

## Research Article

## Structure of intertidal sessile communities before and after the invasion of *Isognomon bicolor* (C.B. Adams, 1845) (Bivalvia, Isognomonidae) in southeastern Brazil

María Soledad López<sup>1,2\*</sup>, Helena Passeri Lavrado<sup>3</sup> and Ricardo Coutinho<sup>1</sup>

<sup>1</sup>Dpto. Oceanografía, Instituto de Estudos do Mar Almirante Paulo Moreira, Marinha do Brasil, Arraial do Cabo, RJ, Brasil

<sup>2</sup>Present address: Centro de Biologia Marinha, Universidade de São Paulo, Rod. Manoel Hipólito do Rego km 131,5, São Sebastião, SP, Brasil

<sup>3</sup>Laboratório de Bentos, Depto. Biologia Marinha, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brasil

E-mail: [msolelopez@yahoo.com.ar](mailto:msolelopez@yahoo.com.ar) (MSL), [hplavrado@gmail.com](mailto:hplavrado@gmail.com) (HPL), [rcoutinhosa@yahoo.com](mailto:rcoutinhosa@yahoo.com) (RC)

\*Corresponding author

Received: 27 December 2013 / Accepted: 11 May 2014 / Published online: 4 August 2014

Handling editor: Demetrio Boltovskoy

### Abstract

Scientists recognize the importance of ecological data prior to invasion by non-native species in order to evaluate changes in the recipient community. Here we assess the potential impact of the invasion of the bivalve *Isognomon bicolor* (C.B. Adams, 1845) on Brazilian rocky shores through the use of surveys both before and after the arrival of this non-native species. The invader was mostly distributed across the mid and low shore levels of the intertidal zone with relative abundance ranging from 9.0 to 36.7 percent cover. The mid shore, previously dominated by the native barnacle *Tetraclita stalactifera* (Lamarck, 1818), was co-dominated by this barnacle species and *I. bicolor* after invasion. The relative abundance of these species, and presumably the interaction strength between them, differed between sites. At the site where *I. bicolor* reached the highest abundance (around 30% on average), the abundance of *T. stalactifera* decreased on average 70% compared to baseline values obtained before the *I. bicolor* invasion. Finally, conspicuous and extensive *I. bicolor* beds such as those observed in this study have not been reported in its original distribution range. Beds of *I. bicolor* may create a much more intricate biogenic matrix than the extents of bare rock and barnacle clumps it replaced. This bivalve may act as an ecosystem engineer and, thus a functionally different component of the intertidal community in its invaded range compared to its native distribution.

**Key words:** bicolor purse oyster, alien species, marine, rocky shores, macro invertebrate assemblages, baseline data

### Introduction

Invasion of marine and freshwater systems by non-native species can cause significant change in the abundance and distribution of species in recipient communities (see review in Carlton 1996; Ricciardi and MacIsaac 2011). The effect of invasive species on native species is now the second most addressed topic in studies of biological invasion (Lowry et al. 2013). In marine habitats, most of these impacts have been investigated once the exotic species have already become invasive either by comparisons of sites with different levels of invasion (e.g. Grosholz and Ruiz 1995; Crooks and Khim 1999; Rilov et al. 2004; Bownes and McQuaid 2009) or by field experiments in which the presence or density of invasive species

were manipulated (e.g. Ross et al. 2003; Byers 2005; Eastwood et al. 2007; Salvaterra et al. 2013). The analysis of pre- and post-invasion datasets is central to unequivocally identify changes in the recipient community associated with the establishment of the invader (Grosholz et al. 2000; Grosholz 2005; Sánchez et al. 2005; Cuevas et al. 2006; Robinson et al. 2007; Hanekom 2008). Unfortunately, pre-invasion baseline data are not available in most cases (Forrest and Taylor 2002; Junqueira 2013). In this work, we present data from the southeast coast of Brazil on the structure of rocky intertidal sessile assemblages both before and after the shores were invaded by the bivalve *Isognomon bicolor* (C. B. Adams, 1845).

The bicolor purse oyster *Isognomon bicolor*, originally distributed in the Gulf of Mexico,

south of Florida and the Caribbean region, has been recorded as an exotic species at several sites along 4,956 km of the Brazilian coast, from Piauí to Santa Catarina (Domaneschi and Martins 2002; Loebmann et al. 2010; Dias et al. 2013). *Isognomon bicolor* was first reported for the Brazilian coast in 1994 on a rocky shore at Barequeçaba (23°49' S; 45°26' W) beach in the state of São Paulo where this exotic species was found in dense aggregations at shore levels previously occupied by oysters and the bivalve *Brachidontes* sp. (Domaneschi and Martins 2002). At Arraial do Cabo, our study area, this species was not detected in surveys carried out before 1991 (Lavrado 1992) but it was recorded on two rocky shores, Ponta da Fortaleza and Prainha, during a survey performed between 1994 and 1999 along the southeast coast of Brazil (Domaneschi and Martins 2002). Later, in 2002–2003, *I. bicolor* densities of more than  $1 \times 10^5$  individuals  $m^{-2}$  were reported for shores of Rio de Janeiro state, including Ponta da Fortaleza at Arraial do Cabo (Breves-Ramos et al. 2010).

The published information on the *I. bicolor* invasion is focused on the population ecology of this species, including its distribution, abundance, and size structure (Fernandes et al. 2004; Oliveira and Creed 2008; Breves-Ramos et al. 2010; Ignacio et al. 2010; Zamprognio et al. 2010; Martinez 2012; Dias et al. 2013). Nevertheless, recent experimental studies have reported biological interactions of *I. bicolor* with some native species such as the positive association with the macroalgae *Sargassum* sp. (López and Coutinho 2010) and its consumption by two guilds of predators (López et al. 2010). Despite great concern on the possible negative effects of *I. bicolor*, there is no information about broader consequences of this invasion at the community level. Since substrate is often a limiting resource, and competition among sessile organisms is one of the main ecological processes structuring communities on rocky shores (Connell 1983), changes in the structure of intertidal sessile communities can be expected as a consequence of the *I. bicolor* invasion. In this study, our hypotheses were: (i) modifications in the structure of sessile assemblages are related to changes in the abundance of those resident species that overlap most of their vertical distribution with that of the invasive bivalve and (ii) *I. bicolor* and bare substrate cover percent will be negatively correlated. We compared the abundance and distribution of the dominant resident sessile invertebrates before (1990–1991) and after (2002–2003) the invasion by *I. bicolor*

at two rocky-shore sites. Throughout this study, we refer to existing communities as resident or recipient, avoiding the use of the terms 'native' and 'indigenous' since there are other species in the intertidal assemblages on the sampled rocky shores which may represent older, naturalized, introductions such as the brown mussel *Perna perna* (Linnaeus, 1758) and the titan acorn barnacle *Megabalanus coccopoma* (Darwin, 1854) (Junqueira et al. 2009).

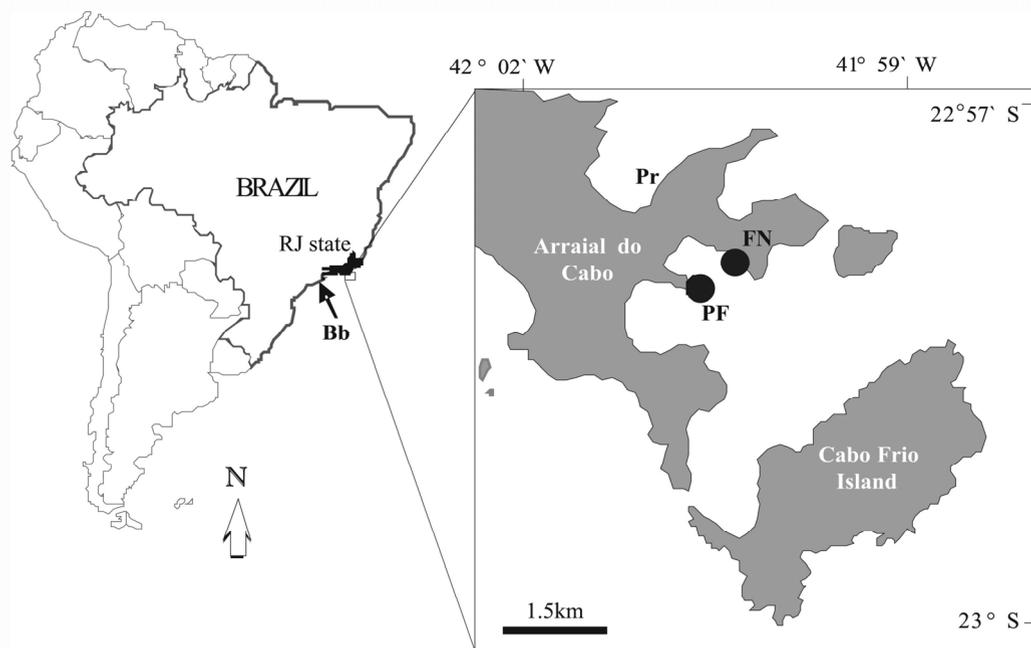
## Methods

This study was carried out on intertidal rocky shores at the Cabo Frio upwelling region in southeastern Brazil (Figure 1). The tidal regime is semi-diurnal with a maximum range of 1.3 m during spring tides. We surveyed two sites, 650 m away from each other: Forno (FN, 22°58'05"S; 42°00'20"W) and Ponta da Fortaleza (PF, 22°58'12"S; 42°00'43"W). An assessment of the structure of intertidal communities at both sites was conducted in spring 1990 and summer 1991, before the invasive bivalve was detected (Lavrado 1992). We used these datasets as baseline, pre-invasion information, on the vertical distribution and abundance of sessile organisms. We re-surveyed these sites in spring 2002 and summer 2003, after the *I. bicolor* invasion.

The same sampling protocol was used during both sampling periods. Three transects were randomly positioned on the shore perpendicular to the water line. Along each transect,  $0.2 \times 0.2$  m quadrats were consecutively placed from the low to the high shore level encompassing the intertidal zone. Each quadrat contained a grid of one-hundred equally spaced intersections. The organisms or bare substrate below each intersection was recorded to estimate the percent cover. The width of the intertidal zone varied from 1.6 to 2.0 m and from 3.0 to 4.6 m at FN and PF, respectively. This resulted in a surveyed area of approximately 20  $m^2$  and 58  $m^2$  at FN and PF, respectively.

## Data analyses

The vertical distribution of sessile invertebrates was qualitatively analyzed by graphically representing the percent cover of each species from the low to the high shore level. Changes in invertebrate assemblages between seasons (spring vs. summer) and alterations associated with the establishment of *I. bicolor* (before vs. after comparisons) were evaluated for each shore separately



**Figure 1.** The study area, situated on the coast of Rio de Janeiro (RJ) state, is represented in the larger map on the right side. Ponta da Fortaleza (PF) and Forno (FN) are the two study sites indicated with black spots. The arrow points out the site where *I. bicolor* was first recorded on the southeast coast of Brazil (Barequeçaba – Bb, São Paulo state). Praia (Pr) and Ponta da Fortaleza (PF) are the two shores where the exotic bivalve had been reported at the study region before this study was carried out (Domaneschi and Martins 2002).

using multivariate analysis. The relative abundance was calculated as the sum of the intersection points where each species was recorded divided by the sum of all the intersection points where sessile invertebrate species occurred in the whole transect. After the square root transformation of the relative abundances, a resemblance matrix based on the Bray-Curtis similarity index was used to perform the non-metric multidimensional scaling (nMDS) ordination and the permutational analysis of variance (PERMANOVA) (Clark and Warwick 2001; Anderson et al. 2008). The data transformation was applied to down-weight the contribution of dominant species to the between-sample similarities (Clarke and Warwick 2001). When a significant effect was detected using PERMANOVA, the permutational analysis of homogeneity of multivariate dispersions (PERMDISP) (both based on 999 permutations) was performed to investigate the nature of the multivariate effects (i.e. location and/or dispersion effects). *Isognomon bicolor* was not included in the analyses to avoid magnification of differences between assemblages due to the absence of the invader in 1990–1991. The contribution of each species to dissimi-

larities among groups was assessed using the Similarity Percentage Procedure (SIMPER).

Additionally, we analyzed the correlation between *I. bicolor* and those resident species that overlapped their vertical distribution with the invasive bivalve (i) *Tetraclita stalactifera*, (ii) *Perna perna*, (iii) *Brachidontes solisianus* as well as bare substrate. Each correlation was performed using the percent cover (arcsin  $\sqrt{p}$  transformation) along the shore level where each resident species (or bare substrate) overlapped with the invader after invasion. We included the three transects from the two sites and the two seasons that were sampled only after the invasion by *I. bicolor* (n=12). We pooled data from sites and seasons to increase the number of observations in each correlation analysis. Further-more, the scatter-plots for each season displayed similar patterns of relationship, even at PF where the invertebrate assemblages differed between seasons (see results below). Pearson product-moment correlation was used when data met the assumption of normality; otherwise the non-parametric Spearman's rank correlation was performed. Statistical analyses were done with STATISTICA 10.0 (for univariate

**Table 1.** Mean (SD; n=3) relative abundance of sessile invertebrates on two rocky intertidal shores in southeastern Brazil in spring and summer of 1990–1991 and 2002–2003, before and after *Isognomon bicolor* invasion, respectively.

Species	Ponta da Fortaleza				Forno			
	Spring		Summer		Spring		Summer	
	1990	2002	1991	2003	1990	2002	1991	2003
<i>Megabalanus</i> spp	5.76(2.63)	7.32(2.50)	2.81(1.87)	3.38(1.82)	9.12(3.32)	12.89(9.36)	4.10(4.19)	5.45(2.91)
<i>Perna perna</i>	4.14(2.16)	15.19(6.01)	26.89(3.24)	21.97(7.64)	0.71(0.66)	7.97(8.37)	3.25(2.82)	13.33(7.26)
<i>Tetraclita stalactifera</i>	31.84(17.24)	8.37(2.22)	18.67(11.02)	5.21(1.77)	31.11(6.67)	22.30(4.26)	27.37(4.99)	24.81(2.07)
<i>Isognomon bicolor</i>	0	20.68(1.51)	0	30.03(7.12)	0	15.80(11.01)	0	15.51(6.35)
<i>Brachidontes solisianus</i>	21.41(2.85)	15.73(2.92)	16.15(0.85)	9.24(0.84)	12.43(11.59)	9.25(1.54)	14.01(11.12)	9.67(4.33)
<i>Chthamalus bisinuatus</i>	36.84(16.56)	32.72(7.31)	35.47(8.26)	30.17(2.87)	46.61(14.85)	31.77(4.23)	51.26(13.64)	31.23(5.24)

analysis) and PRIMER V6 and PERMANOVA+ for PRIMER software packages (for multivariate analysis) (Clarke and Gorley 2006; Anderson et al. 2008).

## Results

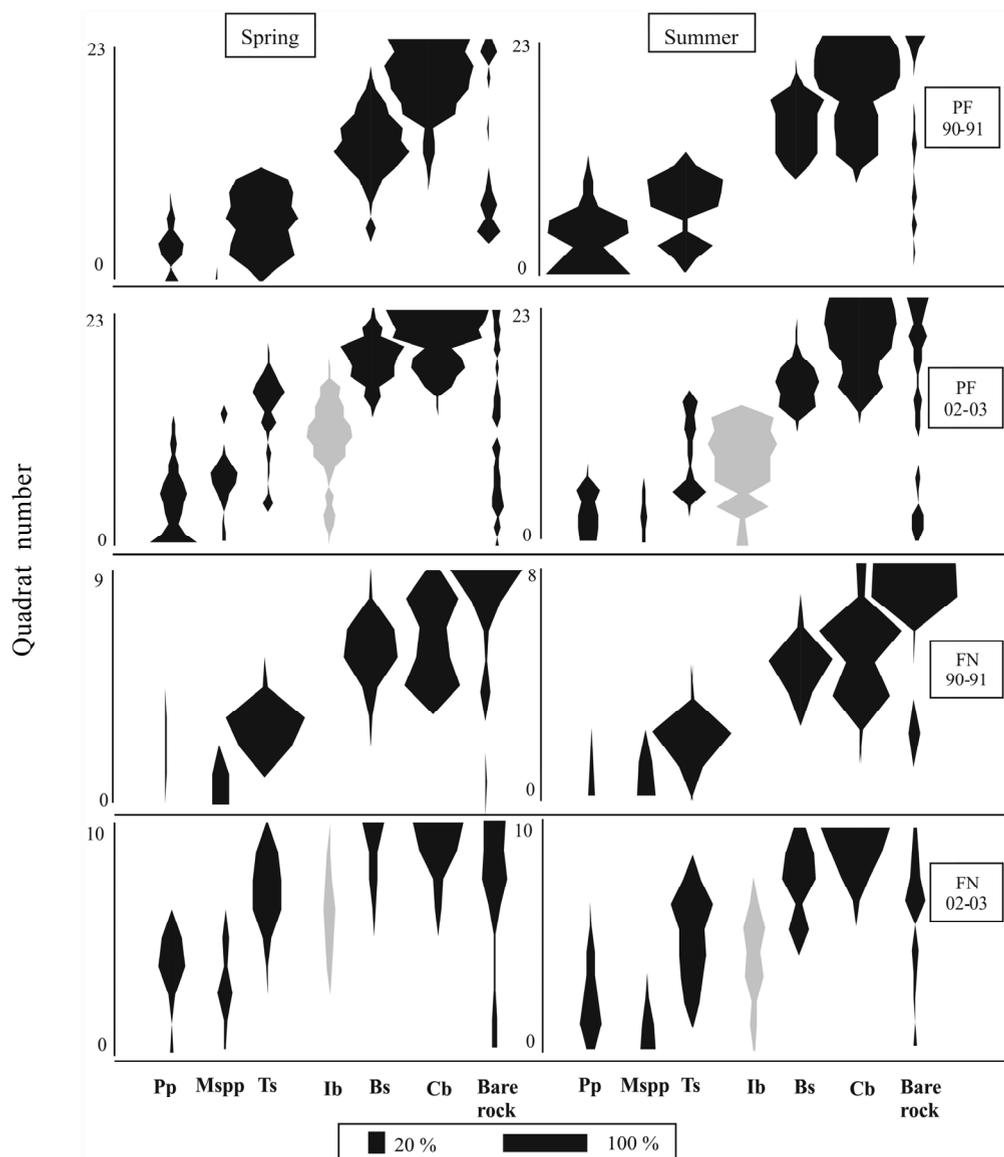
### *Spatial overlapping between Isognomon bicolor and resident species*

The intertidal zone was wider at PF than at FN. To illustrate the vertical profile of the sessile invertebrates, only one of the sampled transects in each shore, season and period was graphically represented because the three sampled transects varied little in terms of species distribution (Figure 2). In the pre-invasion period, there were three zones dominated by: (i) *Chthamalus bisinuatus* and *Brachidontes solisianus* in the high shore; (ii) *T. stalactifera* in the mid shore and (iii) *Megabalanus* spp. and *P. perna* in the low shore (Figure 2). In 2002–2003 (after invasion), *Isognomon bicolor* was distributed from the mid to the low intertidal at PF and from the high to the low intertidal at FN. At PF, the mid-intertidal zone dominated by *T. stalactifera* before invasion was co-dominated by this barnacle and *I. bicolor* after invasion. At FN, *I. bicolor* was conspicuous (20 to 40 percent cover) along the same shore level as *T. stalactifera* but also overlapped with the lower distribution ends of *B. solisianus* and *Chthamalus bisinuatus* (Pilsbry, 1916). During summer, *I. bicolor* extended its vertical distribution downward on the shore and increased the spatial overlap with the mussel *Perna perna* and barnacles of the genus *Megabalanus* on both shores.

### *Temporal variation in sessile invertebrate assemblages*

In all surveys, the barnacle *Chthamalus bisinuatus* was the most abundant sessile species. The relative abundance of the other sessile species on each shore changed between periods and seasons (Table 1). Before the invasion, in 1990–1991, the barnacle *Tetraclita stalactifera* was the second most abundant species except during summer at PF when the mussel *Perna perna* ranked second. In general, *P. perna* abundance was low (less than 5%, on average) during this period, but a 6-fold increase of its cover was detected at PF from spring to summer. In 2002–2003, the invasive bivalve *Isognomon bicolor* ranked second and third at PF and FN, respectively. The relative abundances of this species ranged from 9.1 to 28.5% at FN and from 19.1 to 36.7% at PF. After the invasion *T. stalactifera* was still the second most abundant species at FN, but at PF it was one of the least abundant species. In contrast, *Brachidontes solisianus* was one of the most abundant species before invasion but one of the least abundant species after invasion at FN. At PF, however, it ranked similarly between periods.

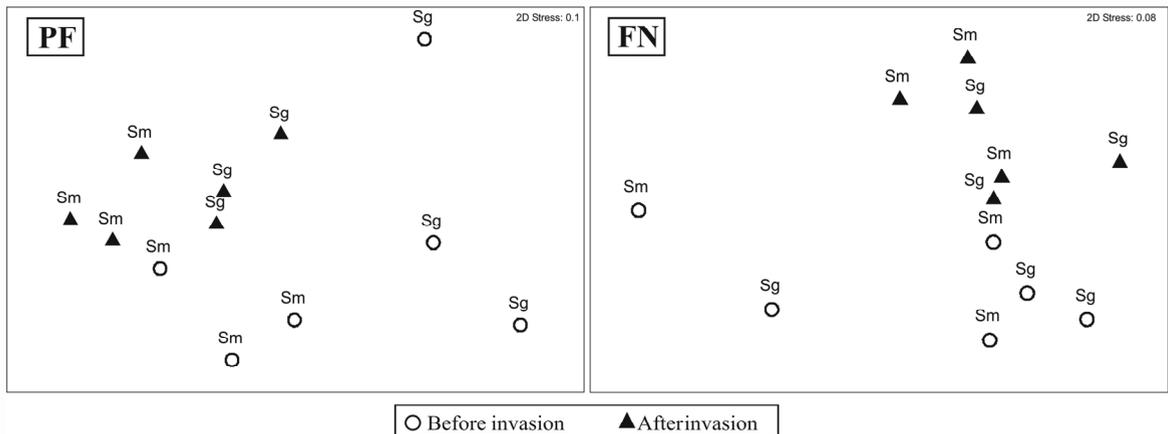
Multivariate analysis of sessile invertebrate assemblages (omitting the invasive species *Isognomon bicolor*) did not show interaction between the factors 'period' and 'season' (Table 2) and differences between periods, before (1990–1991) and after (2002–2003) the invasion, were clear and significant on both shores (Figure 3; Table 2). Regardless of whether the sampling was conducted before or after the invasion, seasonal differences were detected only at PF (Figure 3;



**Figure 2.** Intertidal zonation pattern of sessile macro invertebrates on two rocky shores in southeastern Brazil. One of the three replicated transects is represented for each season of the two periods, before (90–91) and after (02–03) *I. bicolor* invasion. PF=Fortaleza, FN= Forno. P.p= *Perna perna*, M.spp= *Megabalanus* spp., T.s= *Tetraclita stalactifera*, I.b= *Isognomon bicolor* (grey area), B.s= *Brachidontes solisianus*, C.b= *Chthamalus bisinuatus*. Quadrat zero is low shore.

**Table 2.** Summary of PERMANOVA results testing for differences in the intertidal sessile assemblages on the two surveyed shores according to the factors period (P; two levels: before and after the *I. bicolor* invasion) and season (Se; two levels: spring and summer). The contribution of *I. bicolor* was excluded from the analysis to avoid over magnification of the differences. Analyses were based on Bray-Curtis dissimilarities, and each test was performed using 999 permutations. Significant p-values are given in bold.

Source of variation	df	Ponta da Fortaleza			Forno		
		MS	Pseudo-F	p	MS	Pseudo-F	p
P	1	456.9	7.71	<b>0.003</b>	407.13	3.32	<b>0.024</b>
Se	1	457.58	7.72	<b>0.002</b>	183.33	1.49	0.245
P x Se	1	14.57	0.25	0.803	15.98	0.13	0.907
Res	8	59.27			122.56		



**Figure 3.** Two dimensional nMDS ordination (on square root transformed relative abundances) of the sessile invertebrate assemblages on two rocky intertidal shores (PF: Ponta da Fortaleza and FN: Forno) in southeastern Brazil. Surveys were performed before (1990–91, open round symbol) and after (2002–03, filled triangle symbol) the *Isognomon bicolor* invasion. Sg: Spring. Sm: Summer. The contribution of *I. bicolor* was excluded from the analysis.

Table 2). In addition, differences in the multivariate dispersion (PERMDISP analysis) of invertebrate assemblages were detected between periods ( $F = 6.93$ ,  $p = 0.043$ ) and season ( $F = 5.34$ ,  $p = 0.023$ ) at PF. Then, at this site, groups differed not only in their location but also in their dispersion. The variability of the assemblages at PF (mean of deviations from the centroid  $\pm$  SE) was higher before than after the invasion (before:  $10.24 \pm 1.21$ ; after:  $6.58 \pm 0.69$ ), and also larger in spring compared to summer (spring:  $9.92 \pm 0.86$ ; summer:  $7.24 \pm 0.78$ ) (Figure 3).

Since the taxonomic composition stayed the same, the differences detected among sessile assemblages over the surveys were a consequence of changes in the abundance of species. At PF, the SIMPER analysis revealed an average dissimilarity of 16.7% between the before and after invasion periods. The species *T. stalactifera*, *P. perna*, *B. solisianus* and *C. bisinuatus* contributed 35.9, 25.4, 13.8 and 13.7% respectively to this dissimilarity. *Tetraclita stalactifera*, *B. solisianus* and *C. bisinuatus* were less abundant while *P. perna* was more abundant after invasion than before invasion. At FN, the average dissimilarity between periods was 17.6% and the species *P. perna*, *B. solisianus*, *C. bisinuatus* and *Megabalanus* spp were the main contributors to this dissimilarity with 29.4, 23.3, 20.4 and 18.0%, respectively. Here, the abundances of *B. solisianus* and *C. bisinuatus* were lower while the abundance of *P. perna* and *Megabalanus* spp.

were higher after than before invasion. The average dissimilarity between spring and summer at PF was 16.5%. *Perna perna*, *T. stalactifera*, *Megabalanus* spp and *B. solisianus* contributed with 32.1, 27.9, 13.6 and 13.5% to this distinction. *Perna perna* increased its abundance in summer but *T. stalactifera*, *Megabalanus* spp. and *B. solisianus* were more abundant in spring.

The percent cover of *I. bicolor* was negatively correlated with that of *T. stalactifera* ( $r = -0.79$ ,  $p = 0.002$ ) and bare substrate cover ( $r = -0.84$ ,  $p = 0.001$ ) while *I. bicolor* percent cover did not show any significant correlation with that of *Perna perna* ( $r = -0.27$ ;  $p = 0.40$ ) and *B. solisianus* ( $r_s = 0.38$ ;  $p = 0.22$ ).

## Discussion

In this study we report changes in the intertidal sessile community of rocky shores at two sites in southeastern Brazil over a period of 11 years. The most obvious difference was the inclusion of the bivalve *Isognomon bicolor* as a dominant component of the sessile assemblages. This bivalve has been classified as an invasive species on the Brazilian coast with the potential for a high impact on resident species (Junqueira et al. 2009). Local extinction of the most common sessile invertebrates was not observed (as yet) following the invasion, but our results suggest that *I. bicolor* may strongly interact with other major components by overlapping its vertical range on the shore.

*Isognomon bicolor* and the barnacle *T. stalactifera* co-dominated the mid-intertidal zone but before the invasion this barnacle was the main sessile species occupying the mid shore. Nearly matching distributions of the invasive bivalve and *T. stalactifera*, as well as the negative correlation between the percent cover of these two species, suggest that *T. stalactifera* was the species most affected by the invasion of *I. bicolor*.

Although the shore levels occupied by *I. bicolor* were similar at the two sites, there were differences in the magnitude of this invasion and on the changes of the resident sessile assemblage. On the shore where *I. bicolor* reached its maximum abundance, the barnacle *T. stalactifera* was around 70% less abundant after than before the invasion. In contrast, no changes in the abundance of *T. stalactifera* were evident at FN, where the invader was less abundant. At present, we cannot elucidate the mechanisms underlying the apparent negative effect on *T. stalactifera* populations. Recruits of this barnacle species are often observed on bare substrate (Skinner and Coutinho 2005), so one possibility is that the extensive beds formed by *I. bicolor* interfere with *T. stalactifera* larval settlement by reducing availability of bare substrate. In addition, bivalves are known to include cyprid larvae in their diet (Davenport et al. 2000); thus, *I. bicolor* may decrease the supply of potential settlers to the intertidal zone. Future research is needed to test whether either or both of these interactions is occurring.

Previous studies have suggested negative effects of *I. bicolor* on *P. perna* populations (Domaneschi and Martins 2002; Fernandez et al. 2004; Casarini and Henriques 2011). *Isognomon bicolor* has been observed to colonize the byssus threads of *P. perna* in high densities (Casarini and Henriques 2011), which could cause mussel detachment by strong wave action. In general, our study detected higher percent cover of *Perna perna* after invasion. At PF we observed a high recruitment of *P. perna* and the formation of an extensive mussel bed in the low intertidal zone. Increases in *Perna perna* cover are unlikely to be a direct effect of the *I. bicolor* invasion, since their abundances did not show any correlation and the invasive species was not a major component at the low shore level at the time of the survey.

The differences in *I. bicolor* abundances between the two sampled sites may be the consequence of differences in the stage of the invasion. Thus far, detailed information about the initial stages and the spreading direction of *I. bicolor* invasion is not known for our study

region; therefore, it is difficult to interpret our results in this context. Moreover, site-specific factors can regulate the established populations of this invasive bivalve. For example, *I. bicolor* abundance and wave action were negatively associated in some invaded (Domaneschi and Martins 2002; Casarini and Henriques 2011) and native areas (Whorff et al. 1995; Malavé and Prieto 2007). However, in our study we observed higher abundances at PF, which is a moderately exposed shore. Similar to our results, Martinez (2012) found higher *I. bicolor* abundance on wave exposed shores in Santa Catarina, southern Brazil. Spatial variation in predation pressure on *I. bicolor* was observed in southeastern Brazil (López et al. 2010). Thus, the controlling mechanisms that explain the differences we observed between sites deserve further investigation with larger spatial replication.

Besides the negative effects of invasive bivalves on resident communities due to primary substrate monopolization (Branch and Steffani 2004; Rilov et al. 2004), species that form structurally complex beds can also host a diverse and abundant associated fauna (reviewed Sousa et al. 2009). For example, the diversity and density of intertidal invertebrates increased after the *Mytilus galloprovincialis* invasion in South Africa, because the matrix created by the mussel replaced bare rock or less complex biogenic substrates (Robinson et al. 2007). In our study, the mid intertidal shifted from a heterogeneous mosaic of barnacles and bare substrate to extensive beds of *I. bicolor*, with some individuals of the native barnacle *T. stalactifera* remaining in between. A diverse group of organisms have been found to inhabit *I. bicolor* beds (Fernandez et al. 2004; Ferreira and Rosso 2009), and some of these species, including the bivalve itself, recruit on this matrix (Lopez, MS pers. obs.). However, the impact of *I. bicolor* has not been fully investigated on the shores considered in the study. In addition, the importance of *T. stalactifera* as provider of habitat to other organisms has not been investigated in the study area and cannot be ruled out, since an exclusive fauna was found to be associated with both live and dead tests of *Tetraclita stalactifera panamensis* in the midlittoral zone of Panama (Reimer 1976).

Interestingly, the bed-forming colonization pattern of *I. bicolor* observed in this work, and in other studies carried out along the Brazilian coast (Breves-Ramos et al. 2010; Martinez 2012), has not been reported in its native range. Actually, ecological information of *I. bicolor* in

the Caribbean region is scarce, and most of the published papers only report its occurrence. When referred to as an abundant component of intertidal communities, *I. bicolor* occupied mainly the mid shore (Almanza et al. 2004; Malavé and Prieto 2007), associated with heterogeneous substrates such as crevices (Almanza et al. 2004) and algal turfs (Whorff et al. 1995). Thus *I. bicolor* may act as a functionally different member of the intertidal community in its invaded range in Brazil compared to its native range.

In this study, as in others where pre- and post-invasion comparisons were attempted, we have had to tailor the post-invasion sampling design to match previous survey protocols. But even using low spatial replication, our data suggest important spatial variability in the establishment of *I. bicolor* beds between sites and shore heights. The conspicuous colonization of the mid shore by *I. bicolor* as well as the spatial overlapping and negative correlation between *T. stalactifera* and *I. bicolor* abundances strongly suggested this native barnacle as the species most affected by the invasion. However, since no continuous monitoring has taken place between the pre and post invasion survey and the lack of control sites (non-invaded areas), the extent to which the decrease in *Tetraclita stalactifera* abundance was merely a consequence of the *I. bicolor* invasion stands as an interesting subject for future studies. In this way, being aware of the limitations already mentioned, our study provided ecological information to support further long-term monitoring and experimental work to test processes associated with this recent invasion, and mechanisms that may scale up to a major potential threat to intertidal communities along the Brazilian coast.

## Acknowledgements

We would like to thank the Instituto de Estudos do Mar Almirante Paulo Moreira (IEAPM) for providing the logistical support and to L.V. Granthom, S. A. Coelho Souza, C. E. Leite Ferreira and J.E. Arruda for their assistance during field work, species identification and discussions during this study. G. Rilov, S. A. Coelho Souza, B. Lage Ignacio, S. Jenkins, A.A. V. Flores, and K. Bohn reviewed earlier versions of this manuscript and together with the comments from the Associate Editor D. Boltovskoy and three anonymous reviewers greatly improved the quality of this manuscript. RC was granted by CNPq. The results were part of the master thesis of H.P.L under the supervision of Dr. L. F. Lembo Duarte (UNICAMP, Brazil) and of M.S.L (UIA, Baeza, Spain).

## References

- Almanza L, Bolívar F, Borrero S, Caiafa I, De Las Salas K, Luque MG, Valdemar JC (2004) Preliminary study of the macrobenthonic community from the Rocky Coast of Bahía Concha (Parque Nacional Natural Tayrona, Magdalena, Colombia), August 2002. *Acta Biológica Colombiana* 9(1): 3–9
- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth
- Bownes SJ, McQuaid CD (2009) Mechanisms of habitat segregation between an invasive and an indigenous mussel: settlement, post-settlement mortality and recruitment. *Marine Biology* 156: 991–1006, <http://dx.doi.org/10.1007/s00227-009-1143-z>
- Branch GM, Steffani CN (2004) Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). *Journal of Experimental Marine Biology and Ecology* 300 (1–2): 189–215, <http://dx.doi.org/10.1016/j.jembe.2003.12.007>
- Breves-Ramos A, Junqueira AOR, Lavrado HP, Silva SHG, Ferreira-Silva MAG (2010) Population structure of the invasive bivalve *Isognomon bicolor* on rocky shores of Rio de Janeiro State (Brazil). *Journal of the Marine Biological Association of the United Kingdom* 90(3): 453–459, <http://dx.doi.org/10.1017/S0025315409990919>
- Byers JE (2005) Marine reserves enhance abundance but not competitive impacts of a harvested nonindigenous species. *Ecology* 86(2): 487–500, <http://dx.doi.org/10.1890/03-0580>
- Carlton JT (1996) Marine Bioinvasions: The alteration of marine ecosystems by non-indigenous species. *Oceanography* 9(1): 36–43, <http://dx.doi.org/10.5670/oceanog.1996.25>
- Casarini LM, Henriques MB (2011) Estimativa de estoque do mexilhão *Perna perna* e da espécie invasora *Isognomon bicolor* em bancos naturais da Baía de Santos, São Paulo, Brasil. *Boletim do Instituto de Pesca de São Paulo* 37(1): 1–11
- Clarke KR, Gorley RN (2006) Primer v6: User Manual/Tutorial. PRIMER-E, Plymouth
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E, Plymouth
- Connell JH (1983) On the prevalence and relative importance of inter-specific competition: evidence from field experiments. *American Naturalist* 122: 661–696, <http://dx.doi.org/10.1086/284165>
- Crooks JA, Khim HS (1999) Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculita senhousia*. *Journal of Experimental Marine Biology and Ecology* 240: 53–75, [http://dx.doi.org/10.1016/S0022-0981\(99\)00041-6](http://dx.doi.org/10.1016/S0022-0981(99)00041-6)
- Cuevas JM, Martin JP, Bastida R (2006) Benthic community changes in a Patagonian intertidal: a forty years later comparison. *Thalassas* 22 (1): 29–37
- Davenport J, Smith RJW, Packer M (2000) Mussels *Mytilus edulis*: significant consumers and destroyers of mesozooplankton. *Marine Ecology Progress Series* 198: 131–137, <http://dx.doi.org/10.3354/meps198131>
- Dias TLP, Mota ELS, Gondim AI, Oliveira JM, Rabelo EF, Almeida SM, Christoffersen ML (2013) *Isognomon bicolor* (C. B. Adams, 1845) (Mollusca: Bivalvia): First record of this invasive species for the States of Paraíba and Alagoas and new records for other localities of Northeastern Brazil. *Check List* 9(1): 157–161
- Domaneschi O, Martins CM (2002) *Isognomon bicolor* (C.B. Adams) (Bivalvia, Isognomonidae): primeiro registro para o Brasil, redescritção da espécie e considerações sobre a ocorrência e distribuição de *Isognomon* na costa brasileira. *Revista Brasileira de Zoologia* 19(2): 611–627, <http://dx.doi.org/10.1590/S0101-81752002000200017>

- Eastwood MM, Donahue MJ, Fowler AE (2007) Reconstructing past biological invasions: niche shifts in response to invasive predators and competitors. *Biological Invasions* 9: 397–407, <http://dx.doi.org/10.1007/s10530-006-9041-5>
- Fernandes FC, Rapagnã LC, Bueno GBD (2004) Estudo da população do bivalve exótico *Isognomon bicolor* (C.B. Adams, 1845) (Bivalvia: Isognomonidae) na Ponta da Fortaleza em Arraial do Cabo—RJ. In: Silva JSV, Souza RCC (eds), Água de Lastro e Bioinvasão. Editora Interciência, Rio de Janeiro, Brasil, pp 133–141
- Ferreira MN, Rosso S (2009) Effects of human trampling on a rocky shore fauna on the Sao Paulo coast, Southeastern Brazil. *Brazilian Journal of Biology* 69(4): 993–999, <http://dx.doi.org/10.1590/S1519-69842009000500003>
- Forrest BM, Taylor MD (2002) Assessing invasion impact: survey design considerations and implications for management of an invasive marine plant. *Biological Invasions* 4: 375–386, <http://dx.doi.org/10.1023/A:1023613428351>
- Grosholz ED, Ruiz GM (1995) Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. *Marine Biology* 122 (2): 239–247
- Grosholz ED, Ruiz GM, Dean CA, Shirley KA, Maron JL, Connors PG (2000) The impacts of a non-indigenous marine predator in a California Bay. *Ecology* 81(5): 1206–1224, [http://dx.doi.org/10.1890/0012-9658\(2000\)081\[1206:TIOANM\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2000)081[1206:TIOANM]2.0.CO;2)
- Grosholz ED (2005) Recent biological invasion may hasten invasional meltdown by accelerating historical introduction. *Ecology* 102(4): 1088–1091
- Hanekom N (2008) Invasion of an indigenous *Perna perna* mussel bed on the south coast of South Africa by an alien mussel *Mytilus galloprovincialis* and its effect on the associated fauna. *Biological Invasions* 10: 233–244, <http://dx.doi.org/10.1007/s10530-007-9125-x>
- Ignacio BL, Julio LM, Junqueira AOR, Ferreira-Silva MAG (2010) Bioinvasion in a Brazilian bay: filling gaps in the knowledge of Southwestern Atlantic Biota. *PLoS ONE* 5(9): e13065, <http://dx.doi.org/10.1371/journal.pone.0013065>
- Junqueira AOR, Tavares MDS, Schaeffer-Novelli Y, Radashevsky VI, Cirelli J, Julio LM, Romagnoli FC, dos Santos KC, Ferreira-Silva MAG (2009) Capítulo 6: Zoobentos. In: Lopes RM (ed), Informe sobre as espécies exóticas invasoras marinhas no Brasil, Ministério do Meio Ambiente, Brasil, pp 145–371
- Junqueira AOR (2013) Guilty or innocent? The need to improve the assessment of impacts caused by non-native species. *Aquatic Conservation: Marine and Freshwater Ecosystem* 23: 641–645
- Lavrado HP (1992) Seleção de presas pelo gastrópodo *Thais haemastoma* (L.) na região de Arraial do Cabo, RJ. 1992. Master Thesis, Universidade Estadual de Campinas, São Paulo, Brasil, 104 pp
- Loebmann D, Mai ACG, Lee JT (2010) The invasion of five alien species in the Delta do Parnaíba Environmental Protection Area, Northeastern Brazil. *Revista de Biologia Tropical (Int. J. Trop. Biol. ISSN-0034-7744)* 58 (3): 909–923
- López MS, Coutinho R, Ferreira CEL, Rilov G (2010) Predator–prey interactions in a bioinvasion scenario: differential predation by native predators on two exotic rocky intertidal bivalves. *Marine Ecology Progress Series* 403: 101–112, <http://dx.doi.org/10.3354/meps08409>
- López MS, Coutinho R (2010) Positive interaction between the native macroalgae *Sargassum* sp. and the exotic bivalve *Isognomon bicolor*? *Brazilian Journal of Oceanography* 58 (special issue IICBBM): 69–72
- Lowry E, Rollinson EJ, Laybourn AJ, Scott TE, Aiello-Lammens ME, Gray SM, Mickleby J, Gurevitch J (2013) Biological invasions: a field synopsis, systematic review, and database of the literature. *Ecology and Evolution* 3(1): 182–196, <http://dx.doi.org/10.1002/ece3.431>
- Malavé JRF, Prieto MMJ (2007) Fauna malacológica del litoral rocoso de la costa sur del Golfo de Cariaco y costa norte del Estado Sucre, Venezuela. *Boletín del Instituto Oceanográfico de Venezuela* 46 (1): 3–11
- Martinez AS (2012) Spatial distribution of the invasive bivalve *Isognomon bicolor* on rocky shores of Arvoredo Island (Santa Catarina, Brazil). *Journal of the Marine Biological Association of the United Kingdom* 92(3): 495–503, <http://dx.doi.org/10.1017/S0025315411000865>
- Oliveira AES, Creed JC (2008) Mollusca, Bivalvia, *Isognomon bicolor* (C. B. Adams 1845): Distribution extension. *Check List* 4(4): 386–388
- Reimer AA (1976) Description of a *Tetraclita stalactifera* panamensis community on a rocky intertidal Pacific shore of Panama. *Marine Biology* 35: 225–238, <http://dx.doi.org/10.1007/BF00396871>
- Ricciardi A, MacIsaac HJ (2011) Impacts of biological invasions on freshwater ecosystems. In: Richardson DM (ed), Fifty Years of Invasion Ecology: The Legacy of Charles Elton, 1st edition. Blackwell Publishing Ltd, pp 211–224
- Rilov G, Benayahu Y, Gasith A (2004) Prolonged lag in population outbreak of an invasive mussel: a shifting-habitat model. *Biological Invasions* 6: 347–364, <http://dx.doi.org/10.1023/B:BINV.0000034614.07427.96>
- Robinson TB, Branch GM, Griffiths CL, Govender A, Hockey PAR (2007) Changes in South African rocky intertidal invertebrate community structure associated with the invasion of the mussel *Mytilus galloprovincialis*. *Marine Ecology Progress Series* 340: 163–171, <http://dx.doi.org/10.3354/meps340163>
- Ross DJ, Craig RJ, Hewitt CL (2003) Assessing the ecological impacts of an introduced seastar: the importance of multiple methods. *Biological Invasions* 5: 3–21, <http://dx.doi.org/10.1023/A:1024019428616>
- Salvaterra T, Green DS, Crowe TP, O’Gorman EJ (2013) Impacts of the invasive alga *Sargassum muticum* on ecosystem functioning and food web structure. *Biological Invasions* 15: 2563–2576, <http://dx.doi.org/10.1007/s10530-013-0473-4>
- Sánchez I, Fernández C, Arrontes J (2005) Long-term changes in the structure of intertidal assemblages after invasion by *Sargassum muticum* (Phaeophyta). *Journal of Phycology* 41: 942–949, <http://dx.doi.org/10.1111/j.1529-8817.2005.00122.x>
- Skinner LF, Coutinho R (2005) Effect of microhabitat distribution and substrate roughness on barnacle *Tetraclita stalactifera* (Lamarck, 1818) settlement. *Brazilian Archives of Biology and Technology* 48: 109–113, <http://dx.doi.org/10.1590/S1516-89132005000100014>
- Sousa R, Gutierrez JL, Aldridge DC (2009) Non-indigenous invasive bivalves as ecosystem engineers. *Biological Invasions* 11: 2367–2385, <http://dx.doi.org/10.1007/s10530-009-9422-7>
- Whorff JS, Whorff LL, Sweet III MH (1995) Spatial variation in an algal turf community with respect to substratum slope and wave height. *Journal of the Marine Biological Association of the United Kingdom* 75: 429–444, <http://dx.doi.org/10.1017/S0025315400018282>
- Zamprogno GC, Fernandes LL, Fernandes FC (2010) Spatial variability in the population of *Isognomon bicolor* (C.B. Adams, 1845) (Mollusca, Bivalvia) on rocky shores in Espirito Santo, Brazil. *Brazilian Journal of Oceanography* 58(1): 23–29, <http://dx.doi.org/10.1590/S1679-87592010000100003>