different foraging tactics. Sometimes, they made short runs or flights to the lower swash zone when the waves recede, pecking and probing actively in the sand, and returning up fast when waves come again; other times, they ran or flew directly to a prey in the same zone. Occasionally, they were also observed pecking actively in the sand while walking along the swash zone. Predation rates of *L. modestus* on fouled *E. analoga* were higher than on non-fouled animals (Kolmogorov–Smirnov 2-sample test, $P < 0.001$; Fig. 5).

Haematopus ater was not particularly abundant throughout the observation days (mean = 0.36 individuals day⁻¹, Table 2), but it was observed actively searching and preying on *E. analoga* when was present in the beach. Focal observations of 38 *H. ater* were performed for a total of 190 min. Like *L. modestus*, *H. ater* fed mainly along the swash zone (98% of the observations). Predation rates on fouled and non-fouled individuals were not different (Kolmogorov–Smirnov 2-sample test, $P > 0.1$; Fig. 5). A high proportion of small unidentified items (23% of the total prey consumed) were also consumed.

Table 2 Summary of the results of the bird censuses and focal observations

	<i>Larus modestus</i>	<i>Larus pipixcan</i>	<i>Larus belcheri</i>	<i>Haematopus ater</i>	<i>Haematopus palliatus</i>	<i>Numenius phaeopus</i>
No. of days observed	33	12	8	13	3	8
Individual day ⁻¹ (mean, SD)	34.79 (23.72)	1.91 (4.23)	1.82 (8.42)	0.36 (0.56)	0.14 (0.55)	0.17 (0.32)
Time of observation (min)	1,354	70	40	190	25	35

N of days observed is the total number of days that each bird species was observed in the beach, individuals day⁻¹ is the mean number of individuals present in the beach each day, and time of observation is the total time (in minutes) each bird species was observed during the focal observations

**Fig. 5** Predation rates (individuals min⁻¹) on non-fouled (squares, gray boxes) and fouled (triangles, white boxes) *Emerita analoga* for each bird species. Asterisks indicate significant differences ($P < 0.05$) between fouled and non-fouled individuals. LM, *Larus modestus*; LB, *Larus belcheri*; LP, *Larus pipixcan*; HA, *Haematopus ater*; HP, *Haematopus palliatus*; NP, *Numenius phaeopus*

The other bird species (*L. belcheri*, *L. pipixcan*, *H. palliatus*, and *N. phaeopus*) occurred sporadically in the beach or preyed on *E. analoga* only occasionally (Table 2). Their predation rates on fouled and non-fouled *E. analoga* were variable and no differences were found (Kolmogorov–Smirnov 2-sample test, $P > 0.05$ for all of the cases; Fig. 5).

Despite this variability in the predation rates, all of the bird species preferred fouled over non-fouled *E. analoga* (Chesson's alpha > 0.96 in all of the cases), being eaten at a much higher proportion than their availability in the intertidal.

Mortality of *Emerita analoga* caused by birds

Only *L. modestus* was able to consume, on average, 35.4% of the intertidal fouled *E. analoga* day⁻¹, and 0.1% of non-fouled intertidal *E. analoga* day⁻¹. Estimated confidence limits indicated that this difference was significant (proportion of fouled individuals consumed: $X_{\text{fouled}} = 0.354$, SD = 0.519; median = 0.171; 95% confidence limits:

0–1.524; proportion of non-fouled individuals consumed: $X_{\text{non-fouled}} = 0.001$, $SD = 0.002$; median = 0; 95% confidence limits: 0–0.006). When considering that only animals within or larger than the size range of fouled *E. analoga* (i.e., ≥ 18 mm CL) were consumed, mortality was still different (proportion of non-fouled individuals consumed: $X_{\text{non-fouled}} = 0.035$, $SD = 0.058$; median = 0; 95% confidence limits: 0–0.140).

Discussion

Our results showed that the epibiotic association between green macroalgae and *E. analoga* has important effects on fouled individuals. The association is more frequent in larger animals, being adult females particularly affected. Bird observations and calculation of mortality rates indicate that fouled animals are more heavily consumed than those non-fouled of the same size class and hence of the same sex. We discuss here the factors associated with fouling that could have enhanced the susceptibility to predation.

At our study site and during the study period, *E. analoga* density increased from the upper to the lower sampled zones, and fouled individuals were only found in the lowest zones (i.e., the lower swash and subtidal zones). The pattern of increased densities of *E. analoga* to the lower zones is also present throughout the year at our study site (Firstater et al. 2009) and matches well with its across-shore zonation in beaches close to the end of the reflective state (e.g., Jaramillo et al. 2000; Lastra et al. 2004); although the abundance of *E. analoga* across the shore can also vary seasonally, across the tidal cycle and with the beach morphodynamics (e.g., Cubit 1969; Jaramillo et al. 2000; Dugan et al. 2004).

The epibiosis prevalence during the study period was relatively low for the entire population; however, larger animals, mainly adult females, were mostly susceptible to fouling. In decapod crustaceans, the epibiosis prevalence commonly increase with the size and age of individuals (e.g., Gili et al. 1993; Lovrich et al. 2003), since the intermolt duration increases with the age and size of the crabs (Siegel 1984; Gili et al. 1993; Lovrich et al. 2003) and epibionts are shed along with their exuvia during molting (e.g., Gili et al. 1993). Female *E. analoga* are larger and their longevity is twice than that of males (e.g., Contreras et al. 1999) and thus they offer more time for fouling species to settle and grow (Firstater et al. 2009). In addition, *E. analoga* is normally buried leaving the anterior part of the carapace and the first appendices out of the sand (e.g., Villegas et al. 2005), and hence larger individuals may also have a larger area for algae sporelings to settle and growth.

A differential size distribution across the beach has been commonly reported for *E. analoga* populations, being the larger animals relatively more abundant in the lower zones (e.g., Penchaszadeh 1971; Sánchez and Alamo 1974; Alvitres et al. 1998). This pattern was also found at our study site and may explain the higher prevalence of epibiosis at low shore levels. In addition, fouling by itself can affect the across-shore distribution of the animals via swash currents (see Dugan et al. 2000; Manning and Lindquist 2003). Fouling usually increases dragging and buoyancy of the animals (e.g., Wahl 1996) and thus fouled animals, less capable of dealing with swash conditions because of different burrowing abilities and swash behaviors (see Dugan et al. 2000; Manning and Lindquist 2003), can shift from the swash zone to the shallow subtidal, where physical conditions are more stable. In addition, it has been experimentally demonstrated that the reported epibiosis increases the burrowing time of *E. analoga* (Firstater et al. 2009). This negative effect of epibiosis on burrowing behavior may be particularly important during the tidal migrations of *E. analoga*. Tidal migrations may allow animals to maintain a position at a water depth not easily accessible to predatory fishes and birds (Jaramillo et al. 2000). When mole crabs moves up or down the shore along the tidal cycle with the wave wash or swash (e.g., Cubit 1969; Dugan et al. 2000; Jaramillo et al. 2000), the macroalgal epibionts would lead to a reduction or even impede the animals to burrow in the swash zone, exposing them for longer time and making them more vulnerable to detection and predation by birds. Our observations of birds that captured *E. analoga* by making short runs to the lower shore when waves recede and exposed the area, using a similar visual feeding tactic previously reported for *L. modestus* preying on *E. analoga* (e.g., Ryan et al. 1987; Blokpoel et al. 1992), support this explanation. Furthermore, the feeding behavior and prey preference of birds could be related not only with a reduced burrowing ability of fouled individuals, but also with the attractive effect of the algae mat that could make them more conspicuous and readily detectable by visual predators. Although we were not able to differentiate whether birds preyed on fouled animals in the active swash because they burrowed slowly (or were unable to burrow) or because they were more conspicuous, the visual feeding tactic employed by the more abundant birds (i.e., *L. modestus*) indicate that they can promptly detected them, even if they are already buried, as the macroalgae frond remains above the sediment surface evidencing their presence. In addition, it has been shown that body condition is positively correlated with fouling in *E. analoga*, probably because fouling forces animals to spend more time feeding in the shallow subtidal rather than dealing with the harsh conditions of the swash zone (Firstater et al. 2009). Thus, increased profitability of

the animals induced by fouling may also explain the bird preference.

It has been demonstrated that the prevalence and abundance of parasites in *E. analoga* relates with the abundance of birds preying on them (Smith 2007). In our case, because parasites may affect the burrowing behavior of their hosts (e.g., Swennen 1969; Curtis 1987; Poulin and Latham 2002), it would be reasonable to suppose that parasitized *E. analoga* are more susceptible to fouling and in turn to predation. However, since fouled animals burrow at similar rates than those non-fouled when the epibiotic algae is experimentally removed (Firstater et al. 2009), we suggest that parasites are not related to epibiosis and thus with increased predation on *E. analoga*, at least by affecting their burrowing ability. In addition, despite the size of the prey may also influence the food preference by birds (e.g., Goss-Custard 1977), *L. modestus* consumes a broad range of *E. analoga* sizes (range between 0.2 and $1 \times$ bill length, mean = $0.52 \times$ bill length; Ryan et al. 1987). Furthermore, mortality of fouled individuals was still higher than that of those non-fouled when considering that *L. modestus* consumed only large animals; thus, we suppose that their preference for fouled mole crabs relates epibiosis or with the associated factors above mentioned, but not with the larger size of the animals, at least within the size ranges affected.

Only *L. modestus* is able to remove 35% of the fouled animals from the intertidal zone everyday, indicating that predation may be an important factor regulating the abundance of fouled animals in the intertidal. Nevertheless, to keep removal rates in the calculated levels, fouled *E. analoga* must be replaced continuously from the subtidal; otherwise they would disappear from the intertidal within a few days. Despite epibiosis prevalence increases to the subtidal zone, the subtidal fraction of the fouled population should be huge to replace the fouled individuals eliminated by predation. Instead, rates of attachment and growth of macroalgae may be high enough to rapidly produce new fouled animals. *Enteromorpha* spp. can germinate within few hours once spores have attached on a suitable surface (Callow et al. 1997; Callow and Callow 2002), and adults can grow up to 21% per day when environmental conditions are optimal (Taylor et al. 2001). Water temperature, high nutrient input due to upwelling, and low oxygen concentration due to stagnation (Tarazona et al. 2003) might facilitate macroalgal growth at our study site during warmer months, when fouled animals are present in the beach (Firstater et al. 2009).

Beaches close to the end of the reflective state are characterized by high variability due to the increased magnitude of the erosion–accretion dynamics (Brown and McLachlan 1990; Brazeiro 2001) and hence beach macrofauna is generally considered to be mainly physically

controlled (e.g., Defeo and McLachlan 2005). During periods of beach erosion, *E. analoga* may disappear from the intertidal zone and become subtidal (Jaramillo et al. 2000), but also to get locally extinct if climatic conditions get harsher (see Brazeiro 2001). Thus, it would be expected that the occurrence of large numbers of fouled *E. analoga* in the intertidal zone of our beach, and thus to be available for predatory birds, takes place when the swash zone is stable due to steady weather conditions and when environmental variables facilitates rapid algal growth.

Because predation pressure changed as a consequence of altered behavior and not an abundance increase of the predator, this interaction qualifies as an “interaction modification”, as opposed to an “interaction chain”, with serial direct effects (Wootton 1993). This is, by directly affecting the burrowing ability of mole crabs, by enhancing its visual attractiveness, or by increasing its profitability (i.e., increasing its body condition); the interaction represents a negative indirect effect on the host by increasing the predation pressure by birds. Besides those observed at our study site, other resident and migratory birds, including the Common Tern *Sterna hirundo* and the Rudy Turnstone *Arenaria interpres*, have been observed preying on *E. analoga* (Blokpoel et al. 1992). We have also seen large flocks of *N. phaeopus* (>90 individuals) feeding on *E. analoga*, including fouled individuals, in small beaches within the Ancón Bay, next to our study sites (F. Hidalgo, personal observation.). In addition to birds, other visual and tactile predators such as crabs (e.g., ghost crab *Ocyroide gaudichaudii*: Koepcke and Koepcke 1953) and fishes (e.g., the sciaenids *Menticirrhus ophicephalus*, *Sciaena deliciosa*, *Cilus gilberti*: Alvitres et al. 1999; Vargas et al. 1999) usually prey on *E. analoga* in the region and might take advantage of fouled animals, both in the intertidal but also in the subtidal zone, where birds are less effective. Nevertheless, macroalgae may not be equally attractive for each predator species. For example, epibiosis by hydrozoans in the infaunal clam *Donax variabilis* facilitates predation by crabs through increasing their ability to detect them, but protects clams against a fish predator via chemical signaling (Manning and Lindquist 2003). Similarly, barnacle epibionts in *Mytilus edulis* enhance predation by shore crabs, while they decrease predation by a starfish (Wahl et al. 1997; Laudien and Wahl 1999). In our study, whether macroalgae facilitates or inhibits predation by crabs and fishes on *E. analoga* was not assessed; thus, it is unclear which are the combined effects of all predators on the entire *E. analoga* population. Nevertheless, whatever the net effect on the host, *Enteromorpha* spp. may benefit from the association by gaining a hard substrate for attachment in an environment where it could not otherwise occur (e.g., Wahl 1996; Creed 2000; Manning and Lindquist 2003), although it can also be consumed with the host.

In summary, our results show that epibiosis, possibly by affecting the appearance, burrowing ability or profitability, has important consequences for larger *E. analoga* by increasing their mortality rate due to bird predation in the intertidal zone. This may be particularly important if it is taken into account that the larger adult females, as is this case, can represent the major reproductive output of the population (e.g., Dugan et al. 1991; Contreras et al. 1999). Nevertheless, the importance of birds in restricting the abundance of fouled *E. analoga* in the intertidal must be limited to periods when calm swash conditions prevails, allowing the persistence of *E. analoga* in the intertidal, and when environmental factors (e.g., water temperature, nutrient, and oxygen concentration) benefit rapid settlement and growth of *Enteromorpha* spp. on the animals.

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