THE DISTRIBUTION AND ECOLOGICAL EFFECTS OF THE INTRODUCED PACIFIC OYSTER *CRASSOSTREA GIGAS* (THUNBERG, 1793) IN NORTHERN PATAGONIA

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ABSTRACT In this work we studied the actual coverage, distribution patterns and ecologic effects of the introduced oyster *Crassostrea gigas* 20 y after their introduction to the Northern Argentinean Patagonia (Bahía Anegada; 39°50′S to 40°40′S and 61°59 to 62°28 W). Using satellite imagery and field and aerial inspections we found 10 oyster beds that cover less than 0.05% of the bay intertidal (area covered: 36.45 ha). These beds are restricted to intertidal zones with superficial hard substrata (limestone outcrops). Most epifaunal organisms (the crabs *Cyrtograpsus angulatus, Chasmagnathus granulatus,* the isopod *Melita palmata*, and the snail *Heleobia australis*) showed higher densities inside oyster beds compared with outside and experiments showed that artificially deployed oyster beds increased the densities of their at three intertidal zones (high intertidal marsh, low intertidal marsh, and low intertidal with hard substrata) and also increased densities of infaunal organisms (the polychaetes *Laeonereis acuta*, *Nepthys fluviatilis*, and the priapulid *Priapulus tuberculatospinosus*) at the low intertidal with hard substrata. This may be the result of increasing habitat structure and refuge for epifaunal organisms, and enhancement of deposition and sediment stability that may benefit infaunal organisms. Densities bird species (Local species: *Larus dominicanus, Haematopus palliatus*; Regional migratory shorebird: *Charadrius falklandicus*; Long range migratory shorebirds: *Pluvialis dominica, Calidris canutus, Tringa flavipes*) were higher inside oyster beds compared with similar zones without oysters, which may be the result of higher prey availability. Foraging rate was also higher for some of these species (*P. dominica, C. falklandicus*). However, due to the limited availability of hard substratum the aerial distribution of oysters is small. In conclusion, no negative effects were observed as a result of this introduction. There was an increase in species abundance and the area was preferred by local and migratory bird species, which also showed higher feeding rates.

KEY WORDS: biologic invasions, *Crassostrea gigas*, ecosystem engineers, migratory shorebirds

INTRODUCTION

The effect of invasive nonindigenous species on native communities had become a major problem in conservation biology (Lodge 1993, Mack et al. 2000, Bax et al. 2001, Byers et al. 2002) mainly because their negative effects on native species, communities and ecosystems (e.g., Vitousek & Walker 1989, Settle & Wilson 1990, Vitousek 1990, Spencer et al. 1991, Carlton 1992, Petren & Case 1996, Juliano 1998, Mack et al. 2000, Byers 1999, Byers 2000, Byers et al. 2002). Marine ecosystems are especially vulnerable to invasive species (Carlton 1996) showing some dramatic effects on biologic diversity and productivity (Bax et al. 2001). However, little attention has been paid to the role of physical ecosystem engineer species (*sensu* Jones et al. 1994) as habitat modifiers when introduced to new habitats. The change of the physical structure of the ecosystem is not currently accounted for in the evaluation of invader's impact (Crooks 2002), but a large effect in the native community is expected when the invader change habitat complexity or heterogeneity (Posey 1988, Crooks & Khim 1999, Crooks 2002, Bruno et al. 2003).

Physical ecosystem engineer species (*sensu* Jones et al. 1994) that create biogenic structure are known to affect community structure (Jones et al. 1997). This effect is because biogenic structure can affect competitive interactions (Fletcher & Underwood 1987), modify the relative importance of predation (Gilinsky 1984, Orth et al. 1984, Dean & Connell 1987, Schwindt et al. 2001, Hamilton

& Nudds 2003) and, ameliorate physical stress (Nixon et al. 1971) and disturbance (Whorff et al. 1995), generally leading to an increase in the density and diversity of associated organisms (Gilinsky 1984, Downes et al. 1998, Zühlke 2001, Bolam & Fernandes 2003, but see Kelaher 2003). Oysters are a good example of substrate and structure creators (see Jones et al. 1997, Gutiérrez et al. 2003), serving as refuge for numerous mobile and sessile species and having a large effect on community structure (Ulanowicz & Tuttle 1992, Kennedy 1996, Dumbauld et al. 2000, Meyer & Townsend 2000, Lenihan et al. 2001) but oysters are also a good example of invasive species in marine and estuarine environments (Carlton 1992, Reise 1998), usually introduced for aquaculture purposes (Carlton 1992, Shatkin et al. 1997, Wasson et al. 2001, Miller et al. 2002). Although ecologic impacts of mollusk farming are known to be small compared with other forms of aquaculture (Naylor et al. 2000), there are several examples of native community modification as a result of *Crassostrea spp.* introduction by direct competition with native species (Shatkin et al. 1997, Reise 1998), by spreading other invasive species (Carlton 1992, de Montaudouin et al. 1999, Byers 1999, 2000, Wolff and Reise 2002), diseases (e.g., Grizel & Héral 1991, Mann et al. 1991, Shatkin et al. 1997, Wolff & Reise, 2002), and by decreasing benthic oxygen levels (Castel et al. 1989).

The Pacific Oyster *Crassostra gigas*, a species endemic from Japan, is today the most successful oyster in commercial cultivation of hatchery-produced seed and is the basis of the largest oyster fisheries in the world (Mann et al. 1991, Reise 1998). *C. gigas* has been extensively introduced outside its native range for culture purposes, and established in the field (Mann et al. 1991, Carlton

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1992, Shatkin et al. 1997). In South America, *C. gigas* was introduced on the Pacific Ocean in Chile and Peru (Winter et al. 1984), and in the Atlantic in Brazil and Argentina (Pascual & Orensanz 1996, Orensanz et al. 2002). In Argentina, this species was illegally introduced during 1982 in Bahía Anegada (39°50′S to 40°40′S and 62°10′W; see Figure 1; Orensanz et al. 2002, Penchaszadeh et al. 2003). A small stock of commercial size of *C. gigas* (ca 500 individuals) imported from Coquimbo (Chile), with gastronomic purposes, were introduced to the southern part of Bahía Anegada with the purpose of implementing an aquaculture production (Orensanz et al. 2002). After a year of experimentation, the remainder small stock was abandoned but they established in the field (Orensanz et al. 2002, Penchaszadeh et al. 2003).

Although there are several conflicts rising from the invasion of *Crassostrea gigas* on northern Patagonia, one important concern is related to conservation of shorebird habitats. The SW Atlantic intertidals are main stopover sites of migratory shorebirds that breed in the northern hemisphere and spend their winter in the southern hemisphere (see Botto et al. 1998). However, the distribution patterns and coverage extension of *C. gigas* on the intertidal and its effects on the benthic community and shorebirds remain unknown. In this context, the main purpose of this research is to evaluate the number, distribution, and extension of *C. gigas* beds today and to evaluate, by sampling and by field experiments, its effects on the benthic community and shorebird habitat use.

MATERIALS AND METHODS

The study was performed in Bahía Anegada (Fig. 1; see Spalleti & Isla 2003 for full description) from December 2001 to November 2003. This is a large embayment (2371 km^2) affected by a low amplitude (≤1.5 m) semidiurnal tidal regimen.

Given that oysters showed a wide distribution, an analysis of satellite imagery were performed to identify oyster beds and evaluate their spatial distribution. The satellite imagery used was recorded by Enhanced Thematic Mapper plus sensor on board Landsat 7. It records radiation with a nominal spatial resolution of approximately 30 m for bands 1–7, and 15 m for band 8 (panchromatic). Because the tide level is an important factor in saltmarshes and higher levels can mask some habitats, in this study only the image with the lower tide level of a pool of satellite images was selected. The image selected was from 15 January 2002 and was provided by the Argentinean National Commission of Space Activities (CONAE).

To remove the geometric distortions in Landsat imagery, image was geocoded to a UTM Gauss Kruger coordinate system using a first order transformation and nearest neighbor resampling. The root-mean squared error achieved after resampling was lower than 1.5 pixels in all bands. We used map points to geometric corrections. Points were acquired from topographic maps of the Argentinean Army Geographic Institute (IGM; scale 1:50,000).

The south portion of Bahía Anegada was exhaustively searched by walking and the location of oyster beds and different types of
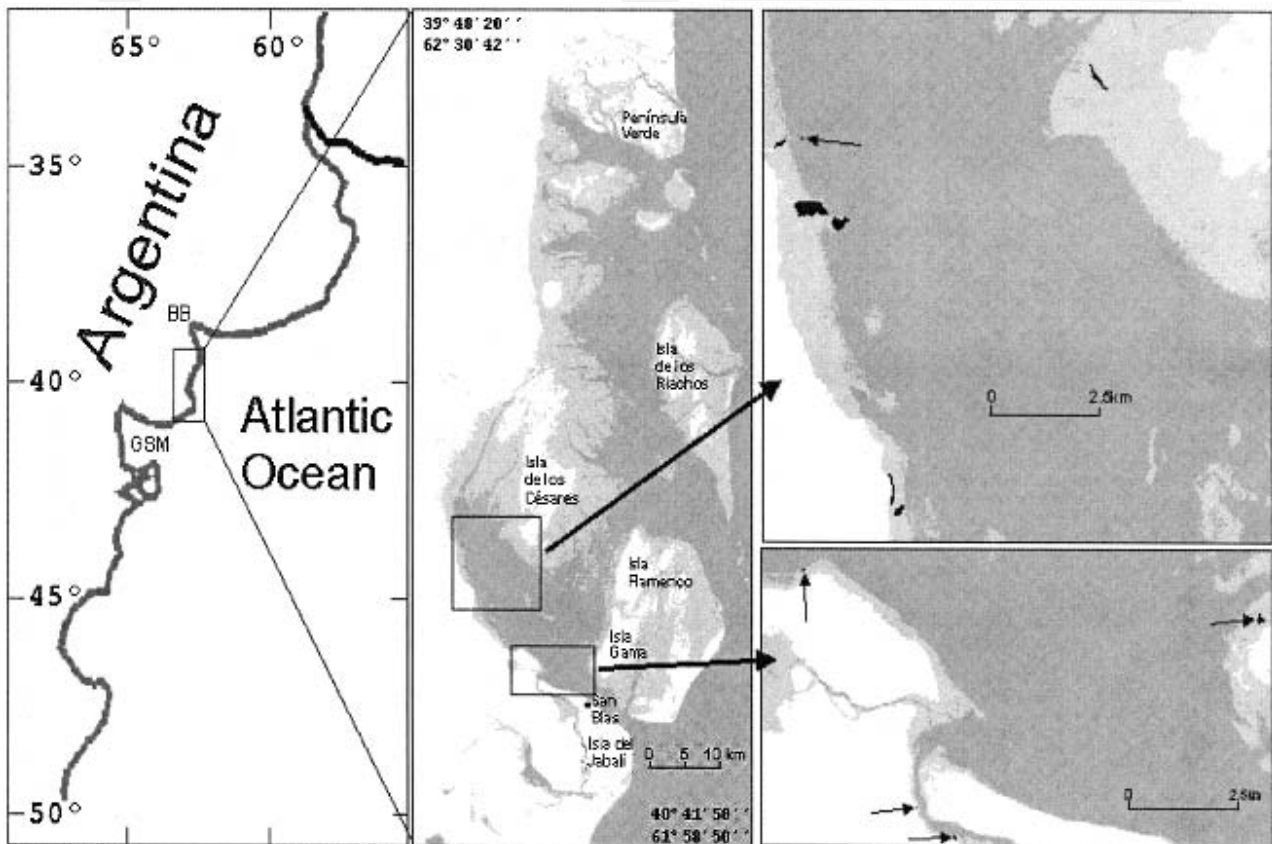

Figure 1. Location and dimension of oyster beds in Bahía Anegada (Argentina). Large oyster beds are shown in black, and smaller ones are indicated by arrows. BB, Bahía Blanca and GSM, Golfo San Matías. Low grey represent intertidal habitat.

environments along the intertidal were registered (position obtained by GPS). A spectral signature analysis of the different kinds of intertidal habitats (tidal flats, saltmarshes dominated by *Spartina alterniflora* Loisel and saltmarshes dominated by *Sarcocornia perennis* (Miller) (formerly *Salicornia ambigua*) were compared with the spectral signature of a known oyster bed. Bahía Anegada intertidal has a mixture of limestone outcrops, sand, silt, and rolling stone bottoms. This variation in substrata, and the variation in water content as a result of field irregularities, generated a bias spectral response that did not allow us to perform a correct classification using common supervised and unsupervised classification methods because of greatly overestimated oyster bed cover. Given this problem, we used a visual analysis of the image, utilizing the Landsat ETM+Panchromatic band (spectral range 520–00 nm), that have a 15 m spatial resolution and allow a good identification of the known oyster beds.

In the Landsat ETM+Panchromatic band, known oyster beds have a particular dendritic pattern that make them conspicuous in the intertidal. This characteristic pattern was used to search for similar structures to make a preliminary oyster beds map. Then, an exhaustive aerial inspection (flying between 60 and 100 m altitude and between 100 and 150 km per hour) of Bahía Anegada coast and islands was done during low tide to verify the presence of oyster beds. No new oyster beds were found but some structures previously identified as oyster beds were discarded. Discrimination of land, intertidal and water was done using the Idrisi32 Maximum Likelihood Software module. The final map (Fig. 1) was done by adding the identified oyster beds to the thematic map.

To study the distribution patterns in relation to intertidal level, transects (100 m) perpendicular to the shoreline were performed (spaced by at least 50 m). In each transect, the number of oysters in 1 m^2 were counted every 0.4 m of intertidal height. The null hypothesis of no differences in oyster densities between tidal levels was analyzed with 1-way ANOVA (Zar 1999). To evaluate the type of substrate used by oysters, the depth at which the hard substratum (i.e., limestone outcrops) was located was measured by pushing a 1.5 m iron stick and noting the buried length of the stick when it touch the hard substratum, and the number of oysters (m^{-2}) were counted. The null hypothesis of no relation between hard substratum depth and oyster densities was analyzed with correlation analysis (Zar 1999).

To evaluate whether there is a relation between oyster beds and densities of epifaunal organisms, samples of 0.25 × 0.25 m were assigned inside and outside oyster beds. In each sample, epifaunal organisms were counted and identified to the lowest taxonomic level possible. For each taxa, the null hypothesis of no differences in densities of organisms were analyzed with *t*-test (or Mann-Whitney when necessary, Zar 1999). To evaluate if there was any relation between oyster densities and the densities of the predominant native grapsid crab *Cyrtograpsus angulatus* Dana, a species that is known to be strongly and positively affected by biogenic structure (see Schwindt & Iribarne 2000, Schwindt et al. 2001, Mendez Casariego et al. 2004), a different sample design was used. The number of oysters and crabs were counted in 83 sampling units of 1m^2, randomly chosen along the intertidal. The null hypothesis of no relation between densities of oysters and crabs were evaluated with correlation analysis. Similarly, to evaluate the relation between oyster beds and densities of the snail *Heleobia australis*, the intertidal substrate was divided into 3 zones (High = 1.3 m above the lower tidal level (ALTL), medium = 0.7 m ALTL and low = 0.2 m ALTL). In each zone, the number of snails in 25 samples of 0.2 × 0.2 m was counted in pools inside and outside oyster beds. For each intertidal level, the null hypothesis of no differences in snail densities between sites was evaluated with *t*-test (Zar 1999).

To experimentally evaluate the effect of *Crassostrea gigas* on natural community on the high marsh, the low marsh and the low intertidal with hard substrata, 60 square plots (1 m^2), 20 in each zone, were randomly chosen on January 2002. Each plot was assigned to one of the following treatments; (1) artificial oyster bed or (2) control. Artificial oyster bed treatments were done by transplanting oysters from natural oyster beds to the plots. These oysters were washed with seawater to eliminate epifauna before transplanting. After 11 mo, epifaunal organisms were counted and classified on a 0.25 × 0.25 m square from the center of the plot. In each plot, a core sample (35-cm depth, 15-cm diameter) was also taken. Infaunal organisms were separated by sieving the samples through a 0.5-mm screen. Organisms were counted and classified to the lowest taxonomic level possible. The null hypotheses of no differences in densities of organisms of each species between treatments (with and without oysters) for each intertidal zone were analyzed with *t*-test or nonparametric Mann-Whitney test (Zar 1999).

One of the main concerns in the region came from the potential effect of oyster beds on habitat use by birds, mainly neotropical migratory shorebirds. To evaluate differential use of areas by shorebirds, 3 sites were selected at the SW part of the bay (Isla Jabali, Fig. 1 lower right) each one had oyster reefs and nearby areas without oysters. Each bed had a mean density of 47.4 oysters m^2 (SD = 12.3) and a mean surface area of 1 ha (Borges 2002, Penchaszadeth et al. 2003). Areas were selected keeping similar characteristics such as tidal level, slope and compass orientation (NW-SE) and known to be used by shorebirds. In each area, a telescope (18 × 36) was used to perform censuses from December 2001 to April 2002 (this period represent the entire migratory season). In each census, individuals were identified and the percentage of them feeding in each area was calculated. Abundance of each shorebird species was compared between sites and months with repeated measures ANOVA (Neter et al. 1990). To evaluate whether there is a relationship between the oyster beds and the shorebird foraging rate and efficiency, focal observations (using a 18 × 36 telescope) were performed. Each bird was observed for a period between 5 and 10 min. Before the observations, and based on a previous sampling, a list of all acts to be recorded was defined (walk, pause, peck, and capture of item) and maintained during the study to ensure standardized observations. The number of probes per minute and the proportion of probes resulting in successful prey capture were calculated. Differences in rate of consumption and foraging efficiency between areas were evaluated independently for each bird species with *t*-test (Zar 1999).

RESULTS

A total of 10 oyster beds were detected, 3 of small size (size range 0.09–0.36 ha), 6 of medium size (size range 1.62–5.67 ha) and 1 large bed (size 16.38 ha), all of them located in the southern part of the bay (Fig. 1). Oyster beds cover a total of 36.45 ha, which is less than 0.05% of the Bahía Anegada intertidal (total intertidal area = 89,689 ha). Both aerial and walk inspection reveals that besides the areas colonized by oysters there were no free superficial hard substrata along the intertidal.
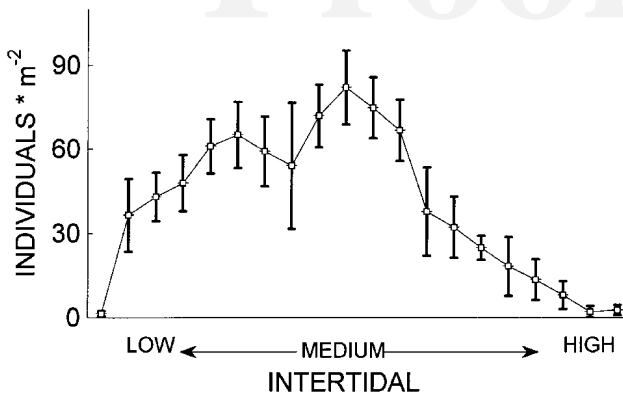
Figure 2. Oyster densities across the intertidal. Squares represent means and bars standard deviation.

Spat were found attached to limestone outcrops, empty shells, shells of a native small mussel *Brachidontes rodriguezi* (d'Orbigny) and the basal portion of *Spartina alterniflora*. Oyster densities were higher in the middle and middle to low intertidal compared with other intertidal zones (ANOVA, $F_{19,177} = 56.404$, $P < 0.001$, Fig. 2). Moreover, there were no oysters in the low intertidal or in the subtidal. There was a negative correlation between hard substratum (i.e., limestone) depth and oyster densities ($r^2 = 0.597$, $n = 100$, $P < 0.001$) and there were no oysters in zones with hard substratum depths higher than 10 cm.

Inside the oyster matrix, the number of juveniles of the crab species *Chasmagnathus granulatus* Dana and *C. angulatus*, and the number of the polychaete *Laeonereis acuta* (Treadwell) and the isopod *Melita palmata* (Montagu) were higher inside oyster beds but the number of the hermit crab *Pagurus criniticornis* (Dana), the snail *Heleobia australis* (d' Orbigny), and unidentified anemones were higher outside oyster beds (Table 1). There were no differences in number of the small mussels *Brachidontes rodriguezi* (d' Orbigny) (Table 1).

There was a positive correlation between oyster density and the density of the crab *Cyrtograpsus angulatus* ($r^2 = 0.27$, df = 43, $P < 0.001$). Similarly, densities of the snail *Heleobia australis* were higher in pools inside oyster beds along the 3 intertidal heights compared with pools outside oyster beds (high: t = 9.79, df = 48, $P < 0.001$; medium: t = 3.402, df = 48, $P < 0.005$; low: t = 2.49, df = 48, $P < 0.05$; Fig. 3).

In the high marsh, the number of the small mussels (square root transformed data; t = 8.63, df = 18, $P < 0.001$), anemones (log

transformed data; t = 2.38, df = 18, $P < 0.05$) and the crab *Cyrtograpsus angulatus* (log transformed data; t = 7.32, df = 18, $P < 0.01$) were higher in artificial oyster beds plots compared with control plots. The amphipods *Corophium sp.* and crabs of the species *Chasmagnathus granulatus* were only present in the artificial oyster bed plots. In contrast, the number of snails (*Heleobia australis*) was higher in the control plots (Z = 2.86, $N_1 = N_2 = 10$, $P < 0.005$). In the low marsh, there were no differences in the number of mussels between treatments (t = 0.45, df = 18, $P > 0.5$). Anemones, amphipods, polychaetes and, the crabs *C. angulatus*, *C. altimanus* Rathbun and *C. granulatus*, were present only in the artificial oyster bed plots. *H. australis* was present only in control plots. In the low intertidal, mussels and the crab *C. angulatus* were present only in artificial oyster bed plots. Inside the sediment, there were no differences in the number of mussels (Z = 1.51, $P > 0.1$), polychaetes of the species *Laeonereis acuta* (Z = 1.57, $P > 0.1$) and *Nepthys fluviatilis* Monro (Z = 0.1, $P > 0.5$), and the priapulid *Priapulus tuberculatospinosus* Baird (Z = 0.1, $P > 0.5$) between plots in the high marsh. In the low marsh, the number of polychaetes (*L. acuta*) were higher in control plots compared with artificial oyster bed plots (Z = 1.256, $N_1 = N_2 = 10$, $P < 0.05$) but there were no differences in the number of mussels between plots ($X_1 = 22.8$, SD = 8.13, $X_2 = 22.4$, SD = 11.8; t = 0.09, df = 18, $P > 0.9$).

The birds present during the study period were the Two Banded Plover *Charadrius falklandicus* (Latham), the American Golden Plover *Pluvialis dominica* (Müller), the Red Knot *Calidris canutus* (Linnaeus), the Lesser Yellowlegs *Tringa flavipes* (Gmelin), the American Oystercatcher *Haematopus palliatus* Temminck, and the Kelp Gull *Larus dominicanus* (Lichtenstein). For all these species (Fig. 4), densities inside oyster beds were higher than in the adjacent areas without oysters (American Oystercatcher: t = 2.955, df = 60, $P < 0.005$, the Two Banded Plover: t = 5.772, df = 60, $P < 0.001$, the American Golden Plover: log transformed data, t = 12.667, df = 60, $P < 0.001$) and the Kelp Gull: log transformed data, t = 4.158, df = 60, $P < 0.001$). The Red-knot (X = 0.024 ind*m^2, SD = 0.0199) and the Lesser Yellowlegs (X = 0.0023, SD = 0.0049) were only present inside oyster beds. Foraging rate (Fig. 5) was higher inside oyster beds for the American Golden Plover (t = 2.172, df = 31, $P < 0.05$) and for the Two Banded Plover (t = 2.294, df = 15, $P < 0.05$) but there was no difference for the Oystercatcher (Mann-Whitney U-test, $Z_{adj} = 0.759$, $N_1 = 10$, $N_2 = 6$, $P > 0.1$) nor for the Red-Knot ($Z_{adj} = 0.039$, $N_1 = 17$, $N_2 = 5$, $P > 0.5$). There were no differences in foraging efficiency between sites (American Golden Plover: t = 0.714, df = 31, $P > 0.1$; Two Banded Plover: t = 0.864, df = 15, $P > 0.1$; Red Knot: t = 0.857,

TABLE 1.

Densities of species of epifauna inside and outside oyster beds. Density was expressed as individuals per sample unit (0.0625 m^2).

|	Inside Oyster Beds	Outside Oyster Beds	d.f.	T or Z Value	P	Observations
Chasmagnathus granulatus	18.67 (7.75)	4.07 (5.35)	28	6.003	<0.001	t-test
Cyrtograpsus angulatus	3.2 (2.14)	0.4 (0.74)	28	5.065	<0.001	t-test, log
Priapulus tuberculatospinosus	0.26 (0.39)	1.24 (0.47)	28	6.26	<0.001	t-test, log
Brachidontes rodriguezi	0.2 (0.77)	1.13 (2.7)	28	1.44	>0.1	M-W
Heleobia australis	3.4 (8.75)	13.07 (10.74)	28	3.038	<0.005	M-W
Laeonereis acuta	1.73 (1.33)	0.67 (0.9)	28	2.19	<0.05	M-W
Melita palmata	1.07 (1.94)	0.13 (0.35)	28	0.79	>0.1	M-W
Unidentified Cnidaria	0.47 (0.52)	3.07 (2.66)	28	2.51	<0.05	M-W
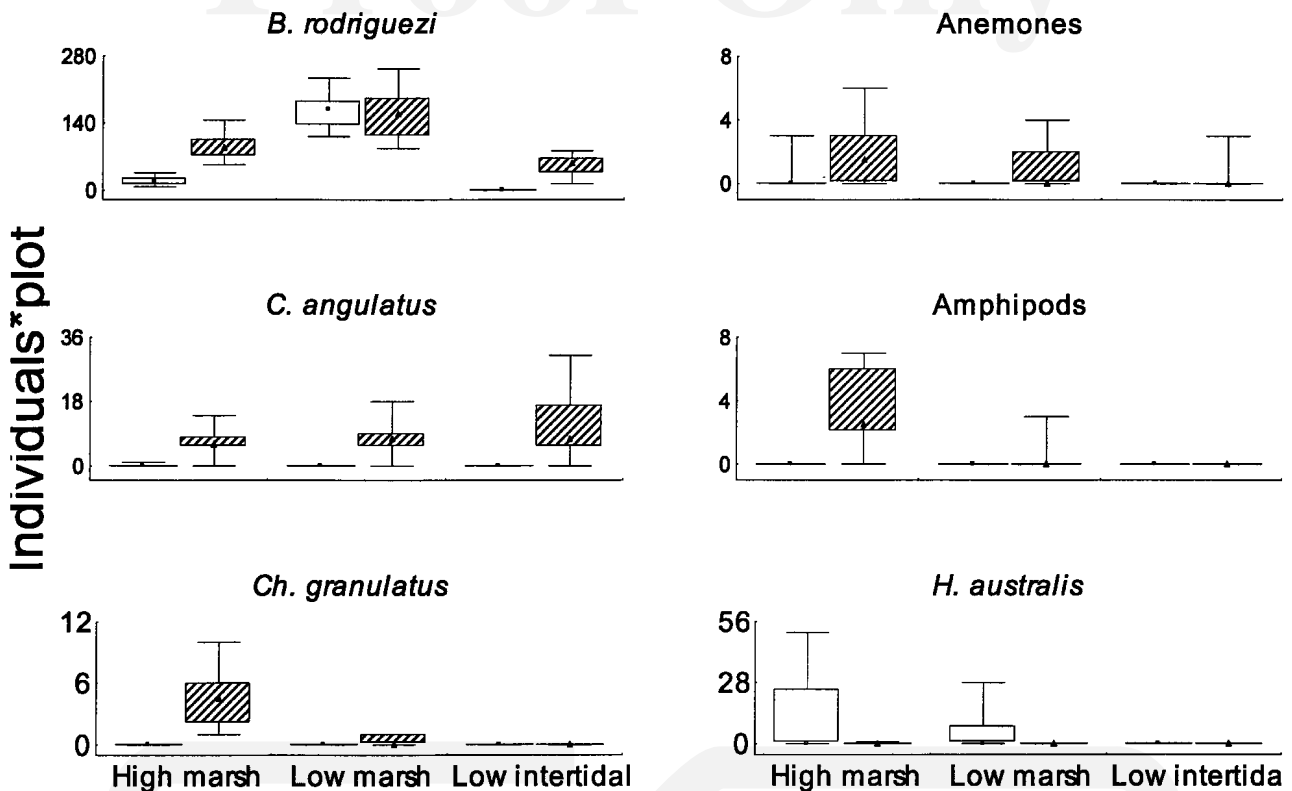
Figure 3. Number of individuals of epifaunal species in control plots (1 m²)(empty boxes) and artificial oyster bed plots (dashed boxes) at three zones of the intertidal. Here and thereafter squares and triangles inside boxes represents medians, limits of boxes are 25th and 75th percentiles, lines represents 1st and 99th percentiles.

df = 20, P > 0.1; American Oystercatcher: t = 0.402, df = 14, P > 0.5).

DISCUSSION

After more than 20 y of introduction, the Pacific oyster *Crassostrea gigas* has established in Bahía Anegada but covers a very small percentage (≤0.05%) of their intertidal area. This contrasts with previous introductions of *C. gigas* around the world (and in wide array of environmental conditions), where *C. gigas* populations expanded in relatively short time (see Shatkin et al. 1997, Sumner 1980, Reise 1998). However, our evidences shows that in this area the distribution is limited by the lack of hard substratum, which is the result of a large sediment discharge from the Colorado River (see Spalleti & Isla 2003 for details). Although this river does not discharge now into the bay, the muddy sediments are still the dominant feature of this area.

We found oysters only in the intertidal zone with higher densities at the middle intertidal. This result contrasts from the pattern found in other sites, where densities of this species are higher in the low intertidal (Reise 1998). This pattern can result from the distribution of hard substrata (limestone outcrops). Oysters were present only in zones with superficial hard substrata; soft bottoms cannot support oysters on the surface (Reise 1998). The local oyster *Ostreola spreta* (d' Orbigny) (formerly known as *Ostrea spreta*) also settle on any hard surface (de Castellanos & Cabrera 1957, de Castellanos 1968), and is the dominant settling species in artificial collection of seed oysters deployed in this area (Borges et al. 2002). However, survival at the intertidal is low probably due low tolerance to higher temperatures (Stenzel 1971), even when

clusters of *C. gigas* offer a good settlement site (Penchazadeth et al. 2003). We have no information on the interaction between the two oysters, but the distribution pattern may in part be the results of competition. Thus, any effects of *C. gigas* on the local community are restricted to zones with superficial hard substrata (mainly limestone outcrop) in the middle intertidal.

Densities of the crabs *Cyrtograpsus angulatus* and *Chasmagnathus granulatus*, and of the amphipod *Corophium sp.* and the isopod *Melita palmata* were higher inside oyster beds and, as expected, experiments indicated densities of epifaunal organisms were higher in oyster beds than outside of the beds. The importance of availability of shelter and structure complexity on inter and subtidal community structure has long been recognized (e.g., Barshaw & Lavalli 1988, Fernández et al. 1993a, Fernández et al. 1993b, Gee & Warwick 1994, Moksnes et al. 1998, Lohrer et al. 2000, Robinson & Tully 2000, Jensen et al. 2002). Oyster shells are an important shelter creator with dramatic effects on crab densities (see Wainwright et al. 1992, Dumbauld et al. 1993, Iribarne [AU1] et al. 1995). The relationship between *C. angulatus* and habitat structure created by an introduced species has also been found in other SW Atlantic estuary (i.e., Mar Chiquita coastal lagoon) invaded by the reef building polychaete *Ficopomatus enigmaticus* Faubel (Schwindt & Iribarne 1999, Schwindt et al. 2001). In this case, oyster shells can increase crabs density not only by enhancing recruitment (see Fernández et al. 1993b) but also by decreasing adult predation risk (Mendez Casariego et al. 2004). In contrast, densities of the snail *Heleobia australis* and the hermit crab *Pagurus criniticornis* were lower inside oyster bed matrix. This can be because, for these two species, availability of shelter may not be a
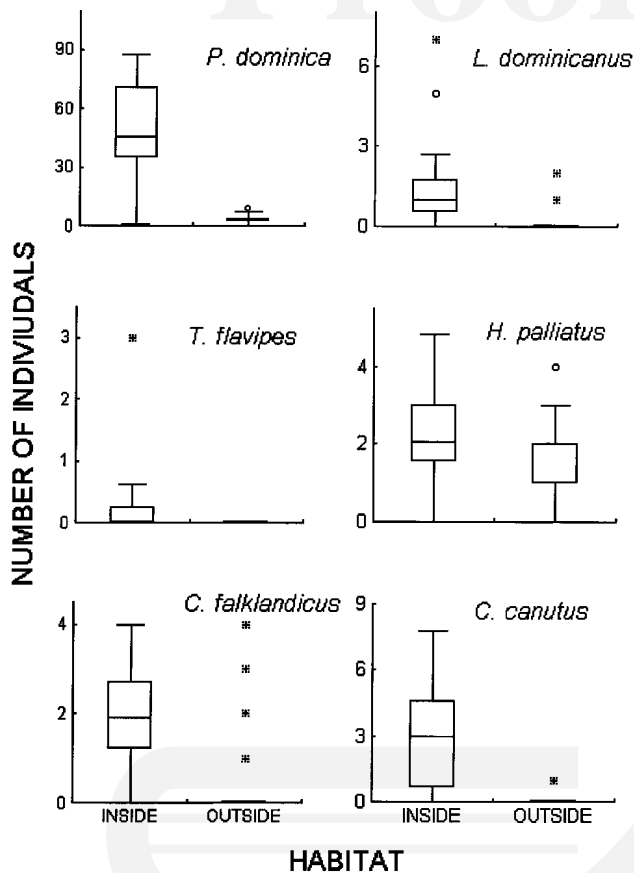
Figure 4. Average counts of number of individuals of different bird species using inside and outside oyster bed habitats. Circles represent outliers and asterisks are extremes.

limiting factor (both species carried their own refuge) and they may be negatively affected by 3-dimension structure (see Kelaher 2003). Alternatively, predation risk may increases inside the oyster matrix because the higher abundance of predators such as crabs. Indeed, *H. australis* shells are usually found in *C. angulatus* stomach contents (P. Martinetto, pers. com.).

The increase of epifauna inside oyster bed plots may be the result of immigration, different mortality and recruitment (Crooks
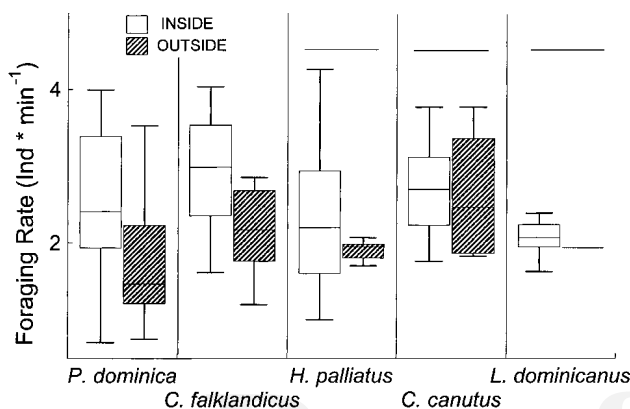

Figure 5. Foraging rate of different bird species compared between inside (empty boxes) and outside (dashed boxes) oyster shell habitats.

& Khim 1999). Individuals of *C. granulatus* that occur in oyster bed plots were only adults suggesting colonization but not recruitment, in contrast, there were recruit and small juveniles of *C. angulatus* and all these stages plus adults of *C. altimanus* suggesting recruitment and colonization.

Densities and foraging rates of shorebirds were higher inside oyster beds and foraging efficiencies, whereas foraging inside or outside oyster beds, were the same. Wolff & Reise (2002) linked the decreases of the oystercatcher *Haematopus ostralegus* Linnaeus populations in the European Wadden Sea, with the introduction of *C. gigas,* and posterior transformation of mussel beds of *Mytilus edulis* d'Orbigny into oyster beds. In addition, bird foraging efficiency, while preying on intertidal invertebrates, are negatively affected by substrate heterogeneity (e.g., Common eiders on Rockweed beds; Hamilton & Nudds 2003; also Marsh 1986). Nevertheless, our results shows that prey abundance (particularly crabs and snails) were positively affected by the presence of biogenic structure created by oysters. Thus, as in mussel cultures (Caldow et al. 2003), higher prey abundance inside oyster beds may be influencing bird habitat choice by positively affecting their foraging rate.

Studies on the effect of naturalized pacific oyster beds on benthic communities also showed strong effects by decreasing O_2 on sediments as a result of organic matter enrichment (Castel et al. 1989, Nugues et al. 1996), by outcompeting local bivalve species (Shatkin et al. 1997, Reise 1998) and, by creating physical structure on otherwise flat zones (Castel et al. 1989). At Bahía Anegada the vascular plant *Spartina alterniflora* and the clumps of the small mussel *Brachydontes rodriguezi* offer settlement sites for this oyster (Borges 2001, Penchaszadeth et al. 2003). Interestingly, oysters and mussels can generate layers of settlement, forming clusters that sometimes can be used as settlement sites by *Ostreola spreta* (Borges 2001, Penchaszadeth et al. 2003). These changes in the physical structure of the ecosystem itself, was postulated as one form in which invaders can have strong ecosystem-level effects (Bertness 1984, Chapin et al. 1997, Crooks & Khim 1999, Crooks 2002) and is supported by some examples (e.g., Posey 1988; see also Crooks 2002 for a review). In contrast, other studies show an increase on macrofaunal abundance as a result of refuge creation (De Grave et al. 1998).

In summary, based in our observations on the distribution and coverage of the reefs of *C. gigas* and the expansion rates reported for other areas worldwide, the success of this oyster is low. However, in terms of the potential expansion, our result may be misleading, given that the distribution is controlled by the availability of substratum.

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