

Similar effects on sediment structure and infaunal community of two competitive intertidal soft-bottom burrowing crab species

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The intertidal crabs Neohelice granulata and Cyrtograpsus angulatus are common on the south-west Atlantic coast but they rarely share the same microhabitat. They are similar in size and in several life history traits which promote competition. Neohelice granulata is the dominant species in intertidal soft-sediment and salt-marsh areas from southern Brazil to northern Patagonia Argentina, where it forms extensive burrowing beds. Its burrowing activity affects sediment characteristics as well as the infaunal community. When both species coexist N. granulata constrains the distribution and modifies some population characteristics and burrowing behaviour of C. angulatus. However, C. angulatus live in burrows forming dense burrowing beds in soft-bottom intertidal areas where N. granulata is absent. Where both species coexist, C. angulatus rarely constructs burrows and N. granulata clearly dominate soft-sediment areas forming conspicuous burrowing beds. This suggests that these crab species could have similar ecological roles in some effects on sediments related to burrowing activities. In this study, we experimentally compare their effects on sediment characteristics and infaunal community. The results of the experiment showed that C. angulatus modify sediment water and organic matter contents and grain size–frequency distributions similarly to N. granulata. Neither N. granulata nor C. angulatus affected the mean abundance of infaunal organisms during the experiment but their variances showed the same patterns in many cases, indicating similar effects. These results indicate that C. angulatus can modify sediment characteristics similarly to N. granulata, and has similar interactions with infaunal species.

Keywords: functional redundancy, *Neohelice granulata*, *Cyrtograpsus angulatus*, bioturbation, competition, soft-bottom intertidal

Submitted 16 August 2010; accepted 19 December 2010; first published online 29 March 2011

INTRODUCTION

The strength of inter-specific competition is affected by the similitude between the involved species (Abrams, 1983). To reduce inter-specific competition, the coexistence requires that the species differ in how they affect and how they are affected by the resources (Chesson, 2000), how and what resources they are using, when and where they use them and the limitations of where they experiment (Amarasekare, 2003). Thus, it is expected to have stronger inter-specific competition as species are more similar.

Life-history traits and other inherent differences between species allow them to escape or minimize competition through different mechanisms (Chesson, 2000). One of these mechanisms, in environments spatially homogeneous where competition is possible, involves some form of intra-specific grouping and inter-specific segregation (Bolker & Pacala, 1999). The dominant competitor cannot exploit all the resources or spaces available leaving gaps in the landscape

that are occupied by the inferior competitor (Murrell & Law, 2003). In this competition by displacement, the coexistence is maintained generating spatial differences in the niche between species (Amarasekare, 2003). Competitive interactions are stronger between species with similar functions operating at the same scale (Peterson *et al.*, 1998). However, this similitude of functions needs to have a threshold to allow the coexistence between competitors (Abrams, 1983).

The role that different species play on the regulation of processes operating at community level has motivated several hypotheses that relate the vulnerability of the systems with the presence of species with similar functions (Johnson *et al.*, 1996; Lawton, 2000). The existence of functionally redundant species (*sensu* Walker, 1992) is one of the more discussed hypotheses. This hypothesis states that in some communities some species are functionally redundant, meaning that they could be lost without much effect on the ecosystem functioning (Walker, 1992). Thus, high conservation effort should go to species with low redundancy to ensure the stability of the whole ecosystem (Walker, 1995). However, there are evidences that the functional roles that the species play are under the influence of local environmental conditions and they may perform the same function under restricted

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conditions but their functions may vary in natural heterogeneous environments (Wellnitz & Poff, 2001). Moreover, species are more likely classified as redundant when less variables are measured (Rosenfeld, 2002). Recently, it has been proposed that the redundancy effect is rare; so, it is more conservative to refer to similar species (instead of redundant species; Chalcraft & Reserits, 2003) that under some circumstances play the same ecological role.

In soft-substratum habitats competition for space and direct interference within and among species is not a dominant process (e.g. Peterson, 1991; Wilson, 1991). This is mostly explained by the vertical and horizontal partitioning of the space that the three-dimensional structure of soft-sediment allows (Wilson, 1991). Thus, direct competition for space is minimized because organisms can live at different depths within sediments. There is, however, some habitat displacement involving dwellers or burrowing species (e.g. Peterson, 1977; Peterson & Andre, 1980; Wilson, 1980; Brenchley & Carlton, 1983; Kurihara *et al.*, 1989). In such cases, given that the space needed to construct a burrow is not magnified by the three-dimensions of soft-sediment, the competition cannot be minimized by inhabiting at different depths. The habitat displacement between the south-west Atlantic intertidal crabs *Neohelice granulata* (formerly known as *Chasmagnathus granulatus*) and *Cyrtograpsus angulatus* is a good example that competition for space may occur between burrowing species in soft-sediment habitat (Iribarne *et al.*, 2003; Martinetto *et al.*, 2007b). These crabs are common in south-west Atlantic coastal and estuarine areas (Boschi, 2000), but there are few places where they share the same microhabitat. They are similar in size and in many life history traits (Boschi, 2000; Luppi *et al.*, 2002) which promote competition. The crab *N. granulata* is the dominant species in soft-sediment and salt-marsh intertidal areas from southern Brazil to northern Patagonia Argentina, where it forms extensive burrowing beds (Spivak *et al.*, 1994; Iribarne *et al.*, 1997; Boschi, 2000). Its burrowing activity leads to deep changes in sediment characteristics as well as on infaunal community (Botto & Iribarne, 1999, 2000). For instance, this species modifies sediment microtopography and granulometry promoting the accumulation of fine particles (Botto & Iribarne, 2000). The presence of *N. granulata* burrowing beds also affects the distribution of meiofaunal organisms (Botto & Iribarne, 1999; Rosa & Bemvenuti, 2005) as well as the habitat use by shorebirds (Botto *et al.*, 2000; Palomo *et al.*, 2003; Escapa *et al.*, 2004; Iribarne *et al.*, 2005) and juvenile fish (Martinetto *et al.*, 2005, 2007a), the distribution of the fiddler crab *Uca uruguayensis* (Daleo *et al.*, 2003), and the feeding behaviour and the distribution of polychaetes (Escapa *et al.*, 2004; Palomo *et al.*, 2004). The geographical distribution of *C. angulatus* overlaps with *N. granulata* but it also extends south to central Patagonia (Spivak, 1997; Boschi, 2000; Iribarne *et al.*, 2003). When these species coexist *N. granulata* constrains the distribution and modifies some population characteristics (e.g. sex-ratio, size and incidence of limb autotomies) and burrowing behaviour of *C. angulatus* (Iribarne *et al.*, 2003; Martinetto *et al.*, 2007b). However, some populations of *C. angulatus* live in burrows forming dense burrowing beds in soft-bottom intertidal areas where *N. granulata* is not present (Iribarne *et al.*, 2003). Where both species coexist, *C. angulatus* rarely constructs burrows and *N. granulata* clearly dominate soft-sediment areas forming conspicuous

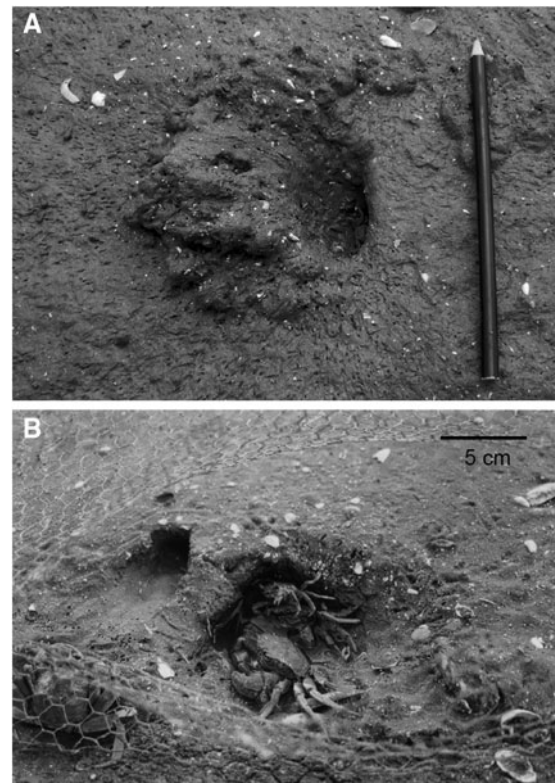


Fig. 1. *Neohelice granulata* (A) and *Cyrtograpsus angulatus* (B) burrows constructed inside the experimental units. Photograph credits: P. Martinetto (A); M. Bruschetti (B).

burrowing beds (Martinetto *et al.*, 2007b). These evidences suggest that these crab species could be 'redundant species' in some effects related to burrowing activities.

To test this hypothesis we experimentally compare the effect of *N. granulata* and *C. angulatus* on sediment characteristics and infaunal community in a soft-sediment intertidal area of the Argentinean biogeographical province where *N. granulata* is the dominant species.

MATERIALS AND METHODS

The experiment was performed in Mar Chiquita coastal lagoon (37°32'S and 57°19'W, northern Argentinean Atlantic coast)

Table 1. Two-way analysis of variance results testing for differences in water content and organic matter content in experimental cages including *Neohelice granulata* or *Cyrtograpsus angulatus*, or excluding crabs (treatments) during 1 and 2 months (time).

Source	df	MS	F	P
Water content				
Time	1	24.820	39.748	<0.001
Treatment	2	5.009	8.022	0.003
Interaction	2	0.783	1.253	0.306
Error	21	0.624		
Organic matter content				
Time	1	31.030	41.647	<0.001
Treatment	2	11.012	14.780	<0.001
Interaction	2	1.513	2.031	0.156
Error	21	0.745		

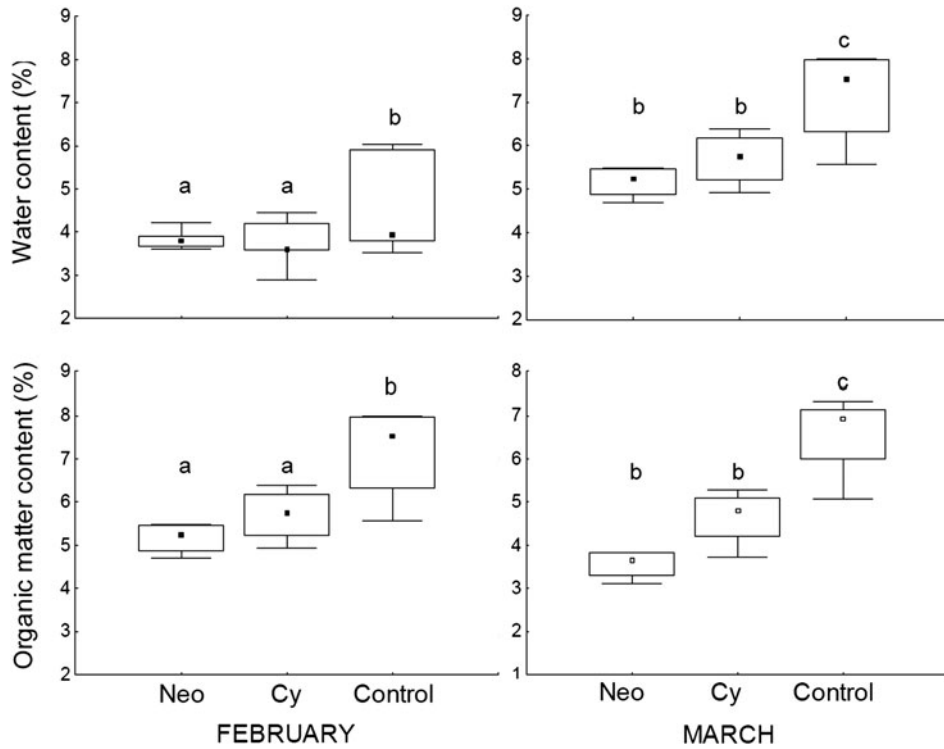


Fig. 2. Percentages of water content and organic matter content after one (February) and two (March) months of different treatments manipulating crab presence. Treatments are: Neo, *Neohelice granulata* inclusion; Cy, *Cyrtograpsus angulatus* inclusion; and control, exclusion of both crab species. Different letters indicate differences in mean values among treatments. Here and thereafter, box plots are constructed with limits being the 75th and 25th percentile, lines represent 10th and 90th percentile, and points inside boxes are medians.

where both crab species coexist. The lagoon is a body of brackish water affected by a semidiurnal tidal regime and characterized by mud flats surrounded by a large cord grass area (*Spartina densiflora*; Iribarne *et al.*, 1997; Bortolus & Iribarne, 1999). The crab *N. granulata* lives in burrows and *C. angulatus* lives free in the subtidal, in sandy or muddy flats avoiding the other crab species (Martinetto *et al.*, 2007b).

To evaluate whether *C. angulatus* and *N. granulata* are similar in their effects on the sediment and on the infaunal community we ran an experiment in the intertidal area where *N. granulata* often forms a conspicuous burrowing bed. We used 27 wire cages (1 m² area, 0.2 m high, with a mesh size of 5 cm) that were inserted into the sediment and randomly assigned 9 replicates to each of the following treatments: (1) inclusion of *N. granulata*; (2) inclusion of *C. angulatus*; and (3) control cages without crabs. Weekly, cages were checked and the construction of burrows by both species was verified. To test if treatment effect changed through time, 5 replicates were obtained after 1 month and 4 after 2 months. Similar cages have been used in former studies in this area without artefact effect on the variables measured in this study (Botto & Iribarne, 1999; Botto *et al.*, 2000; Escapa *et al.*, 2004).

To evaluate differences among treatments on sediment structure, water content, organic matter content and grain size-frequency distributions were determined. Water content of the sediment was obtained as the difference between wet and dry weight (after dried at 70°C for 72 hours). Organic matter was evaluated as the percentage of ash free dry weight (AFDW; combustion of a 10 g subsample at 550°C for 8 hours; Crisp, 1971). Grain size distributions were obtained by sieving following Carver (1971). Samples were sieved

through three mesh sizes (2000 µm, 500 µm and 63 µm) separating the samples into gravel, sand, fine sand and silt.

To compare the effect of both crab species on the infaunal community samples of sediment were taken from each cage.

Table 2. Two-way analysis of variance results testing for differences in grain size proportions in experimental cages including *Neohelice granulata* or *Cyrtograpsus angulatus*, or excluding crabs (treatments) during 1 and 2 months (time).

Source	df	MS	F	P
Gravel				
Time	1	299.416	27.663	<0.001
Treatment	2	31.814	2.939	0.007
Interaction	2	3.592	0.332	0.721
Error	21	10.824		
Sand				
Time	1	172.276	34.866	<0.001
Treatment	2	10.635	2.152	0.141
Interaction	2	2.650	0.536	0.593
Error	21	4.941		
Fine sand				
Time	1	414.96	9.973	0.005
Treatment	2	137.10	3.295	0.057
Interaction	2	49.94	1.200	0.321
Error	21	41.61		
Silt				
Time	1	2580.60	29.493	<0.001
Treatment	2	423.03	4.835	0.019
Interaction	2	17.47	0.200	0.820
Error	21	87.50		

Samples of 5 cm diameter and 2 cm depth were taken to determine meiofauna abundances and samples of 10 cm diameter and 5 cm depth for macrofauna. Meiofauna samples were homogenized and subsamples of 2 cm diameter and 2 cm depth were stained with Bengal rose to visualize the organisms and preserved in formalin 4%. Samples were sieved through 0.1 mm mesh size and the organisms quantified and grouped in broad taxonomic categories under microscope (4 ×). Macrofaunal samples were sieved through a 500 μm mesh and all the retained organisms were sorted, identified, and counted.

All the results were evaluated with two-way analysis of variance with treatment (*C. angulatus*, *N. granulata* and no crabs) and time (1 and 2 months) as factors (Zar, 1999). Homogeneity of variance was tested with the Cochran test. Square root transformation was applied when homogeneity of variance was not met. Because treatments can differ because they cause different patterns of variation among replicates rather than differences among means (Underwood, 1997), we reported the results of the Cochran test as an experimental outcome.

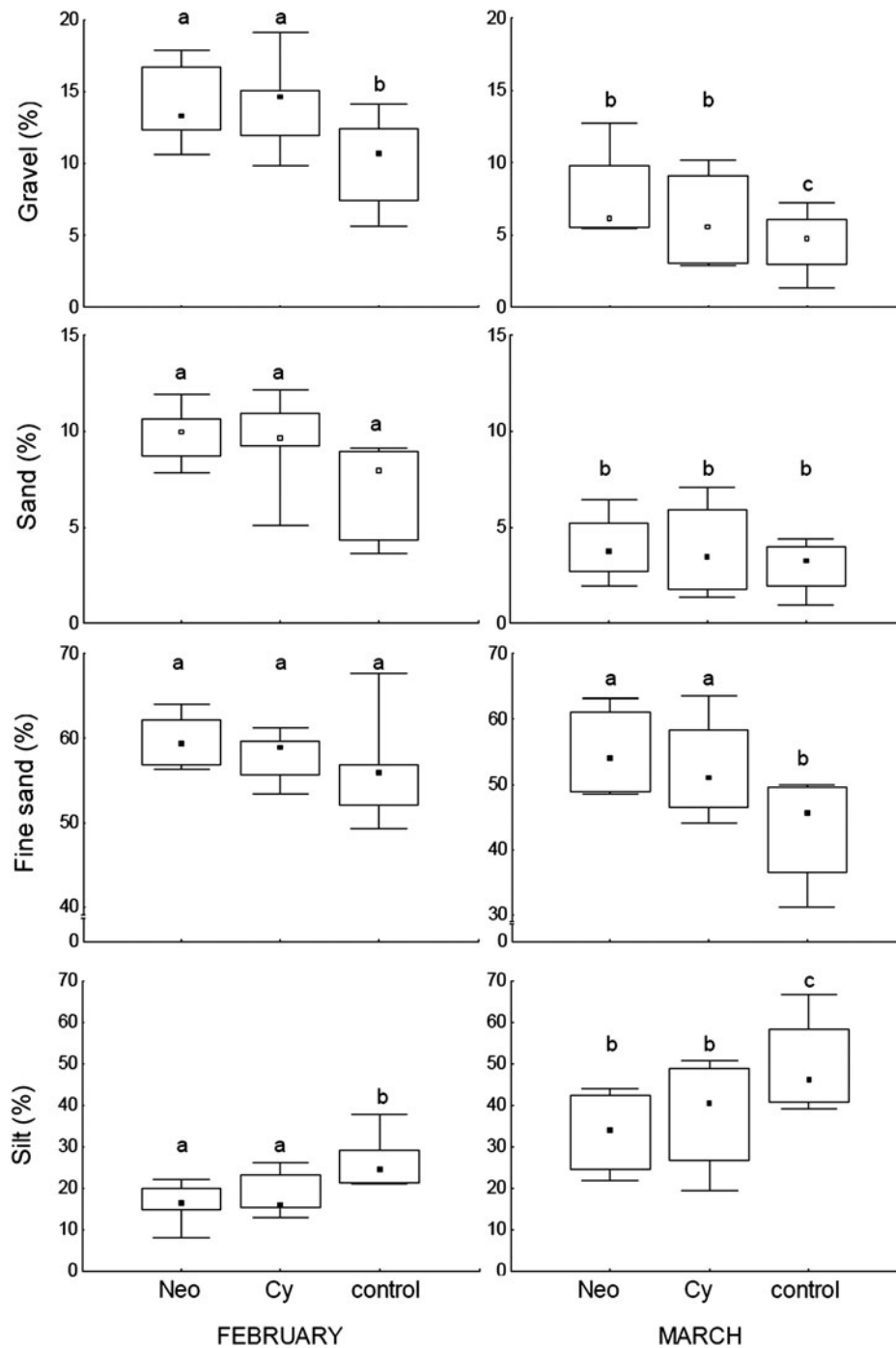


Fig. 3. Proportion of gravel, sand, and silt after one (February) and two (March) months of different treatments manipulating crab presence. Treatments are: Neo, *Neohelice granulata* inclusion; Cy, *Cyrtograpsus angulatus* inclusion; and control, exclusion of both crab species. Different letters indicate differences among treatments.

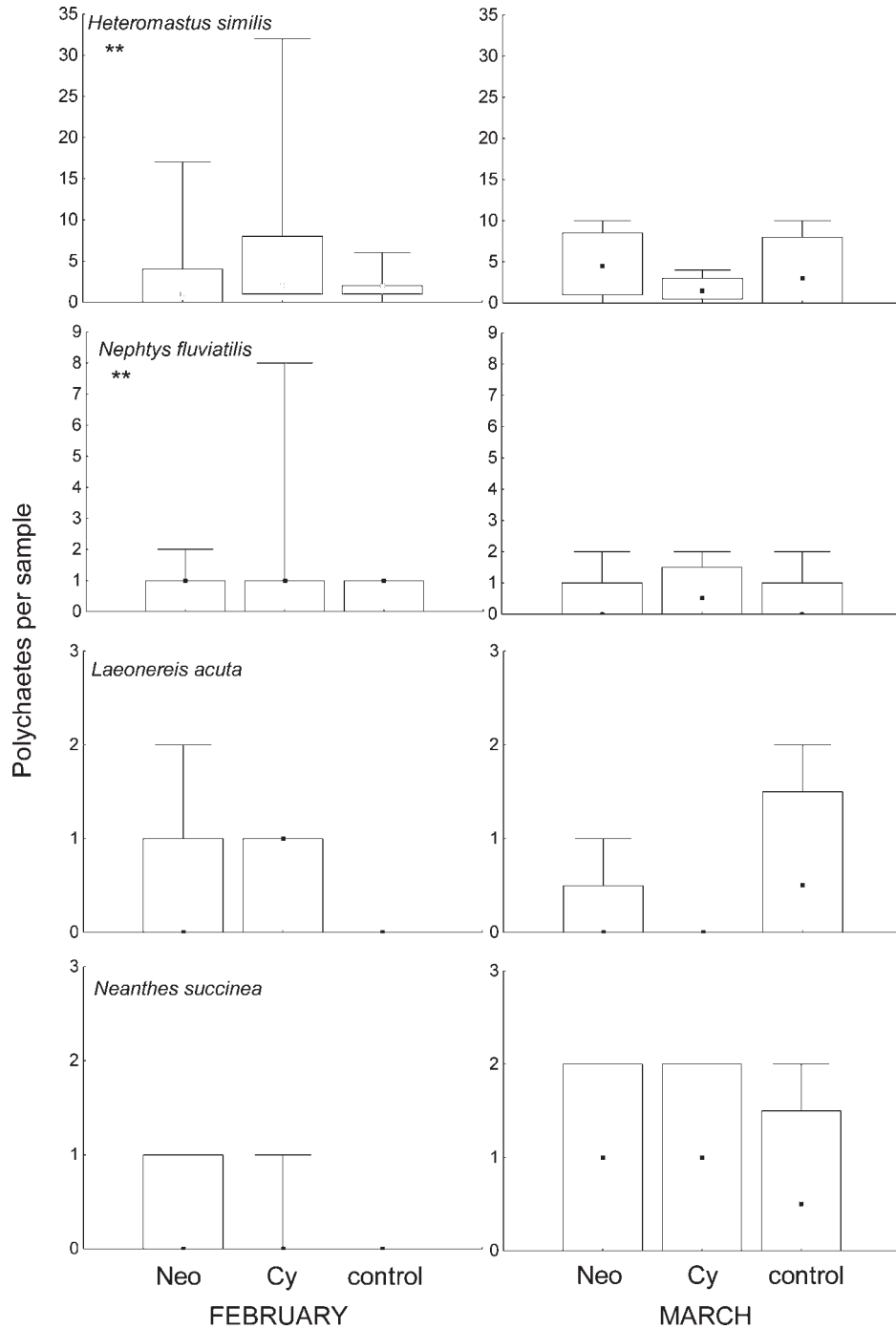


Fig. 4. Abundance of polychaetes after one (February) and two (March) months of different treatments manipulating crab presence. Treatments are: Neo, *Neohelice granulata* inclusion; Cy, *Cyrtograpsus angulatus* inclusion; and control, exclusion of both crab species. Sample size is 10 cm diameter and 5 cm depth. Asterisks indicate heterogeneity of variances (**: $P < 0.010$; Cochran test).

RESULTS

During the eight weeks experiment, crabs built burrows in all the inclusion treatments. *Neohelice granulata* burrows were easily distinguished from those of *C. angulatus* (Figure 1a, b). The burrows of *N. granulata* had a funnel tunnel entrance while *C. angulatus* built burrows with a simple straight tunnel entrance (Botto & Iribarne, 1999; Iribarne *et al.*, 2003). In addition, the sediment removed from the burrows

was disposed differently. *Neohelice granulata* built a mound near the entrance of the burrow, whereas *C. angulatus* spread the sediment over the surface with no structure or mound.

The variances in sediment water content (WC) and organic matter content (OMC) were homogeneous. Sediment WC and OMC were both higher in the control cages than in the crab inclusion cages (Table 1; Figure 2). There were no differences in WC and OMC between inclusion of *N. granulata* and

Table 3. Two-way analysis of variance results testing for differences in abundance of polychaetes in experimental cages including *Neohelice granulata* or *Cyrtograpsus angulatus*, or excluding crabs (treatments) during 1 and 2 months (time).

	df	MS	F	P
<i>Heteromastus similis</i>				
Time	1	17.785	0.346	0.563
Treatment	2	10.957	0.213	0.810
Interaction	2	50.068	0.973	0.394
Error	21	51.443		
<i>Nephtys fluviatilis</i>				
Time	1	2.017	0.721	0.405
Treatment	2	1.802	0.644	0.535
Interaction	2	0.839	0.230	0.744
Error	21	2.798		
<i>Laeonereis acuta</i>				
Time	1	0.030	0.079	0.782
Treatment	2	0.035	0.093	0.911
Interaction	2	1.146	3.047	0.069
Error	21	0.376		
<i>Neanthes succinea</i>				
Time	1	3.424	5.640	0.027
Treatment	2	0.246	0.406	0.672
Interaction	2	0.024	0.040	0.961
Error	21	0.607		

C. angulatus treatments. In addition, WC and OMC were higher in March than in February (Table 1; Figure 2).

The variances in percentage of gravel, sand, fine sand and silt were homogeneous. Percentages of gravel and sand were higher in the crab inclusion treatments than in the control and also higher in February than in March (Table 2; Figure 3). Percentage of fine sand was lower in control cages in March than in the control cages in February or the crab inclusion cages in February and in March (Table 2; Figure 3). Silt percentage was higher in the control than in the crab inclusion cages either in February or in March (Table 2; Figure 3). In addition, silt percentage was higher during March (Table 2; Figure 3).

Four polychaete species were found in macrofaunal samples (*Heteromastus similis*, *Nephtys fluviatilis*, *Laeonereis acuta* and *Neanthes succinea*) and 4 groups were identified in the meiofaunal samples (nematodes, foraminifers, ostracods and copepods). Higher variances were observed in *H. similis* ($C_5 = 0.626$, $P = 0.007$) and *N. fluviatilis* ($C_5 = 0.746$, $P = 0.006$), in treatments with crab inclusion (Figure 4). Mean densities of *H. similis*, *N. fluviatilis* and *L. acuta* did not show difference among treatments nor between months (Table 3; Figure 4). The density of *N. succinea* was higher in March than in February, while it was no different among treatments (Table 3; Figure 4). The variances of ostracods, foraminifers and copepods were not homogeneous ($C_5 = 0.390$, $P = 0.004$; $C_5 = 0.489$, $P = 0.014$; $C_5 = 0.780$, $P < 0.001$ respectively). Variances in ostracods were higher in February than in March (Figure 5). Foraminifers showed higher variances in the *N. granulata* inclusion treatment and in the control than in the *C. angulatus* inclusion (Figure 5). Copepods had higher variances in the control than in the treatments with crab inclusions (Figure 5). Mean densities of meiofaunal organisms were not different among treatments but ostracods, foraminifers and copepods showed a significant

effect of time being more abundant in February (Table 4; Figure 5).

DISCUSSION

The results of the experiment showed that *C. angulatus* modify sediment water and organic matter contents and grain size–frequency distributions similarly to *N. granulata*. These results were also consistent through the experimental time. There were neither mean effects of *N. granulata* nor *C. angulatus* on the abundance of infaunal organisms during the experiment. However, their variances showed the same patterns in many cases, indicating effects. Thus, in addition to the similarities in life history traits, our results show that these species have similar effects on sediment structure and species interactions supporting the hypothesis that these crab species play some sort of redundant role. It has implications for the competitive interaction, but also for the possibility of recovery of an ecosystem.

Competition between similar species should be stronger (Abrams, 1983) than between non-related species. In our studied system, the plasticity of *C. angulatus* to live in the subtidal when *N. granulata* is present allows for their coexistence. The burrows play a key role in the life of *N. granulata*, whereas for *C. angulatus*, burrows seem to be less important (Iribarne *et al.*, 2003, Martinetto *et al.*, 2007b). However, when *N. granulata* is absent *C. angulatus* can construct burrows and have similar effects on the sediment and infauna. Inside *N. granulata* burrowing beds, *C. angulatus* has lower density, larger sizes, lower incidence of limb autotomies, and a higher percentage of males than in adjacent areas without *N. granulata* burrows (Martinetto *et al.*, 2007b). When *N. granulata* were experimentally excluded within their burrowing beds, new settlers of *C. angulatus* colonized these areas, made burrows and maintained them until they reached large size (Botto & Iribarne, 1999). Another field experiment shows that in absence of *N. granulata*, adults of *C. angulatus* construct their own burrows and never use empty *N. granulata* burrows (Martinetto *et al.*, 2007b). Thus, *C. angulatus* burrowing activity is constrained when it is sharing the habitat with *N. granulata* indicating that competitive interaction is strong and *N. granulata* is the dominant species. The similarity in ecological roles regarding effects on sediment characteristics and abundance of infaunal organisms reported in this study add evidence that the strength of the competitive interaction between these crab species is strong.

Co-occurring species with similar ecological roles turn the ecosystem less vulnerable to disturbance or random species extinction (Walker, 1995). This concept has been discussed under different hypotheses (Peterson *et al.*, 1998). The major criticism that these hypotheses have received, specially the ‘redundant species’ one (Walker, 1992), is that species that are redundant in some ecosystem functions could not be necessarily redundant in their responses to environmental changes or in all the food web interactions (Rosenfeld, 2002). Indeed, the two species here studied do not have potential for redundancy in their food web participation. A stable isotopic study shows that in Mar Chiquita the signature of C differs between them (Botto *et al.*, 2005), indicating that these species have different nutrient sources and that their roles in the food web are

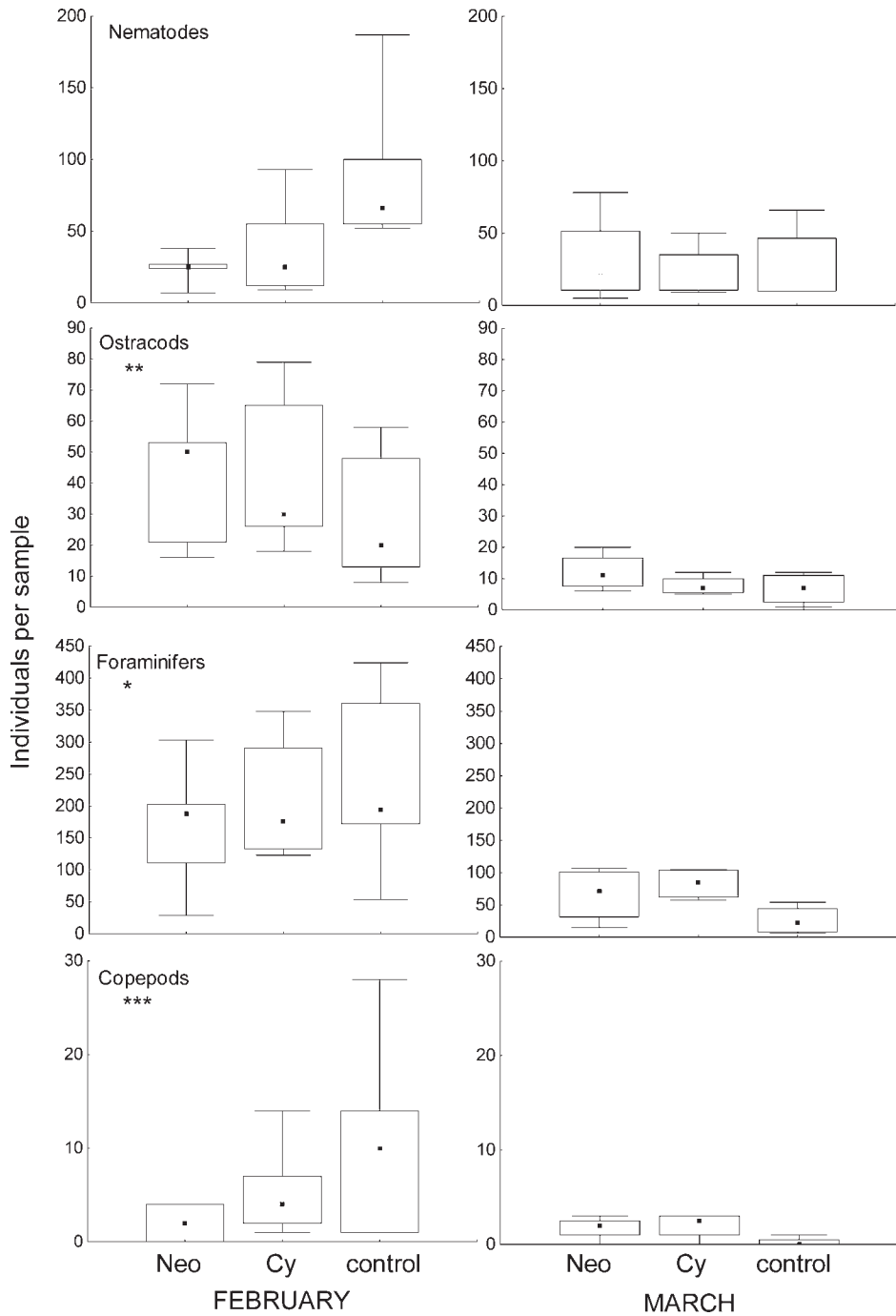


Fig. 5. Abundance of meiofaunal organisms after one (February) and two (March) months of different treatments manipulating crab presence. Treatments are: Neo, *Neohelice granulata* inclusion; Cy, *Cyrtograpsus angulatus* inclusion; and control, exclusion of both crab species. Sample size is 2 cm diameter and 2 cm depth. Asterisks indicate heterogeneity of variances (*: $P < 0.050$, **: $P < 0.010$, and ***: $P < 0.001$; Cochran test).

different. However, our results support the prediction that the effect of *C. angulatus* on the sediment and infaunal organisms is similar to the effect of the dominant species. Thus, *C. angulatus* can potentially play a similar role to *N. granulata* in the effect on sediment structure and abundance of infauna but it is unknown if other roles, such as food web interactions, can be also similar to *N. granulata* when it is absent. Given its high abundance and the many ecological interactions mediated by *N. granulata* (e.g.

Botto & Iribarne, 2000; Daleo *et al.*, 2003; Palomo *et al.*, 2004; Martinetto *et al.*, 2005, 2007a) it is important to know if there are species in these ecosystems with similar ecological functions. As mentioned above, competition is stronger among species with similar functions and this enhances the functional diversity through and across an ecosystem. This diversity is necessary to maintain the possibility of ecosystem recovery. Our results are evidences that, at least partially, *C. angulatus* play a redundant role.

Table 4. Two-way analysis of variance results testing for differences in abundance of meiofaunal taxa in experimental cages including *Neohelice granulata* or *Cyrtograpsus angulatus*, or excluding crabs (treatments) during 1 and 2 months (time).

	df	MS	F	P
Nematodes				
Time	1	3947.41	3.381	0.080
Treatment	2	2858.34	2.448	0.111
Interaction	2	2879.52	2.466	0.109
Error	21	1167.58		
Ostracods				
Time	1	147543.5	17.065	<0.001
Treatment	2	2289.0	0.265	0.770
Interaction	2	7734.3	0.894	0.424
Error	21	8646.2		
Foraminifers				
Time	1	5854.23	16.936	<0.001
Treatment	2	212.37	0.614	0.550
Interaction	2	97.78	0.283	0.756
Error	21	345.67		
Copepods				
Time	1	153.600	5.076	0.035
Treatment	2	29.635	0.979	0.392
Interaction	2	61.339	2.027	0.157
Error	21	30.262		

ACKNOWLEDGEMENTS

This project was supported by Universidad Nacional de Mar del Plata, ANPCyT and CONICET.

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