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Foraging by the omnivorous crab *Pachygrapsus transversus* affects the structure of assemblages on sub-tropical rocky shores

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ABSTRACT: The roles of herbivory and predation in determining the structure and diversity of communities have been tested across most intertidal systems. In contrast, the importance of omnivorous consumers remains untested in many rocky shore communities. We tested the role of a small omnivorous crab in an intertidal food web on rocky shores of the sub-tropical southwest Atlantic. Exclusion of the grapsid crab *Pachygrapsus transversus* in the field resulted in significant changes in the abundance of functional groups in the sublittoral fringe of sheltered shores, where the dominant cover changed from a suite of macroalgae to an assemblage of filter-feeding animals (ascidians, sponges, mussels). In contrast, limpets, whelks, large crabs and fish did not significantly affect community composition of the assemblage. To examine the omnivorous feeding pattern of *P. transversus*, we did laboratory experiments to test its foraging behaviour among animal and algal groups. The crab showed selective behaviour, preferring invertebrate groups to macroalgae, and opportunistic behaviour among types of prey within those major groups. According to our results, the role of slow-moving and large fast-moving consumers is apparently negligible compared to the effect of an omnivorous consumer. *P. transversus* plays an important role in determining the intertidal community composition on these subtropical rocky shores, causing changes in the balance of functional groups and controlling invasive species.

KEY WORDS: Omnivory · Predation · Community ecology · Top-down control · Functional groups · Food web · Foraging behaviour

INTRODUCTION

The effects of consumers in complex food webs are still debated, because increased diversity makes a large number of links possible (e.g. Polis & Strong 1996, Finke & Denno 2004). The presence of omnivorous consumers makes the situation even more complex, owing to their interaction with many trophic levels (e.g. Bruno & O'Connor 2005). Although studies during the last 30 yr have shown the importance of slow-moving and fast-moving predators and herbivores in intertidal food webs, the influence of omnivores in this system has seldom been addressed.

In rocky shore communities, herbivory often plays a very important role, as repeatedly demonstrated by experimental studies showing a clear reduction of algal cover by molluscan grazing, with similar intercontinental patterns (e.g. Underwood 1980, Bustamante et al. 1995, Menge et al. 1999, Williams et al. 2000, Jenkins et al. 2005). Yet, some geographical differences can be noted in predator–prey relationships. On temperate and

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sub-tropical shores, single groups of slow-moving (e.g. starfish, whelks) or fast-moving predators of large size (e.g. crabs, fish) consume large numbers of mussels and barnacles, and indirectly affect the abundance of other invertebrates and algae by removing their competitors (e.g. Paine 1971, Fairweather & Underwood 1991, Navarrete & Castilla 2003, Rilov & Schiel 2006, reviewed by Jenkins et al. 2008). In contrast, there have been fewer studies on tropical shores, although some experimental work on the coast of Panama showed that single groups of consumers do not separately impact sessile species assemblages (Menge & Lubchenco 1981). Instead, their cumulative foraging effect may drive changes in community structure (Menge et al. 1985, 1986a,b). Therefore, greater diversity of consumers in tropical regions increases the complexity of food webs and, based on the few published data, has so far prevented the identification of important consumers and the ways in which they influence the structure of assemblages on tropical rocky shores.

Small omnivorous crabs of the genus *Pachygrapsus* are abundant and fast-moving on intertidal shores, where their feeding activity can potentially impact assemblages (e.g. Abele et al. 1986, Cannicci et al. 2002, Silva et al. 2009). However, their role in the food web is still controversial. An experimental study reported an important influence of the crab *P. transversus* on both algae and invertebrates near crevices that these animals use as shelter (Menge et al. 1983). On the other hand, other short-term experiments did not show any significant impact of *P. marmoratus* on animal prey (Brazão et al. 2009) and *P. transversus* on algal assemblages (Sauer Machado et al. 1996).

Small fast-moving consumers are abundant along the coast of the tropical and sub-tropical southwest Atlantic, for which there is very limited information on the structure of rocky shore communities and the underlying ecological processes ruling their dynamics (but see Sauer Machado et al. 1996). Given that *Pachygrapsus transversus* is very abundant across our study region (Flores et al. 2009), in contrast to the low density of slow-moving (Christofoletti et al. in press b) and large fast-moving consumers (pers. obs.), we hypothesised that this crab influences the structure of intertidal assemblages through its feeding pattern. We manipulated the access of different types of consumers in the field to test this hypothesis. As *P. transversus* is an omnivorous consumer with a wide range of prey available, it is also important to verify whether such an effect is a result of an opportunistic or selective feeding pattern. In a complementary experiment in the laboratory, we offered prey under equal conditions to remove any effect of availability, which is expected to vary in natural conditions due to biological processes, to test the opportunistic behaviour of the consumer.

MATERIALS AND METHODS

Study area. Field experiments were conducted at the sheltered shores of Lamberto Beach (23° 29′ 48″ S, 45° 06′ 54″ W) and Enseada (23° 30′ 00″ S, 45° 05′ 02″ W) in the north coast of São Paulo State, in the sub-tropical area of Brazil. Tidal amplitude in this region varies from 0.4 to 1.4 m, on neap and spring tides, respectively. Below the dominant cover of chthamalid barnacles, the lower midlittoral and the sublittoral fringe zones along this coast tend to be dominated by sessile filter-feeding invertebrates at exposed sites. These include mainly mussels, sabellariid reef-building polychaetes and barnacles, while canopy-forming macroalgae dominate at sheltered sites (Christofoletti et al. in press b).

Activity of mobile predators. The abundance and foraging activity of mobile consumers on intertidal assemblages was estimated from February to April 2008 using video recordings. A Canon PowerShot SD1000 digital camera was attached to a metal frame which was held 1 m from the substratum, allowing an area of 0.3 × 0.4 m to be recorded. The frame was screwed to the rock a few hours before the images were recorded, thus allowing observations to be taken with minimal disturbance to the behaviour of the animals. Areas of the sublittoral fringe and the low midlittoral were selected on different rocks to ensure independent sampling. Images were recorded during daylight high (n = 13) and nocturnal low (n = 11) tides, at times of greater activity of intertidal fish and crabs, respectively (e.g. Menge & Lubchenco 1981, Burrows et al. 1999). Videos were recorded continuously for 1 h, centred on the time of extreme tide. The total time that crabs, isopods and fish visited the area was registered by fully examining video recordings. In each area, the total visiting time of a given group was chosen as a response variable because it would allow more reliable estimation of the impact of predators upon prey than the number of visiting consumers (Burrows et al. 1999). We also measured the time of feeding behaviour displayed by fish and crabs, which was not possible to quantify for isopods because they use ventral appendages for feeding.

Predator-exclusion experiments. Experimental manipulations were conducted to test the influence of consumers on intertidal assemblages of sheltered shores. The experiment consisted of 4 treatments: (1) ‘control’, an area without any manipulation; (2) ‘procedural control’, corresponding to a roof, thus allowing foraging by slow-moving and fast-moving animals, but also testing possible effects of experimental manipulation, such as shading and restricted circulation of water; (3) ‘partial exclusion’, allowing access of *Pachygrapsus transversus* into the experimental plot, but excluding fish, large crabs and slow-moving animals; and (4) 'total exclusion'. Therefore, differences between treatments (3) and (4) should only be due to the impact of *P. transversus* foraging.

Cages of 20 × 20 × 8 cm were made with a microfibre net (1.4 mm mesh), cable-tied to a top and lateral PVC structure and to a basal EVA 6 mm thick foam sheet. Cages were screwed to the rock, and layers of tulle mesh fabric were squeezed between the EVA layer and the surface of the rock, providing a better fit without retaining water during low-tide, and also preventing consumers getting into the cages through the lower edges. In the 'partial exclusion' treatment, 2 small windows (3 × 6 cm) were open in each side of the cage. During the first month, observations were made to confirm the efficiency of this treatment. Fish and gastropods were unable to enter through the lateral windows. Larger crabs were never seen near the cages, neither during preliminary observations nor over the course of the experiment. *Pachygrapsus transversus* avoided the cages during the first 10 d but afterwards exhibited natural behaviour and walked over and inside them. Cages were cleaned every 15 d and meshes were replaced after 6 mo.

All treatments were randomly allocated in patches of full cover from the prevailing assemblages described above at both the low midlittoral and sublittoral fringe zones, across a 300 m sampling coastline along the sheltered Lamberto and Enseada shores. All slow-moving consumers were removed from experimental plots before the cages were fixed. Initial assemblages were examined (0 d), and subsequent changes assessed during the course of the experiment at 3 different times (150, 270 and 390 d), using independent random samples ($n = 3$ replicates per treatment) at each visit. Surveys were carried out by estimating the percentage cover of sessile invertebrates, macroalgae and bare rock, at the 15 × 15 cm inner core of plots, using a square grid of 100 intersecting points. Given that our hypotheses were about changes in the abundance of functional groups and not species, assemblages were coarsely identified to high hierarchical systematic groups (e.g. macroalgae, sponges, bivalves, ascidians). As groups are potential competitors for space, their percentage cover was analysed separately to guarantee independence of data. The changes in abundance for each prey over time were analysed separately for each of the 2 shore habitats with analyses of variance (ANOVA) with 'shore' as a random factor with 2 levels and the fixed orthogonal factors 'treatment' (4 levels) and 'time' (4 levels). Homoscedasticity was tested using Cochran's *C*-test and the arcsine transformation was applied when necessary. As ANOVA is still robust to variance heterogeneity in large balanced designs, raw data was used in the model when transformation was not sufficient to achieve homoscedasticity, and we used a conservative level of significance ($p < 0.01$, Underwood 1997). In cases when the power of the test could be increased, post hoc pooling was performed when the p-values of higher order interactions were greater than 0.25 (Underwood 1997). When necessary, the post hoc Student-Newman-Keuls test was applied for multiple comparisons of means.

Foraging behaviour: opportunist × selective consumer. Based on the most common prey found in the field and in stomach contents (R. A. Christofoletti et al. unpubl. data), we designed 3 different multiple choice experiments to test the foraging behaviour of *Pachygrapsus transversus*. Therefore, in contrast to what happens in the field, prey were offered in equal amounts. We assumed that an opportunist consumer should forage equally among prey as opposed to a selective consumer which should forage differently among prey. This design does not test preference among prey (see the ongoing debate Underwood et al. 2004, Underwood & Clarke 2005, 2006, Manly 2006, Taplin 2007), but the opportunistic behaviour of a consumer and was designed to confirm the results of the previous field experiment.

First, we tested *Pachygrapsus transversus* foraging activity among 4 different algal morpho-functional groups: filamentous (*Callithamnion* sp.), corticoid (*Acanthophora* sp.), calcareous (*Amphiroa* sp.) and microalgae (biofilm). Secondly, the consumption of animal prey was compared among barnacles (*Chthamalus* sp.), mussels (*Brachidontes* sp.), polychaetes (*Phragmatopoma* sp.) and sponges. Finally, to compare algae and invertebrates, we conducted a third experiment using 2 prey of each type simultaneously. If selective behaviour was observed in Expt 1 and 2, the 2 most foraged prey would be used. If opportunist behaviour was observed, prey items would be chosen by chance. In all protocols, different *P. transversus* specimens were used in each trial.

Trials were conducted under natural photoperiod conditions (~ 12 h light:12 h dark) and temperature (~20°C) with a constant flow of sea water covering the bottom (10 cm) of the aquaria. A central shelter (8 cm width × 3 cm diameter) was introduced into the experimental aquaria (20 × 20 × 30 cm, $n = 16$), with opaque walls to avoid external interference. Adult *Pachygrapsus transversus* of both sexes, with no missing appendages, were collected during low tides and kept unfed in individual containers for a period of 48 h. Crabs were then transferred to experimental aquaria and allowed to acclimatise for 24 h. All prey were collected 2 d before the beginning of the experiments and kept in running sea water. Prey were fragmented in pieces of similar size and kept attached to rock chips. Initial tests showed that either loss of prey weight or cover area were not accurate measures of consumption, because prey were very different in shape and volume, and *P. transversus* is an active small crab, consuming amounts of food too small to be quantified but releasing a great amount of small pieces of prey into the aquarium during ingestion. Instead, we video recorded all aquaria using cameras with infrared lights and used consumption time spent by the crab on each prey as the response variable. The consumption was determined by the handling and ingestion time visualised by the action of the chelipeds and maxilipedes.

Prey were offered simultaneously, each one placed at random in each of the 4 corners of the aquarium. As *Pachygrapsus transversus* presents greater activity during low tides, multiple choice experiments were done for all animals during a period encompassing 3 consecutive low tide periods in nature. By doing so, results from the beginning, when starving individuals would probably be less selective, could be distinguished from those obtained later in the trial. To ensure independence of data, each sampling time was analysed separately and only 1 randomly selected prey per aquarium was considered. Experiments started 2 h before the time of low tide and filming was continuous over the following 4 h. Food items were then removed and the same procedure was repeated over the next 2 low tide periods. Rock chips were used only once to avoid the influence of chemical cues from the consumer.

There were 8 replicates per prey and, hence, a total of 32 experimental trials per experiment. In a few cases, crabs managed to escape; therefore, a number of replicates were randomly removed to maintain a balanced analysis. In the first 2 experiments, separately testing foraging behaviour among algal groups and among invertebrates, data were analysed using a 1-way ANOVA. A specific model was tested in the third experiment, comparing the foraging behaviour among algal and animal groups, in which 'group' (algae × animal) was a fixed factor corresponding to the functional level, and 'species' (nested in group) was a random factor corresponding to the systematic level. Post hoc pooling and procedures to deal with variance heterogeneity followed the protocol described above.

RESULTS

Activity of mobile predators

At low tides, crabs (*Pachygrapsus transversus*) were seen during 63.4% ± 97.2 (mean ± SD) of the time over the area, with frequent foraging activity (37.7% ± 49.2 of the time), while isopods (*Ligia exotica*) were present (45.0% ± 40.4) mainly at the midlittoral level. Crabs and isopods were not seen during high tide, whilst fish were observed for 6.8% ± 16.4 of the time, almost always foraging (6.4% ± 15.7). The predation activity of crabs, based on foraging time, was greater than fish (*t*-test = 2.26, df = 22, p = 0.0344). Large crabs were never observed in the video records.

Predator-exclusion experiments

There was no influence of predation on the low midlittoral assemblages, where only a temporal difference in settlement of barnacles between shores was observed (Table 1) which failed to persist as adults. However, there was a significant effect of *Pachygrapsus transversus* on the sublittoral fringe community (Table 2), where a significant effect of the total exclusion treatment, in relation to the partial treatment and controls, was obtained for all prey (Table 2). The single significant change for the partial exclusion treatment in relation to the others was a decrease of macroalgal density after 150 d on the Lamberto shore (Table 2, Fig. 1A). Nevertheless, the macroalgae returned as the main cover after 270 d, while there was less cover in the total exclusion plots. The exclusion of *P. transversus* caused a similar pattern of species succession and diversity at both shores, differing only in time (Table 2) or the density at which these taxa settled on experimental plots (Fig. 1A).

At the beginning of the experiment there was a full dominance of macroalgae in the sublittoral fringe, which were covered by a colonial ascidian (*Didemnum psammatodes*) by 150 d (Fig. 1A). In sequence, a succession of sessile invertebrates was observed in experimental units where all consumers were excluded. The abundance of the colonial ascidians decreased after 150 d (Fig. 1A), coinciding with the development of solitary species at both shores, hence increasing the diversity of ascidians. Later on, bivalves, including oysters, *Brachidontes* spp. and the invasive *Isognomon bicolor*, became important colonisers after 270 and 390 d at Enseada and Lamberto, respectively (Fig. 1A, Table 2). Consistently, on both shores, sponges increased significantly after 270 d and bare rock space at 390 d (Fig. 1B, Table 2). Therefore, by excluding *Pachygrapsus transversus*, the assemblage at the sublittoral fringe changed from a rather homogeneous cover of macroalgae to an assemblage of sessile invertebrates, with ascidians, sponges, bivalves and bare rock occupying comparable surface areas (up to 25%).

Foraging pattern: opportunist × selective consumer

Pachygrapsus transversus showed opportunist behaviour with either algal or animal species presented separately (Table 3). On the other hand, the

Table 1. Effects of consumer exclusion on the abundance of prey in the low midlittoral of sampled shores. Results of the Student-Newman-Keuls (SNK) procedure are shown for significant sources of variation (underlined) for the variation in abundance of prey over time (0, 150, 270, 390 d) in each shore (En = Enseada, La = Lamberto) and treatment (TE = Total Exclusion, PE = Partial Exclusion). *C* = Cochran's *C*-test; ns = not significant

	df	Bare rock			*Chthamalus*			*Tetraclita*			Macroalgae			Vermetids		
		C = 0.1769 (ns)			*C* = 0.1908 (ns)			*C* = 0.1454 (ns)			*C* = 0.8970 (p < 0.01)			*C* = 0.2825 (p < 0.01)		
		MS	*F*	p	MS	*F*	p	MS	*F*	p	MS	*F*	p	MS	*F*	p
Shore = sh	1	65.78	0.39	0.5346	76.78	1.46	0.2313	5.04	0.06	0.8153	12.04	0.95	0.3328	2.67	0.72	0.3983
Treatment = tr	3	292.26	1.73	0.1692	378.37	3.37	0.1727	18.08	0.2	0.8978	16.57	1.31	0.2788	2.03	0.32	0.8118
Time = ti	3	135.81	0.81	0.4957	363.44	1.04	0.4886	420.36	1.94	0.2993	11.07	0.88	0.4586	3.47	0.94	0.4259
sh × tr	3	172.77	Pooled		112.42	2.14	0.1040	33.52	Pooled		4.35	Pooled		6.31	1.71	0.1738
sh × ti	3	60.87	Pooled		350.68	6.67	0.0005	216.13	2.36	0.0798	9.85	Pooled		0.64	Pooled	
tr × ti	9	62.20	0.37	0.9459	77.94	1.48	0.1736	37.63	0.41	0.9249	14.78	1.17	0.3299	2.48	0.67	0.7302
sh × tr × ti	9	61.09	Pooled		67.40	Pooled		44.08	Pooled		11.52	Pooled		3.94	Pooled	
Residual	64	168.70			52.57			91.60			12.65			3.69		
SNK tests					En, TE: 0 = 150 < 270 = 390 La, TE: 0 = 390 < 150 = 270											

Table 2. Effects of consumer exclusion on the abundance of prey in the sublittoral fringe of sampled shores. Details as in Table 1

	df	Macroalgae			Ascidians			Sponges			Bivalves			Bare rock		
		C = 0.3158 (p < 0.01)			*C* = 0.3407 (p < 0.01)			*C* = 0.4041 (p < 0.01)			*C* = 0.4573 (p < 0.01)			*C* = 0.4597 (p < 0.01)		
		MS	*F*	p	MS	*F*	p	MS	*F*	p	MS	*F*	p	MS	*F*	p
Shore = sh	1	1641.76	17.46	0.0001	625.26	13.42	0.0005	15.04	0.27	0.6023	99.45	12.38	0.0008	137.76	1.1	0.2992
Treatment = tr	3	11039.90	7.35	0.0678	1807.48	4.45	0.1260	610.64	30.94	0.0093	300.11	4.93	0.1113	775.87	5.98	0.0881
Time = ti	3	2501.15	5.95	0.0885	783.26	1.9	0.3058	219.61	3.29	0.1773	130.09	2.94	0.1996	220.48	2.65	0.2223
sh × tr	3	1502.34	15.98	<0.0001	406.59	8.73	0.0001	19.74	0.36	0.7822	60.83	7.57	0.0002	129.84	1.03	0.3843
sh × ti	3	420.09	4.47	0.0065	412.54	8.85	0.0001	66.82	1.22	0.3104	44.22	5.51	0.002	83.18	0.66	0.5789
tr × ti	9	1785.60	4.68	0.0155	603.69	1.69	0.2221	154.23	2.81	0.0076	113.15	4.92	0.0132	487.73	3.88	0.0006
sh × tr × ti	9	381.38	4.06	0.0004	356.32	7.65	<0.0001	40.26	Pooled		22.99	2.86	0.0067	80.74	Pooled	
Residual	64	94.04			46.59			54.85			8.03			125.77		
SNK tests		En, TE: 150 = 270 = 390 < 0 La, PE: 150 < 0 = 270 = 390 La, TE: 390 < 150 < 270 = 0			En, TE: 0 = 270 = 390 < 150 La, TE: 0 = 270 < 150 = 390			TE: 0 = 150 < 270 = 390			En, TE: 0 = 150 < 270 = 390 La, TE: 0 = 150 = 270 < 390			TE: 0 = 150 = 270 < 390		

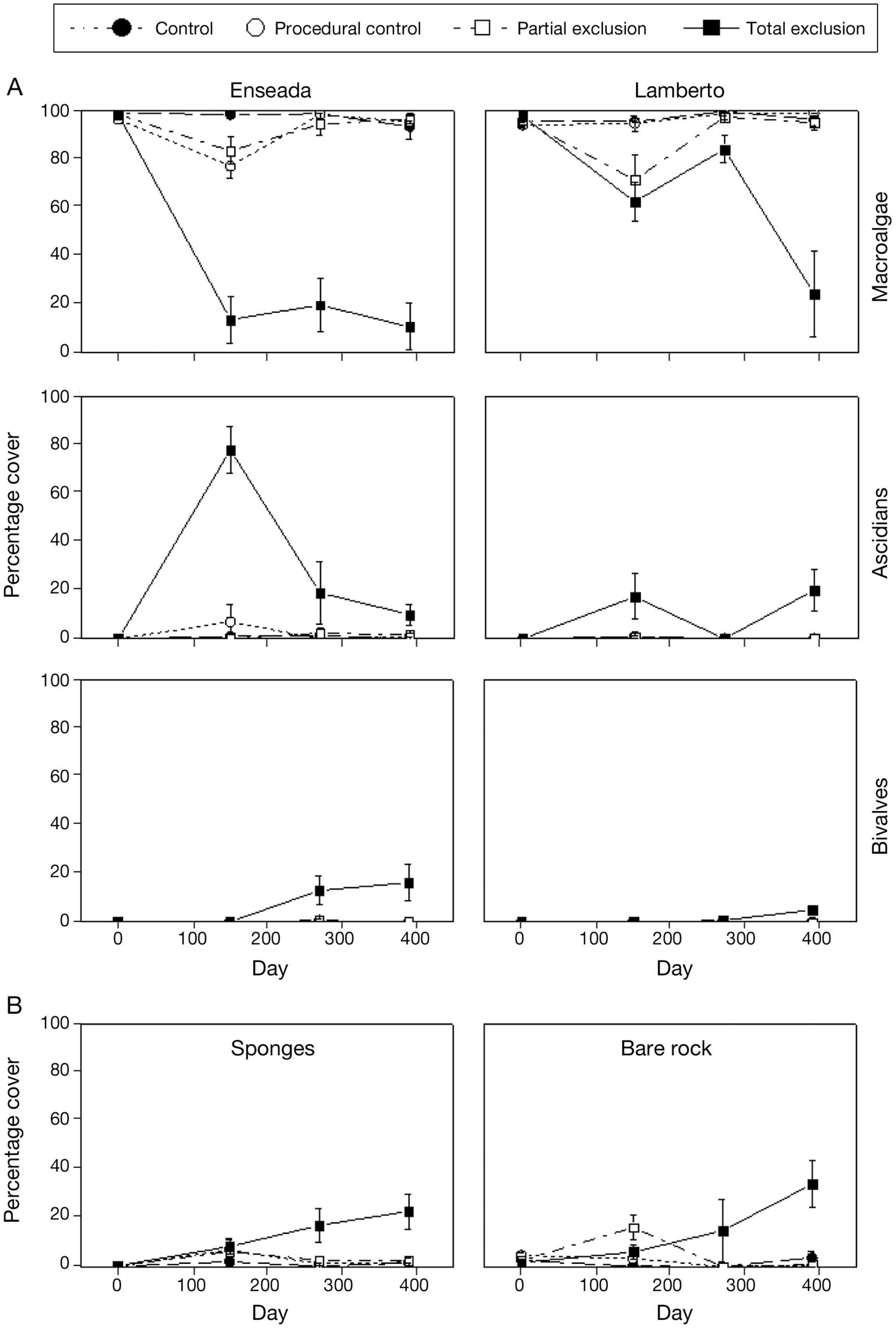

Fig. 1. *Pachygrapsus transversus.* Influence of the omnivorous crab on the abundance of prey (mean ± SE) over time in the sublittoral fringe of sheltered shores (Enseada and Lamberto) in southeastern Brazil. Results are shown (A) separately for each shore, or (B) merged, in accordance with the patterns of significance (see Table 2). Details of treatments are given in 'Materials and methods'

Table 3. *Pachygrapsus transversus.* Foraging pattern. Expt 1: selected prey among morpho-functional groups of algae (filamentous, corticoid, calcareous and biofilm). Expt 2: selected prey among invertebrates (barnacles, mussels, sabellariid polychaetes and sponges). Expt 3: selected prey between algae (corticoid and calcareous) and invertebrates (barnacles and mussels), including both the comparison between high hierarchical groups (plants and animals), and prey type nested in them. Results of the SNK test for the significant factor (underlined) are also presented. *C* = Cochran's *C*-test; ns = not significant

Experiment		1st Low Tide				2nd Low Tide				3rd Low Tide			
		df	MS	*F*	p	df	MS	*F*	p	df	MS	*F*	p
1	Algae species	3	0.063	0.92	0.4443	3	3.933	1.95	0.1534	3	0.003	0.32	0.8097
	Residual	28	0.069			20	2.013			20	0.011		
			C = 0.4045 (ns)				*C* = 0.4178 (ns)				*C* = 0.4928 (ns)		
2	Animal species	3	0.0552	1.55	0.224	3	0.2574	0.12	0.9458	3	4.9006	1.35	0.279
	Residual	28	0.0356			28	2.0951			28	3.6364		
			C = 0.3087 (ns)				*C* = 0.5137 (ns)				*C* = 0.5153 (ns)		
3	Group = gr	1	0.163	3.93	0.0572	1	1921.95	2.86	0.2331	1	0.297	10.67	0.0033
	Species (gr)	2	0.008	Pooled		2	673.17	2.75	0.0811	2	0.034	Pooled	
	Residual	28	0.041			28	244.70			24	0.028		
			C = 0.4415 (ns)				*C* = 0.4471 (ns)				*C* = 0.4573 (ns)		
SNK test											Algae < Animal		

between groups experiment showed a selective behaviour of *P. transversus*, favouring animal prey, regardless of species (Fig. 2A, Table 3). Numerical differences were consistent over the 3 low tide periods, but a statistically significant difference was only found for the third period (Fig. 2, Table 3). This result agrees with our methodology assumption that the starving period would influence the results.

DISCUSSION

Our results show that *Pachygrapsus transversus* can affect the dominance of benthic communities on open rock surfaces of intertidal sheltered shores on the subtropical coast of Brazil. Also, in the presence of *P. transversus*, the effects of limpets, whelks and fish on these assemblages are not important. This is in contrast with previous studies, in which predators and herbivores have been shown to control community dominance through simple, direct food webs (see reviews by Menge 2000, Jenkins et al. 2008). Our results also suggest an important contribution for the role of omnivores in trophic cascades (e.g. Polis & Strong 1996, Finke & Denno 2004, Bruno & O'Connor 2005). A wide range of food resources are usually available to omnivorous consumers, but the strength of their influence in food webs will depend on their foraging behaviour. Opportunistic consumers will ingest prey in proportion to their availability and thus the diversity of prey will

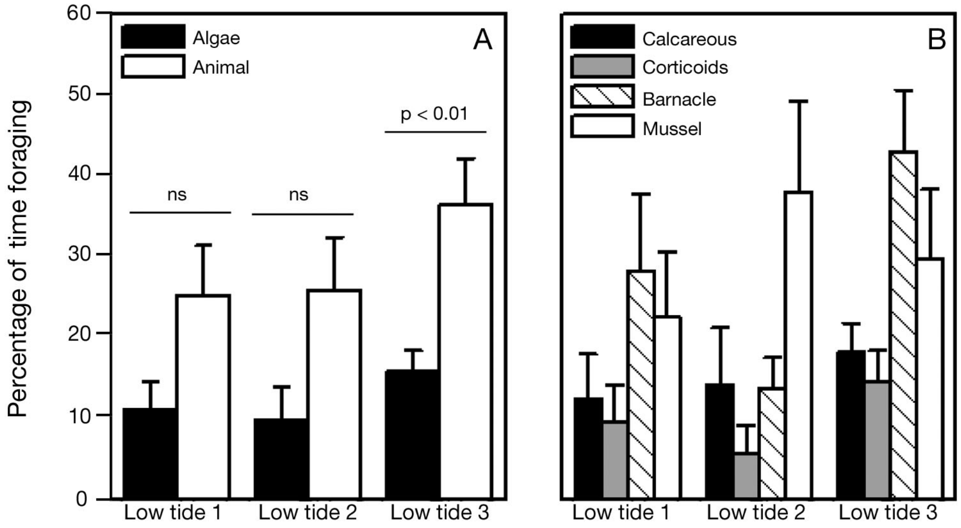

Fig. 2. *Pachygrapsus transversus.* Time spent foraging for algal and invertebrate prey (mean ± SE). Data are presented per (A) higher functional group or (B) low systematic group

largely reflect relative recruitment rates and competition, rather than consumer pressure. In contrast, a selective feeding behaviour will influence not only abundance, but also the richness of prey, hence resulting in a stronger consumer pressure on the assemblage. In our study system, *P. transversus* proved to be a selective consumer with great foraging activity on groups of animals, driving changes in both the abundance and richness of invertebrate assemblages. Yet, the complexity of their influence in the food web has to be evaluated in relation to the level of identity of prey. For instance, *P. transversus* is a selective consumer of animal groups (functional level) while specific identity of prey (systematic level) was not important. Therefore, information on feeding behaviour is an important tool for evaluating the role of such consumers in food webs, for instance to verify if changes occur in high or low hierarchical systematic or functional groups.

Pachygrapsus transversus has a stronger consumer influence on animal prey and its impact renders an indirect positive effect on primary producers, not through changes in herbivory pressure as in other food webs (e.g. Finke & Denno 2004, Byrnes et al. 2006, Snyder et al. 2006), but through competition among sessile organisms due to a negative effect on sessile invertebrates. Abundance of sponges and ascidians increased within a few weeks after *P. transversus* exclusion and, although mussels are never found in these shores, our results show that they can settle and grow in these areas, even the invasive species *Isognomon bicolor*. Since sessile invertebrates are the dominant competitors in intertidal areas (e.g. Menge et al. 1986a,b, Bell 2008), their removal by predation allows the spreading of macroalgae over the shore. Also, as fish and other herbivores are not abundant in this area, their weak grazing pressure is insufficient to decrease algal abundance and create bare rock space, as observed in Panama (see Menge & Lubchenco 1981). Thus, the dominance of macroalgae on the sublittoral fringe at our study area is a consequence of the predation effects of *P. transversus*, and a weak pressure of herbivores. In the absence of consumer effect, filter-feeding animals reached nearly 50% of the sublittoral cover (Fig. 2) and primary producers became the less abundant functional group. Therefore, *P. transversus* plays an important role in the functioning of this ecosystem through changes in balance of the functional groups and control of invasive species (e.g. *I. bicolor*).

Pachygrapsus transversus is very abundant along the tropical western Atlantic coast, but, to our knowledge, only 2 experimental studies have previously tested its role in the regulation of communities. On the Rio de Janeiro coast, it was considered a herbivore, and its foraging pressure, together with other mobile consumers, was not found to be important for determining the algae community structure (Sauer Machado et al. 1996). Indeed, our results place *P. transversus* as an omnivorous crab with preference for animal prey, without any direct effect on the diversity of primary producers. In Panama, where *P. transversus* was only found to have a localised effect on populations of prey inside crevices (Menge et al. 1983), the abundance of top predators (fish and large crabs) is greater (see Lubchenco et al. 1984) than on the north coast of São Paulo State (see 'Results'). We suggest that differences between our results, i.e. broad influence of *P. transversus* and lack of an effect of slow-moving consumers, and those obtained in Panama may be due to a trophic cascade influenced by both density-mediated (DMII) and trait-mediated indirect effects (TMII) (e.g. Trussell et al. 2002, 2003, Griffin et al. 2008), which should be further tested. In this scenario, weaker predation stress by fish on *P. transversus* might be responsible for its greater density (Flores et al. 2009), compared to other areas (Lubchenco et al. 1984, Sauer Machado et al. 1996), and presumably greater activity (DMII and TMII processes). Therefore, the lack of predatory threat may allow wide foraging over larger open surfaces and not restrict activity to crevices and their surroundings. A large population of such a mobile animal, exhibiting an intense foraging activity over wide areas, is thus expected to exert a strong control on prey. Based on our results, we believe large populations of *P. transversus* remove animals and plants over large areas of the shore, which could have considerable consequences for slow-moving consumers (e.g. whelks) through competition.

In Panama, where the diversity of consumers is greater, their cumulative effect, rather than the impact of single groups of consumers, regulates the intertidal assemblages on open rocky surfaces (Menge et al. 1985, 1986a,b), even in the presence of *Pachygrapsus transversus* (Menge & Lubchenco 1981). It is important to point out that our results do show a strong influence of *P. transversus* on intertidal assemblages, but they only suggest a null effect of slow-moving and large fast-moving mobile consumers on prey dynamics. As *P. transversus* was allowed to forage on plots where whelks and large mobile consumers were excluded, the strong predation control by *P. transversus* might be masking a possible influence of other groups. A similar effect has been described for the isopod *Ligia exotica*, masking the impact of slow-moving grazers on biofilm cover over rocky shores (Christofoletti et al. in press a). Further experiments to separate the effect of small mobile consumers and the impact of slow-moving and large fast-moving mobile animals are necessary to evaluate the contribution of limpets, whelks and fish in the top-down control in our region.

The omnivorous feeding strategy of *Pachygrapsus transversus* is an important adaptive behaviour for this species, and explains its presence in all the natural rocky shores or man-made hard structures, such as piers or walls, that we visited along our coastline. Feeding on a variety of prey would decrease intraspecific competition in very dense populations. Also, while maintaining a low abundance and diversity of filter-feeding animals throughout the area under its foraging pressure, the exploitation of a variety of prey enhances the chances of survival of this crab to adulthood under limitation of its preferred food resource. Therefore, the feeding pattern of *P. transversus* appears to be a critical issue in determining its role in the sub-tropical coast of the southwest Atlantic. These results provide important information about changes in functional groups and place small fast-moving consumers as important competitors with slow-moving and large consumers on intertidal rocky shores. Also, our results imply that the foraging strategy of a consumer has to be carefully considered together with its feeding pattern for a more realistic evaluation of the role of omnivores in their communities.

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