

Foraging behaviour and diet of American Oystercatchers in a Patagonian intertidal area affected by nutrient loading

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Abstract. Eutrophication increases the biomass of opportunistic green macroalgae that covers intertidal zones, and macroalgal blooms may affect the intertidal invertebrate community and predation of invertebrates by shorebirds. In San Antonio Bay, Argentina, eutrophication from the discharge of wastewater from a coastal town produces periodic macroalgal blooms. Our aim was to assess if macroalgal blooms affect the foraging behaviour and diet of the American Oystercatcher (*Haematopus palliatus*). A macroalgal transplant experiment was performed in order to evaluate how epifaunal species respond to a macroalgal canopy. The availability of prey for Oystercatchers, and their foraging behaviour and diet, were analysed in two paired channels with different nutrient loadings. Oystercatchers generally ate the most profitable prey and avoided prey with a profitability value lower than the mean rate of energy intake. During the macroalgal blooms, Oystercatchers avoided two prey species with high profitability values, shifting their foraging strategy and feeding onto a suboptimal prey but with a high encounter rate. Our results suggest that nutrient loadings and the macroalgal blooms that they generate have effects on the diet and foraging behaviour of Oystercatchers, which results in an increase of the average rate of energy intake of Oystercatchers foraging along the channel subject to a macroalgal bloom.

Introduction

Shorebirds are conspicuous predators of coastal habitats that can respond to the availability of benthic prey by changing their distribution and behaviour (Goss-Custard *et al.* 2006). Changes in the availability of prey can be induced by natural or anthropogenic factors, or both (Pfister *et al.* 1992). One of the most common anthropogenic factors that changes the composition and abundance of benthic organisms is eutrophication caused by increased nutrient loadings from human activities in coastal ecosystems (Valiela 2006). In naturally low-nutrient coastal systems, such as estuaries and bays, increased nutrients rapidly increase primary productivity through the growth of opportunistic algal species, causing macroalgal blooms (e.g. Valiela *et al.* 1997; Raffaelli *et al.* 1998).

The presence of a macroalgal canopy resulting from eutrophication may affect predation of invertebrates by shorebirds by changing the density, conspicuousness or accessibility of prey. The density of prey can either decrease or increase depending on the species (Hull 1987; Raffaelli *et al.* 1991; Everett 1994). For example, Hull (1987) found that macroalgal blooms resulted in increased density of the deposit feeder *Capitella capitata* – an anoxic tolerant species – but lower densities of a less anoxic tolerant species. Conspicuousness can

be reduced by increased camouflage against the macroalgal mats (Hull 1987; Everett 1994), whereas accessibility may be increased by upward vertical migration of prey (Kalejta and Hockey 1991). However, the extent to which the distribution and behaviour of shorebirds is altered by eutrophication is not obvious (Lopes *et al.* 2006).

The way a bird responds to changes in habitat depends on its degree of plasticity, which may allow it to tolerate or take advantage of that disturbance (Brawn *et al.* 2001). The American Oystercatcher (*Haematopus palliatus*) is a common shorebird that breeds along the coast of San Antonio Bay, Patagonia (Yorio *et al.* 1998), a bay partly affected by eutrophication (Teichberg *et al.*, *in press*). The American Oystercatcher is not considered threatened globally or in Argentina (López Lanús *et al.* 2008; BirdLife International 2009), and has been recorded foraging in estuarine environments in Argentina, mainly feeding on the Stout Razor Clam (*Tagelus plebeius*) and on viscera and eggs of crabs (*Neohelice granulata*, *Cyrtograpsus angulatus*) (Bachmann and Martínez 1999; Daleo *et al.* 2005). Because it feeds mainly on benthic prey, American Oystercatchers are likely to be indirectly affected by eutrophication through changes in the algal canopy (see Nixon *et al.* 1971; Whorff *et al.* 1995; Downes *et al.* 1998; Kelaher 2003).

San Antonio Bay is a provincial Natural Protected Area and a BirdLife International Important Bird Area (IBA) (Di Giacomo 2005). This bay is also a Western Hemisphere Shorebird Reserve Network site owing to its importance as a stop-over site for neotropical migratory shorebirds (González *et al.* 1996). Despite the high tidal amplitude of the bay (up to 9 m), eutrophication produces periodic macroalgal blooms during winter and spring, which may affect the use of this site by shorebirds (Iribarne *et al.* 2004; Teichberg *et al.*, *in press*). The source of this eutrophication is the discharge of wastewater from the coastal town of San Antonio Oeste (population ~25 000 inhabitants). This system offers the possibility of examining the effect of anthropogenic nitrogen discharge on a Patagonian coastal ecosystem.

The aim of this study was to assess if macroalgal blooms affect the diet and foraging behaviour of American Oystercatchers. We would expect to observe differences in foraging behaviour and diet as a consequence of differing availability of prey resulting from the macroalgal bloom. To examine this, we studied two channels in the bay, one with a seasonal occurrence of macroalgal blooms and the other without. We conducted experimental trials, which included the manipulation of the macroalgal canopy, to evaluate the effect of macroalgal blooms on the abundance of benthic organisms, and we assessed the abundance of prey and the diet and foraging behaviour of Oystercatchers.

Materials and methods

Study area

The study was conducted in San Antonio Bay (40°44'S, 54°68'W, Fig. 1), Río Negro Province, Argentina. The bay is 80 km² in area, and is a marine system with a semi-diurnal tidal regime (and a tidal amplitude of up to 9 m); it is characterised by extensive intertidal flats, mainly of sand and pebbles, bordered on the landward side by areas of cord grass (mainly *Spartina alterniflora*; Isacch *et al.* 2006). San Antonio Bay is also a large and hypersaline environment owing to the combination of low annual rainfall (~250 mm year⁻¹) and absence of freshwater riverine inflow to the bay, so the salinity is usually above mean values for sea water (see Pascual *et al.* 2001).

The bay is cut by many channels with similar physical characteristics (e.g. size, depth, time of inundation, type of sediments) (Pickett 1989) and with very little water running during the low tide and completely flooded during the high tide. Of these channels, we selected two that differed markedly in the level of nitrogen input from the sewage system of the town of San Antonio Oeste (3.3×; E. Fanjul, unpubl. data). The first channel, running beside the town (the 'Treatment Channel', TC, Fig. 1) had high levels of dissolved inorganic nitrogen (DIN, in µM) and a seasonal macroalgal bloom during spring (average $DIN \pm s.d. = 57.10 \pm 13.36$). The second channel, running parallel to the first but ~400 m distant from the town (the 'Control Channel', CC, Fig. 1), had lower levels of DIN and no macroalgal blooms during spring (average $DIN = 17.00 \pm 1.97$).

Estimation of the density of the Oystercatchers' prey

The density of prey was estimated in the channels in spring and summer. To discriminate between the effect of a macroalgal canopy effect and a seasonal effect on benthic invertebrates, both channels

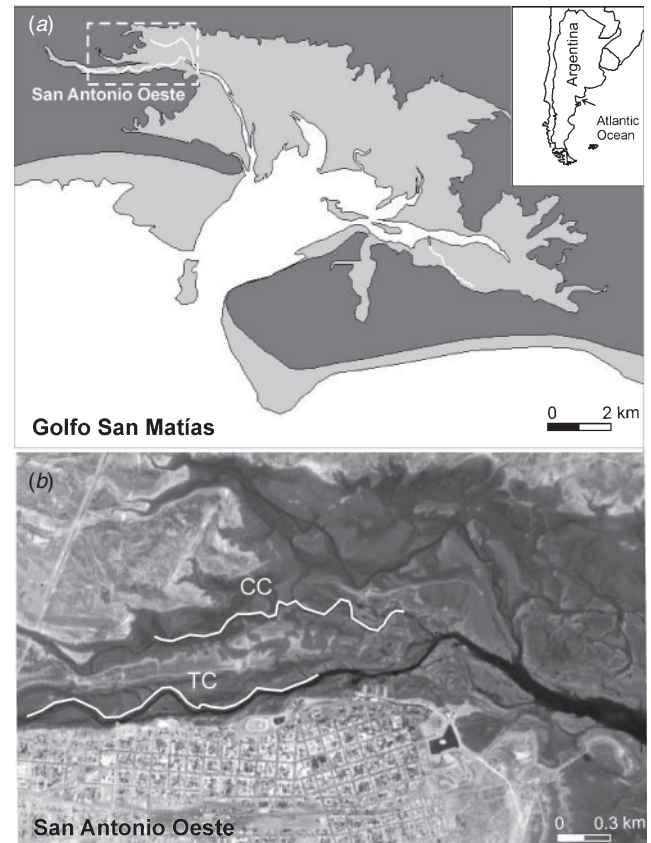


Fig. 1. (a) Illustration of San Antonio Bay, Argentina, during low tide. The three main habitats identified are: uplands (dark grey), intertidal (light grey) and sea (white). The inset in the upper right shows the location of the study area within Argentina. White dotted lines enclose the area enlarged in the lower image. (b) The study area within San Antonio Bay. The white lines show the treatment (TC) and control (CC) channels.

were compared during spring (TC with macroalgal bloom, CC without macroalgal bloom). To discriminate between the channel effect and the macroalgal effect on benthic invertebrates, both channels were compared during summer when neither channel had a macroalgal bloom. For each channel and sampling period, nine randomly selected core samples (26.5-cm diameter × 8-cm depth) were obtained from the mid- to low intertidal range, and sieved through a 1-mm mesh. Both infaunal and epifaunal invertebrates were sampled in each core. During spring in the TC channel, epifaunal organisms were removed by washing the algal canopy. The organisms were preserved in 70% alcohol, identified to the lowest possible taxon and counted using a 20× Olympus SZX7 binocular microscope (Melville, NY, USA). The null hypothesis was that there would be no difference in densities of invertebrates between channels for each season. The hypothesis was evaluated by *t*-test unless data did not satisfy assumptions of parametric tests, even after transformations, when Mann–Whitney tests were used (Zar 1999).

Manipulation of the macroalgal canopy

A macroalgal transplant experiment was conducted to evaluate how epifaunal species responded to a macroalgal canopy during

macroalgal blooms in spring (October–November). The wide tidal range of the study area prevented us from carrying out long-term transplant experiments because the transplanted canopy tended to be quickly washed away through tidal action. Although adding stones or some other structure would assist to retain the algae, this was not done because it would confound the algal effect. Since mobile organisms, such as crabs, respond fairly quickly to the presence of shelter, the experiment was performed under the assumption that consistent results could be obtained in short periods of 2 weeks.

Five 1 × 1-m quadrats were randomly selected in the CC mid-intertidal area during low tide. Macroalgae (a mix of *Ulva* spp. and *Enteromorpha* spp.) obtained from the TC were placed in each quadrat simulating the characteristics of the canopy developed in TC. Before doing that, algae were washed with channel water to remove epifauna. Control quadrats were paired with the experimental ones, and consisted of five 1 × 1-m quadrats delimited with stakes and without any placement of algae. After 16 days, a central core (26.5 cm in diameter × 8 cm deep) was removed from each treatment square and from each control square. Samples were sieved through a 1-mm mesh, and invertebrates were preserved in 70% alcohol, identified to the lowest possible taxon and counted using a 20× binocular microscope. The null hypothesis was that there was no difference in the densities of conspicuous invertebrates between treatment and control quadrats and was evaluated by *t*-test (Zar 1999).

Foraging behaviour and diet of Oystercatchers

The foraging behaviour and diet of the American Oystercatchers were analysed through focal observations made on randomly selected individuals (after Martin and Bateson 1993). The maximum abundance of Oystercatchers was 0.60 individuals ha⁻¹ (mean = 0.48, s.d. = 0.16) in TC and 0.40 individuals ha⁻¹ (mean = 0.37, s.d. = 0.05) in CC (J. P. Isacch, unpubl. data). The observations were grouped into two sets, one for each channel, during spring (October–November) and summer (January–February). During the observations we used Bushnell NatureView binoculars (10×), a Nikon Spotting Scope 80/80 A telescope (12–60×), and AIWA Voice Sensor Recording TP-M131 tape recorder. Individual birds were observed for at least 5 min (see Meire and Ervynck 1986). A total of 214 focal observations were taken ~3 h either side of low tide. The minimum and maximum duration of each sample considered for statistical analysis was 5 and 15 min respectively (mean 10 min each, s.d. = 4). A total of 116 focal observations were made in spring (81 in TC, 35 in CC) and 98 in summer (61 in TC, 37 in CC). To reduce observer bias, all focal observations were made by two observers using the same standardised methodology.

The following behavioural variables were recorded: (1) number of pecks (when only the tip of the bill entered the substrate); (2) number of successful and unsuccessful probes (probe is when the entire bill entered the substrate and the bird made a rapid up and down movement with the head); (3) duration of lateral sweeps (i.e. the time spent performing a lateral sweep search strategy with the bill through the surface of the mud to detect prey, used only sometimes); (4) number and type of prey captured; (5) handling time (i.e. time between capture of a prey

item and it being swallowed); and (6) how prey was detected (Oystercatchers used two search strategies to detect prey: a tactile strategy (see 'Results'), and a visual–tactile strategy, see Bachmann and Martínez 1999). The proportion of time spent using each search strategy (tactile and visual–tactile) was tested using Chi-square test (Zar 1999) comparing frequencies among channels and periods.

The size of prey captured was estimated with the objective of estimating the intake rates of Oystercatchers using the channels as feeding areas. As the number of very small prey items that were entirely ingested was negligible (frequency <3% of observed prey), after focal observation of each individual, all remains of prey (hard parts) left on the substrate were collected to improve the estimates of the size of prey. For crabs, the species and its size (carapace width, CW, relative to the length of the Oystercatcher's bill) of each item was estimated. Three size-categories identified for crabs were: small (CW 15–25 mm), medium (CW 25–35 mm) and large (CW >35 mm).

Further, the following parameters were estimated: (1) encounter rate, defined as the number of prey obtained per unit time (in min); (2) profitability, defined as the total energy obtained per unit time of handling prey (in kJ min⁻¹, calculated for each type of prey; see below for details); and (3) rate of energy intake, which was the total energy obtained per unit time of focal observation (in kJ min⁻¹).

Ivlev's prey selectivity index was used as a measure of prey selectivity (E) for various macroinvertebrate taxa in the diet (Ivlev 1961):

$$E = (r_i - p_i)/(r_i + p_i)$$

where r_i , proportion of each item in the diet; and p_i , proportion of each item in the environment. Values of Ivlev's index range from -1 (complete avoidance) to +1 (exclusive selection). We calculated the Bonferroni interval for the observed proportion of prey eaten (Neu *et al.* 1974; Byers *et al.* 1984) to analyse dietary selectivity. The difference was significant when prey availability (expected percentage of use) did not fall within the respective confidence interval for the observed percentage in the diet.

The null hypothesis of no difference in encounter and intake rates of Oystercatchers between each channel for each season was evaluated by an unequal variance *t*-test (Zar 1999). The null hypothesis of no difference in profitability among prey items of Oystercatchers was calculated by analysis of variance (ANOVA; Zar 1999).

Estimation of the rate of energy intake of Oystercatchers

The main prey items of the Oystercatchers were the crabs *Neohelice granulata* and *Cyrtograpsus angulatus*, the mytilid (bivalve) molluscs *Brachidontes rodriguezii* and *Mytilus edulis* (Common Mussel), the gastropod mollusc *Crepidula aculeata* (Spiny Slippersnail), the gastropod whelk *Buccinanops globulosum*, and undifferentiated polychaetes (see 'Results', Table 1). The fresh weight of the main molluscan and polychaetes prey items was estimated by collecting these from the foraging patches in both channels during both seasons. All invertebrates were randomly collected in different areas where Oystercatchers foraged (30 spiny slipper snail, 20 mytilid, 30 common mussel, 22 whelk and 60 polychaetes). The samples

Table 1. Importance of invertebrates in the diet of the American Oystercatcher and in the areas used for foraging by Oystercatchers (%)

TC, treatment channel (affected by nutrient loading and macroalgal blooms in spring); CC, control channel (not affected by nutrient loading); FA, foraging area

	Spring				Summer			
	TC		CC		TC		CC	
	Diet	FA	Diet	FA	Diet	FA	Diet	FA
<i>Neohelice granulata</i>	0.13	0	1.20	4.55	1.12	1.59	16.96	0
<i>Cyrtograpsus angulatus</i>	38.47	16.83	21.56	7.27	0.37	11.11	1.79	5.00
<i>Brachidontes rodriguezii</i>	56.92	19.80	13.17	3.64	42.83	34.92	9.82	0
<i>Mytilus edulis</i>	0.53	0	0	0	16.95	0	2.68	0
<i>Buccinanops globulosum</i>	1.05	7.92	10.78	7.27	34.45	15.87	36.61	2.00
<i>Crepidula aculeata</i>	0	0.99	34.73	43.64	3.72	0	16.96	4.00
Polychaetes	1.05	54.46	14.97	33.64	0.56	36.51	15.18	89.00

were placed in bags to prevent dehydration and then frozen. In the laboratory, body size was measured (maximum shell length, to 0.1 mm) and all soft parts were extracted and weighed (to 0.001 g). Empirical linear regressions were built and then used to estimate flesh content of prey from the size of hard parts left after Oystercatchers had eaten (e.g. shell length for *Mytilus edulis*).

For the crabs *Neohelice granulata* and *Cyrtograpsus angulatus*, fresh weight (M, in g) was estimated from CW (in mm) using regressions available from pre-existing data (Laboratorio de Vertebrados, UNMdP, unpubl. data). For *Neohelice granulata*, regression equations were: small, $M = 27.11 \text{ CW} + 4.32$; medium, $M = 34.35 \text{ CW} + 6.62$; and large, $M = 36.19 \text{ CW} + 6.62$. For *Cyrtograpsus angulatus*, equations were: small, $M = 29.4 \text{ CW} + 2.89$; medium, $M = 30.53 \text{ CW} + 5.01$; large, $M = 40.27 \text{ CW} + 8.79$.

To estimate the energetic content of prey, soft tissues were chopped, homogenised and dried in an oven at 60–80°C for 24–72 h to a constant weight. For each type of prey, wet and dry weights were determined to the nearest 0.001 g by weighing the homogenate before and after drying. The energetic content of each prey was estimated using empirical linear models that used the percentage dry weight to calculate the energy density (see Ciancio *et al.* 2007). The rate of energy intake was estimated for each focal observation in kJ min^{-1} of observation. The null hypothesis of no difference on energy intake rate of Oystercatchers between TC and CC for each season was evaluated by *t*-test (Zar 1999).

Results

The effect of anthropogenic nutrient input on densities of invertebrates

In total, 29 species of benthic invertebrates were recorded in CC and TC combined during spring and summer, six of which were recorded, either in diet or availability samples at frequencies >5% (Table 1). Polychaetes species were pooled in a single group given the difficulties to identify prey at species level during observations. Of these six species, densities of *Brachidontes rodriguezii*, polychaetes, and *Buccinanops globulosum* were similar in TC and CC during both spring and summer (Fig. 2; *Brachidontes rodriguezii*: $Z_{\text{SPRING}} = 1.76$, $P = 0.077$; $Z_{\text{SUMMER}} = 1.19$, $P = 0.23$; polychaetes: $t_{\text{SPRING}} = 0.62$, $P = 0.54$; $t_{\text{SUMMER}} = 1.09$, $P = 0.29$; *Buccinanops globulosum*: $t_{\text{SPRING}} = 0.01$, $P = 0.99$; $Z_{\text{SUMMER}} = 1.06$, $P = 0.29$). The

density of the crab *Cyrtograpsus angulatus* was higher in TC in spring and similar in both channels during summer (Fig. 2; $t_{\text{SPRING}} = 2.28$, $P = 0.036$; $t_{\text{SUMMER}} = 0.45$, $P = 0.66$), whereas densities of *Crepidula aculeata* were higher in CC during spring and similar in the two channels in summer (Fig. 2; $Z_{\text{SPRING}} = 2.25$, $P = 0.02$; $Z_{\text{SUMMER}} = 1.19$, $P = 0.23$).

Manipulation of the macroalgal canopy

After 16 days of the experimental manipulation of the macroalgal canopy, a total of 11 species of benthic invertebrate were recorded in transplanted plots compared with 7 species in the paired control plots (the number of which was included in the total of 11 species). Of all the species in the plots, only two were eaten by Oystercatchers: the mollusc *Buccinanops globulosum* and the crab *Cyrtograpsus angulatus*. *Buccinanops globulosum* showed similar densities in control and transplant plots (mean densities (individuals plot^{-1}) \pm s.d.: control plots = 2.00 ± 3.46 , transplant plots = 1.00 ± 1.00 ; $t_4 = 0.48$, $P = 0.65$), whereas *Cyrtograpsus angulatus* showed higher densities in transplant plots (control plots = $0.33 + 0.58$, transplant plots = 3.67 ± 1.15 ; $t_4 = 4.47$, $P = 0.011$).

Foraging behaviour and diet of Oystercatchers

Oystercatchers used two different search strategies to detect prey, in both channels and both seasons: tactile detection, and visual–tactile detection. When Oystercatchers explored the substrate using the visual–tactile strategy, they detected cues on the surface and then made pecks and probes, whereas when using the tactile strategy the bill was used to explore for and detect prey by lateral sweeps of the bill through the substrate. The frequency with which each tactic was used differed between the treatment and control channels and between periods ($\chi^2_{11} = 88.60$, $P < 0.0001$). The visual–tactile strategy dominated in all situations except in the TC during spring, where the tactile strategy was the most used (Fig. 3).

Six species and a group of polychaetes comprised the bulk of the diet of American Oystercatchers in San Antonio Bay. The diet varied between channels and periods. During spring, the crab *Cyrtograpsus angulatus* and the mollusc *Brachidontes rodriguezii* comprised 95% of prey in TC, whereas five items comprised 95% of prey in CC (Table 1). During summer, the molluscs *Brachidontes rodriguezii* and *Buccinanops globulosum* comprised 77% of prey in TC, whereas four species comprised 86% of prey in CC (*Buccinanops globulosum* was the most

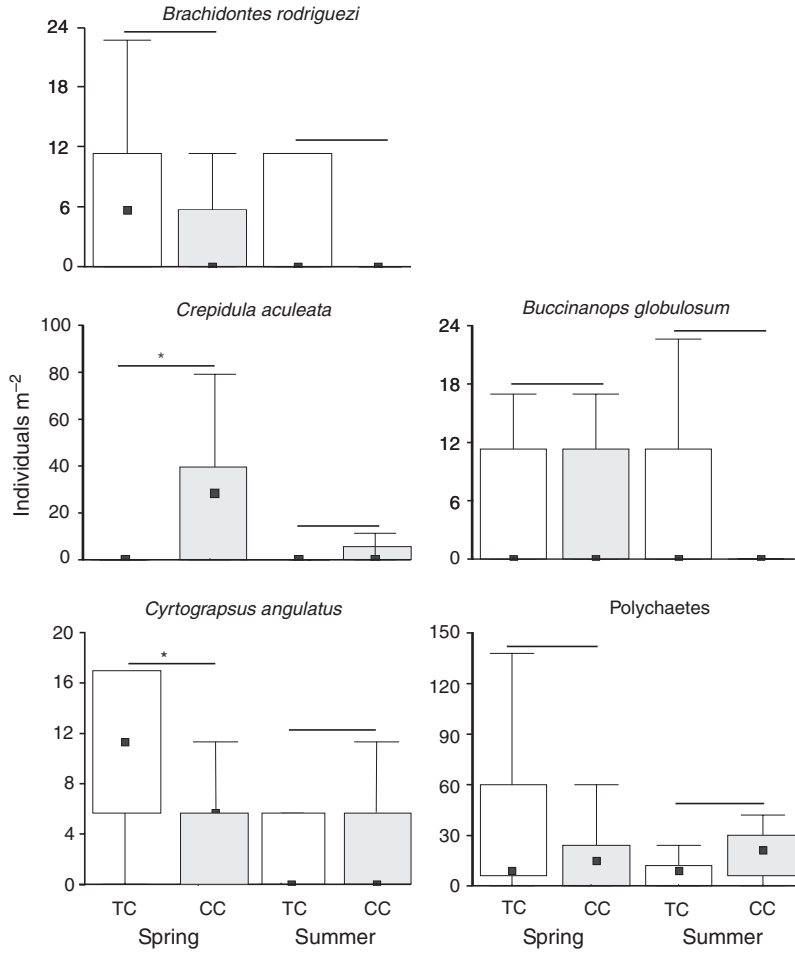


Fig. 2. Average densities of the most abundant benthic species in the treatment (TC; white box) and control (CC; grey box) channels during spring and summer, either subject to macroalgal bloom (spring TC) and without macroalgal blooms (spring CC, summer TC and CC). Bold horizontal lines plots indicate *t*-test comparisons, and asterisks show significant differences ($P < 0.05$). Boxes bounded by the 75th and 25th percentiles, and whisker lines represent the minima and maxima; points inside the boxes are median values.

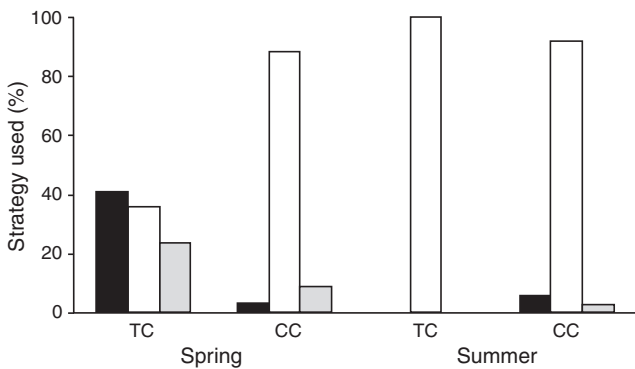


Fig. 3. Frequency of use of search strategies by American Oystercatcher between control (CC) and treatment (TC) channels during spring and summer, either subject to macroalgal bloom (spring TC) or without algal blooms (spring CC, summer TC and CC). Black bars, tactile strategy; open bars, visual-tactile strategy; grey bars, combined of both strategies.

frequently eaten). Profitability was higher when Oystercatchers fed on the molluscs *Buccinanops globulosum*, *Crepidula aculeata* or *Brachidontes rodriguezii*, than when they fed on the crabs *Neohelice granulata* and *Cyrtograpsus angulatus*, the bivalve mollusc *Mytilus edulis*, or on polychaetes ($H_6 = 622.77$; $P < 0.001$; *post hoc* Dunn Test, $P < 0.05$; Fig. 4a).

Prey selectivity by Oystercatchers changed with season and channel. They selected *Cyrtograpsus angulatus* and *Brachidontes rodriguezii* in TC during spring (in CC during spring there was no preference for any prey), whereas during summer they selected *Mytilus edulis* and *Buccinanops globulosum* in TC and *Neohelice granulata* and *Buccinanops globulosum* in CC. In contrast, polychaetes were avoided in all seasons and both channels, *Buccinanops globulosum* and *Crepidula aculeata* were avoided in TC during spring, and *Cyrtograpsus angulatus* was avoided in TC during summer (see Table 1, Fig. 4b).

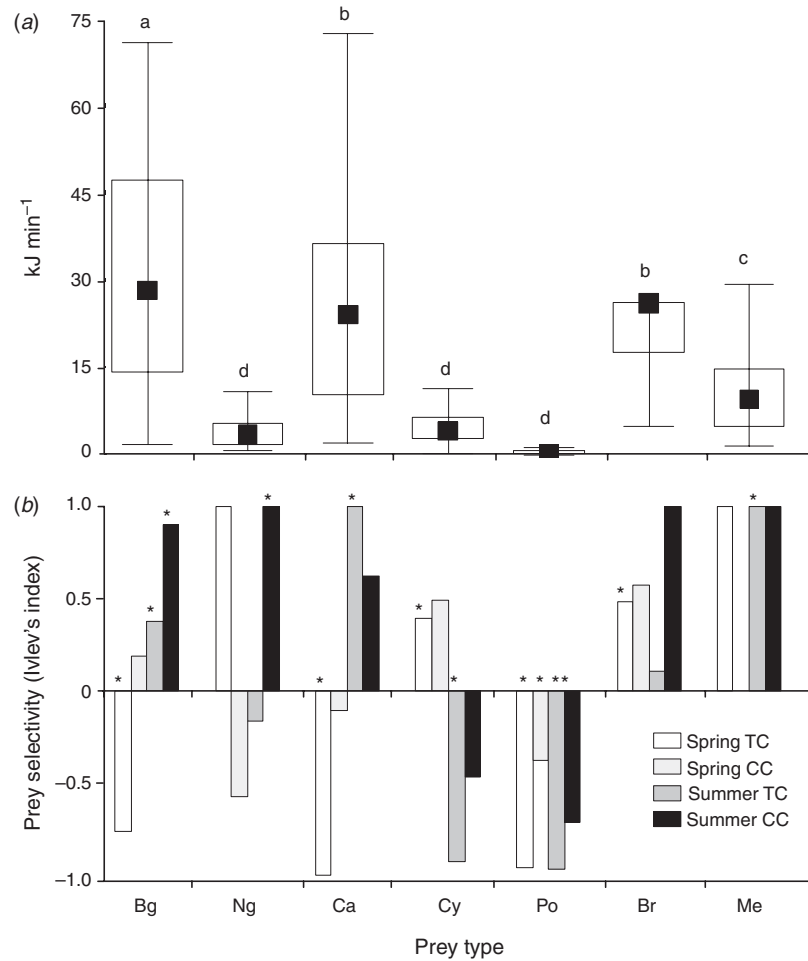


Fig. 4. (a) Profitability of main items in the diet of the American Oystercatcher; and (b) Ivlev's index of prey selectivity. Different letters above whiskers in Fig. 4a represent significant differences ($P < 0.05$) after a *post hoc* Dunns Test. Prey selectivity was compared between control (CC) and treatment (TC) channels during spring and summer, either subject to macroalgal bloom (spring TC) or without macroalgal blooms (spring CC, and summer TC and CC). Statistical significances from Bonferroni test are shown with an asterisk ($P < 0.05$); delimitation of box-plots as given in caption to Fig. 2. Bg, *Buccinanops globulosum*; Ng, *Neohelice granulata*; Ca, *Crepidula aculeata*; Cy, *Cyrtograpsus angulatus*; Po, polychaetes; Br, *Brachidontes rodriguezii*; Me, *Mytilus edulis*.

The encounter rate was higher in TC than in CC during spring and summer (t_{SPRING} (d.f. = 99, 26) = 4.02, $P < 0.001$; t_{SUMMER} (71, 0) = 3.72, $P < 0.001$; Fig. 5). However, the encounter rate for Oystercatchers feeding on the crab *Cyrtograpsus angulatus* was higher in TC (i.e. during algal blooms) than in CC (i.e. without algal bloom) during spring, and similar in both channels during summer (t_{SPRING} (105, 7) = 6.06, $P < 0.001$; t_{SUMMER} (62, 4) = 0.92, $P > 0.05$; Fig. 6). The average energy intake rate was higher in TC than in CC during spring and summer (Z_{SPRING} (71, 31) = 6.09, $P < 0.001$; t_{SUMMER} (49, 24) = 2.68, $P < 0.001$). Energy intake was seven times higher in TC than in CC during spring (energy intake in TC = 1.65 ± 1.19 , in CC = 0.24 ± 0.37) and two times higher during summer (TC = 2.05 ± 1.88 , CC = 1.01 ± 0.70 ; Fig. 7). The highest

rates of energy intake were observed in summer ($F_{\text{SEASON}} = 13.22$, $P < 0.001$).

Discussion

American Oystercatchers ate a relatively small group of organisms compared with the species available in the bay. Six species of molluscs and crustacean and a group of polychaetes, were differentially selected in different areas and periods in the study site. The differential use of prey was linked with the temporal and spatial availability of prey, which was affected by macroalgal blooms. Nutrient loadings and the macroalgal blooms that they generate in San Antonio Bay have effects on the diet and foraging behaviour of the American Oystercatcher,

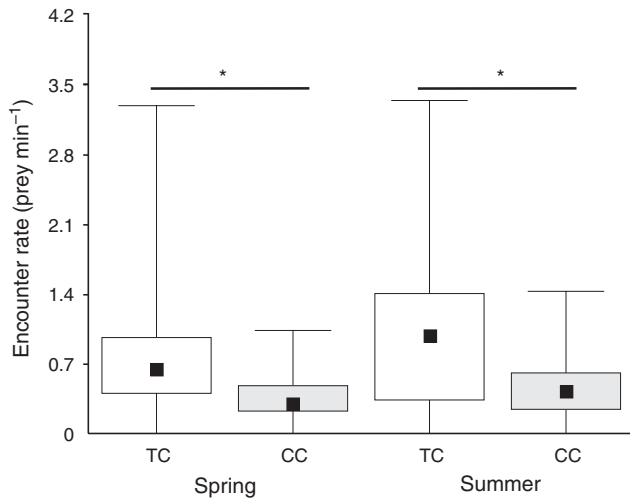


Fig. 5. Encounter rates for American Oystercatchers feeding in treatment (TC) and control (CC) channels during spring and summer, either subject to macroalgal bloom (spring TC) or without macroalgal blooms (spring CC, and summer TC and CC). Bold horizontal lines above plots indicate *t*-test comparisons and asterisks show significant differences ($P < 0.05$); delimitation of box-plots as given in caption to Fig. 2.

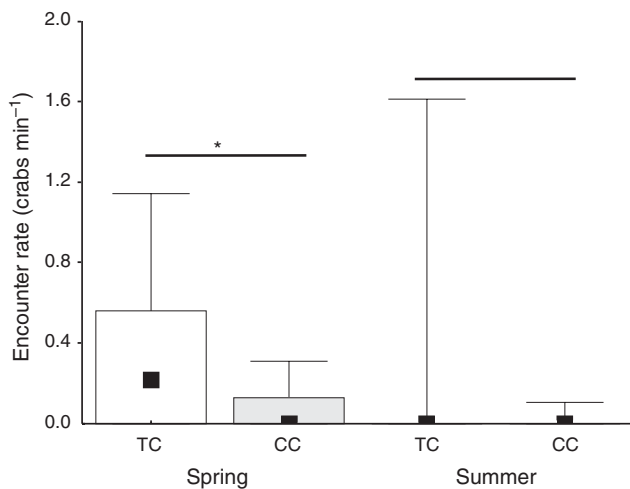


Fig. 6. Encounter rates for American Oystercatchers feeding on the crab *Cyrtograpsus angulatus* in treatment (TC) and control (CC) channels during spring and summer. Heavy horizontal lines above plots indicate *t*-test comparisons and asterisks show significant differences ($P < 0.05$); delimitation of box-plots as given in caption to Fig. 2.

which results in an increased rate of energy intake in areas with macroalgal blooms.

Effect of macroalgal blooms on the densities of invertebrates

The abundance of prey did not differ between the two channels during summer, when no algal blooms were present. However, during spring the crab *Cyrtograpsus angulatus* and the gastropod *Crepidula aculeata* were more and less abundant, respectively,

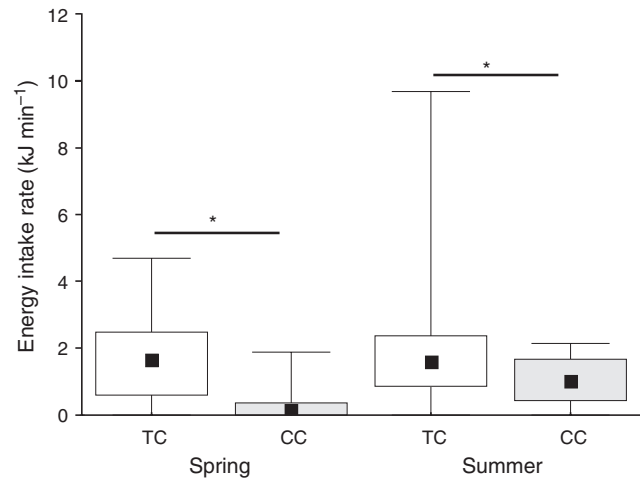


Fig. 7. Rate of energy intake of American Oystercatchers feeding in treatment (TC, white box) and control (CC, grey box) channels during spring and summer. Heavy horizontal lines above plots indicate *t*-test comparisons and asterisks show significant differences ($P < 0.05$); delimitation of box-plots as given in caption to Fig. 2.

in the TC than in the CC. Macroalgal mats offer refuge for macroinvertebrates such as *Cyrtograpsus angulatus* by increasing the physical structure of the intertidal mudflat. Thus, one of the main effects of these macroalgal beds probably relates to their role as autogenic ecosystem engineers by controlling the availability of resources to other species through their physical structure (Jones *et al.* 1997). Of the main species recorded, only the abundance of the crab *Cyrtograpsus angulatus* responded positively and quickly to the presence of macroalgae.

Effect of macroalgal blooms on the diet and foraging strategy of Oystercatchers

The differential use of prey by the American Oystercatcher was linked with the temporal and spatial availability of prey, and can be understood as a functional response (Van de Kam *et al.* 2004; Goss-Custard *et al.* 2006). The basic premise of optimal foraging theory is that organisms maximise their rate of energy intake (Stephens and Krebs 1986). It follows that birds should then only select prey that have a higher profitability than the long-term average rate of energy intake. In line with this prediction, in this study we observed that Oystercatchers always avoided prey with lower profitability than the average rate of energy intake (i.e. polychaetes) and selected prey with higher profitability (i.e. *Buccinanops globulosum*, *Crepidula aculeata*, and *Brachidontes rodriguezii*). Even though the occurrence of polychaetes in the diet was high, they were avoided. This avoidance is clear if we compare the percentage of this prey item in the diet with the percentage in the study site (see Table 1). In the TC the bulk of the diet of the Oystercatchers consisted of prey of high profitability or with high encounter rates or both (i.e. *Cyrtograpsus angulatus* during spring period). Consequently, rates of energy intake were always higher in the TC than in the CC. We can conclude that the higher nutrient loading in the TC improved the feeding condition of the

Oystercatchers. As such, a preference for foraging in the TC should have advantages for the condition of individual Oystercatchers.

During macroalgal blooms, by changing its foraging strategy from visual–tactile to tactile, the American Oystercatcher mainly took *Cyrtograpsus angulatus*. Despite its low profitability, this prey was selected primarily owing to its high encounter rate (perhaps in turn owing to their abundance and size) linked to the high extent of macroalgal patches. The intake rate of Oystercatchers was seven times higher in areas with macroalgal blooms than in those without it. On the other hand, during the macroalgal blooms, Oystercatchers were observed to avoid two highly profitable prey (*Buccinanops globulosum* and *Crepidula aculeata*). This avoidance could be at least partially attributed to the decreased detectability of these prey owing to camouflage against the macroalgal mats. There is thus a trade-off between searching to encounter as many prey as possible in a short period of time versus searching slowly to maximise the profitability of prey that are encountered, leading to an optimal search rate for which the rate of energy intake is maximised (Shuterland *et al.* 1996).

Conclusion

Our results strongly suggest that nutrient loading, by causing macroalgal blooms, may have effects on a common native shorebird of coastal habitats of America. We observed a change in the foraging behaviour and diet of the American Oystercatcher as an indirect effect generated by an anthropogenic nutrient loading on an intertidal community. Owing to their plastic behaviour, American Oystercatchers are able to compensate for the environmental change on the invertebrate community generated by macroalgal blooms. However, these results need to be viewed with some caution because patterns of increased abundance and diversity are usually produced at earlier stages of eutrophication (Crozier and Gawlik 2002; Morris and Keough 2003), as observed here, but there are uncertainties about the long-term effects on other organisms, such as migratory shorebirds.

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