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The role of *Asterina stellifera* (Echinodermata: Asteroidea) as a predator in a rocky intertidal community in southern Brazil

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ABSTRACT. Populations of *Asterina stellifera* Möbius, 1859 are declining in southern Brazil and today the species is on the Brazilian list of endangered species. Here we experimentally investigate the ecological role played by *A. stellifera* as a predator on the rocky substrate community by increasing densities of this species. Starfish taken from other, nearby, locations were added to three replicate plots and their density was maintained every 15 days. None of the total of 32 species that were identified in the encrusting community appeared to be influenced by the experiment. Two species, the barnacle *Chthamalus bisinuatus* Pilsbry, 1916 and the algae *Gracilaria verrucosa* (Hudson), showed small apparent responses to predation. We found that *A. stellifera* only exerts weak predation pressure on the community, even at high densities. This result is strikingly different from that observed for similar species in the northern hemisphere and in Australia.

KEY WORDS. Experiment; predation; rocky coast; starfish.

Predation can maintain high local species diversity if the predator consumes a competitively dominant prey species (Paine 1966, 1971, Menge & Sutherland 1987, Verling *et al.* 2003). In this situation, the predator will have a fundamental influence at the community level by structuring interactions between species and reducing the impact of each, thereby permitting coexistence that would not occur in the absence of the predator. Predators may also influence other processes, such as the induction of phenotypic modifications in prey species (Lima 1998), that in turn can influence species growth, survival and fitness (McPeek *et al.* 2001). Predators have also influenced size limitation of prey within populations (Menge 1976) as well as population dynamics (Bolker *et al.* 2003).

Indirect effects of predation are also important, including cascading effects in which other species (not prey) respond as a result of predation on different, interacting species (Peacor and Werner 1997, Trussell *et al.* 2003). In general, this effect is a result of the interaction between the predator and prey, in which the prey has its own effects that may influence relationships between it and additional species. Thus, the predator can indirectly affect other species which in turn interact with their prey or competing species (Raimondi *et al.* 2000, Peacor & Werner 2004).

Predators not only influence their prey in a community but may have additional complex consequences. Most patterns in intertidal rocky coasts are the result of combined effects of factors that influence the availability of space on rocky substrates, such as intra- and interspecific competition, biological disturbance (*e.g.*, herbivory and predation) and physical factors (e.g., wave action and desiccation) (Dayton 1971, Paine 1971, Menge 1976).

The complexity of these interactions between predators and their communities highlights the importance of experimental field studies to examine and quantify the influence of predation on community structure and process (Peacor & Werner 2004). Controlled laboratory experiments often cannot include many of the interacting components of the predator-prey relationship and therefore may not reflect what happens in the field. On the other hand, controlling important factors is often difficult in the field and as a consequence, field studies may yield results that are complex and difficult to interpret, due to temporal or spatial variability as well as biological interactions. These complex interactions are common, for example, in rocky intertidal habitats where the main predators are crabs, snails, starfish and fish.

Starfish are often important in community structuring processes (Paine 1969a, b, 1976, Dayton 1971, Paine *et al.* 1985, Gaymer *et al.* 2004), mainly in intertidal regions in temperate latitudes (Menge *et al.* 1994, Navarrete & Menge 1996). Most effects are observed in the lowest zones (subtidal) on rocky substrates, where the starfish are protected from desiccation or other abiotic influences that echinoderms, in general, do not tolerate well (Stickle & Diehl 1987). Starfish can be voracious predators that devastate some communities, such as *Acanthaster planci* (Linnaeus, 1758) on coral reefs (Cameron *et al.* 1991) and *Asterias* sp. on mussels (Gaymer *et al.* 2002). Not all asteroids, however, are so voracious and some may maintain heterogeneity and biological diversity of their communities (Verling *et al.* 2003).

Classical studies that showed the importance of predation by starfish in intertidal rocky shores were carried out in the northern hemisphere, with starfish in the genera *Asterias* and *Pisaster* and in Australia, with *Acanthaster*. Experimental removal of the predator *Pisaster ochraceus* (Brandt, 1835) resulted in the increased abundance and distribution of its prey *Mytilus californicus* Conrad, 1837 (Paine 1969b). This resulted in reduced species richness and mussel dominance, which has also been seen elsewhere along the coast of North American due to strong interactions between *Pisaster* and *Mytilus* and suggesting that *Pisaster* is an example of a keystone predator (Paine 1966, 1969a, 1974). In Australia, similar results occurred between the sea star *Stichaster australis* (Verrill, 1871) and the mussel *Perna canaliculus* Gmelin, 1791. Exclusion of the predator led to a 40% increase in the vertical distribution of its prey and decreased species richness from 20 to 14 species (Paine 1971).

In Brazil, the ecological role played by asteroids has not yet been studied, although *Asterina stellifera* Möbius, 1859 is one of the few starfish species in the intertidal rocky coastal habitats of the Atlantic Ocean. Its is found from Cabo Frio, Brazil (23°S, 42°W) to Mar del Plata, Argentina (35°S, 56°W) in the western Atlantic and from Senegal (15°N, 15°W) to Namibia (28°S, 15°E) in the eastern Atlantic Ocean (Clark & Downey 1992). No starfish species of the low intertidal region is very abundant and *A. stellifera* is included in the Brazilian list of endangered species. Its biology is poorly known, with some information suggesting that it can change the permeability of its body wall to avoid desiccation at low tide (Vidolin *et al.* 2002) and that late winter is when gonadal development is greatest with reproduction occurring in the spring or early summer in southern Brazil (Carvalho & Ventura 2002).

Asterina stellifera is a carnivore and therefore may play an important role in community structure. Also, given its extra-oral feeding strategy, it may affect more species than just the prey while feeding on the rocks through cascading interactions as described above. Here we examine the potential role and consequence of *Asterina stellifera* predation in a subtropical rocky intertidal coastal area in Penha, in the southern Brazilian state of Santa Catarina.

MATERIAL AND METHODS

Study area

The study area is the rocky shore at Quilombo beach (26°46'S, 48°38'W), Penha, state of Santa Catarina. Rocks are predominantly granitic with many different shapes and sizes, with protected and exposed areas to wave action and direct sunshine. Rocks form rows more or less perpendicular to shore. The barnacle *Chthamalus bisinuatus* Pilsbry, 1916 and gastropods *Littorina flava* King & Broderip, 1832 and *Littorina ziczac* (Gmelin, 1791) are found on these rocks.

We selected rocks that were exposed during 0.3 m tides for this study and most had three distinct horizontal zones that were visible during low tide. The upper zone had the barnacles *C. bisinuatus*, *Megabalanus* sp. and *Tetraclita stalactifera* Lamarck, 1818 and the gastropods *L. flava* and *L. ziczac*. The intermediate zone had the same barnacles along with the bivalves *Brachidontes solisianus* d´Orbigny, 1846, *Crassostrea rhizophorae* (Guilding, 1828) and *Isognomon bicolor* (Adams, 1845), the gastropods *L. flava*, *L. ziczac*, *Stramonita haemastoma* (Linnaeus, 1758), *Tegula viridula* (Gmelin, 1791), *Leucozonia nassa* (Gmelin, 1791), *Collisella subrugosa* (d'Orbigny, 1846) and *Fissurella clenchi* Farfante, 1943, the polychaete *Phragmatopoma caudata* Mörch, 1863, and the algae *Ulva fasciata* Delile, 1813, *Porphyra spiralis* var. *spiralis* Oliveira & Coll, 1975, and *Centroceras clavulatum* (C. Agardh) Montagne, 1846. The lowest zone had the starfish *A. stellifera* and occasionally *Echinaster brasiliensis* Müller & Troschel, 1842, the sea urchins *Lytechinus variegatus* (Lamarck, 1816) and *Arbacia lixula* (Linnaeus, 1758), the sea cucumber *Holothuria grisea* Selenka, 1867, the anemones *Actinia bermudensis* (McMurrich, 1889), *Bunodosoma caissarum* Correa, 1964, *Anthopleura* sp. and the tunicates *Eudistoma carolinense* Van Name, 1945, *Botrylloides nigrum* Herdman, 1886, *Aplidium accarense* (Millar, 1953), *Polysyncraton amethysteum* (Van Name, 1902) and *Clavelina oblonga* Herdman, 1880, the hydrozoans *Pinauay ralphi* (Bale, 1884) and *Dynamena crisioides* Lamouroux, 1824, the bryozoan *Bugula neritina* (Linnaeus, 1758), the sponge *Hymeniacidon heliophila* Parker, 1910, and the algae *Gracilaria verrucosa* (Hudson) Papenfuss, 1950, *Corallina officinalis* Linnaeus, 1758, and *Padina gymnospora* (Kützing) Sonder, 1871.

Inclusion of *A. stellifera*

Pilot relocation experiments in July 2004 were carried out to test whether moved individuals of *A. stellifera* would remain on the rocks where they were placed. Three rocks were randomly chosen in which three vertical transects were delimited. Six starfish were placed into each of the transects and 20 were placed within a circumference of 1 m radius around the transects (38 individuals per rock). These starfish were followed daily for 15 days at diurnal and nocturnal low tides. The moved individuals (70%) tended to remain within a radius of 1.0-1.5 m from the transects, for one week and in two weeks, 50% were still within that distance. Based on these data, the experiment was possible and the experiment would be monitored and maintained at two week intervals, when starfish that had disappeared during that interval would be replaced.

Six (three experimental and three control) previously unused rocks were chosen to examine the effects of increased density of *Asterina* on the rocky community. Rocks were separated from each other by at least 1 m. Two vertical transects (60 x 10 cm) on each rock, separated by 50 cm, were marked in the lowest horizontal zone, close to the sandy bottom. Six permanent quadrats (100 cm^2) were marked along the transects with epoxy resin (Durepoxi®) at the corners so that the same quadrats would be measured each time.

Prior to placement of the starfish, in late July 2004, quadrats were examined to quantify the organisms already in place, immediately after which the starfish were place in the experimental plots. At one month intervals beginning in late August through late October, quadrats were examined and organisms quantified. Organisms were quantified using visual estimation following Foster *et al.* (1991), within 10cm^2 area that were subdivided into 25 squares.

Data analysis

Starfish, when manipulated, often had everted stomachs as evidence of recent feeding. The preferred prey (if any) is unknown for *A. stellifera* and so all organisms in the encrusting community were measured to test for both direct and indirect effects of the predator. Since the organisms on all replicates were different, rather than a direct comparison between treatments and controls, we compared the change in cover in both treatments during each month, in which each rock acts as its own control. Given that rare occurrences of organisms are uninformative in this study, we included only species whose abundance permitted comparisons between more than one month. Percentage cover by species was compared between control and experimental treatments with Students *t*-test.

Physiological tolerance of *A. stellifera*

Predatory action by *A. stellifera* during low tide depends on its tolerance of air exposure or its ability to survive in tidal pools. To examine this tolerance of temperature and salinity variation, individual were taken into the laboratory for physiological experiments. In the laboratory they were maintained in aquaria (390 L) with sea water under field conditions: 13:11 h light: dark photoperiod (in summer) and 12:12 h (in winter), 28 ± 1ºC in summer, and 18 ± 1ºC in winter, constant salinity 35 g/kg, pH 7.5-8.0).

Winter and summer salinity tolerance experiments (10, 35, 45 g kg^{-1}, n = 10 for each group) and desiccation tolerance experiments (air exposure), with or without sunshine (n = 10 for each group) were carried out. Salinity values were based on values measured *in situ* in tidal pools on Penha beach, during daily analysis, and 35g kg^{-1} is typical of sea water. Measurements during that analysis were gathered every hour in six tidal pools in winter with 1) rainfall and 2) sunshine and in summer with 3) rainfall and 4) sunshine, for a total of four days of measurements, in which salinity varied from 5-39g kg^{-1}. In the lab, water of salinity 10g kg^{-1} was obtained by dilution of sea water with fresh water. High salinity water was obtained using the first thaw of previously frozen natural sea water (salinity 55-85 g/kg) diluted with natural sea water to 45g kg^{-1}. Each starfish was maintained in separate 2.5L aquaria. When tested, each was placed for 3h in the experimental aquaria under constant temperature (summer 28ºC, winter 18ºC).Salinity was measured by Shibuya S-28 salinity refractometer. Coelomic fluid (200-500 µl) was taken from the ambulacral area with syringes and disposable insulin needles. Osmolality (vapor pressure osmometer Wescor, VAPRO 5520) and chloride concentration were measured (n = 6 for each group). Chloride concentration was measured after diluting coelomic fluid samples with deionized water (1:3), by colorimetric assay using a commercially available kit (Labtest®). Absorbency (Ultrospec 2100 PRO Amersham Pharmacia Biotech spectrophotometer) was read at 470 nm (chloride ions react with mercury thiocyanate in the presence of ferric nitrate, yielding orange ferric thiocyanate). Approximate values of chloride concentration for sea water of different salinities were obtained from standard sea water (salinity 34.33 g/kg) concentrations following Prosser (1973). Osmolality of sea water at different salinities was estimated as follows: salinity 35 = 1,050 mOsm/kg H_2O.

In the desiccation experiment starfish were exposed to the air for three hours. During daylight hours, they were placed in open air containers either under sunny or cloudy condition, in summer and winter. In the field, starfish would have had to sustain such conditions for a maximum of two hours.

After air exposure and salinity experiments, survival and "health" of the starfish were assessed by their ability to right themselves. After experimental exposure, starfish were placed upside down in sea water (35g kg^{-1} salinity) and observed for 30 minutes. If they righted themselves within this time they were considered healthy. Those that remained upside down were then each placed in a separate aquarium for 48 h and checked every six hours. Dead starfish remained inverted and those that had righted themselves were also considered healthy. All live starfish were returned to their point of origin in the field.

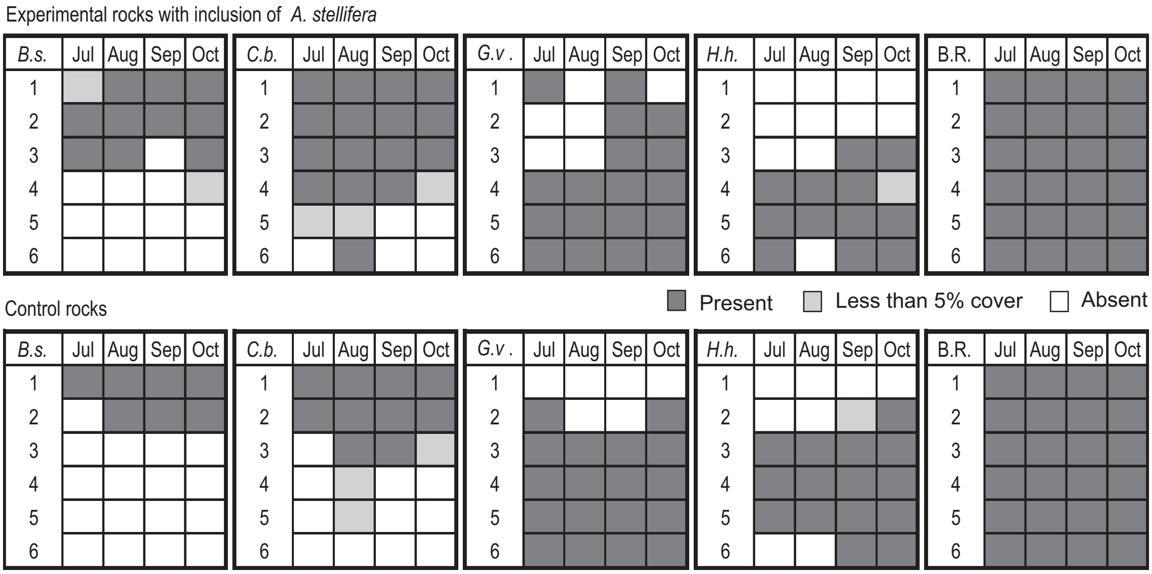
RESULTS

The role of *A. stellifera* in the rocky coastal community

Among the 32 species that were found and quantified in the community, only four species were found consistently throughout the experiment. *C. bisinuatus* and *B. solisianus* occupied the three or four higher quadrats on the vertical transect, while *G. verrucosa* occupied all six quadrats and *H. heliophila* the three or four lower ones (Fig. 1). Variation in spatial distribution between months was similar on control and experimental rocks and therefore the starfish had no apparent effect on any of these species.

Cover in both *C. bisinuatus* and *G. verrucosa* was 50% at the beginning of the experiment. While *G. verrucosa* remained more or less constant during the experiment, *C. bisinuatus* declined on the control treatment in the first month of the experiment. Fluctuation in cover of *C. bisinuatus* was similar in both treatments but somewhat less extreme in the inclusion treatments (Fig. 2). Cover in both *B. solisianus* and *H. heliophila* was low and similarly variable in both treatments except for in August, when cover increased in the inclusion treatment but decreased in the control (Fig. 2).

Change in cover from one month to the next was very low in the inclusion treatment, with little variation among replicates for all species except for *G. verrucosa* (Fig. 3). Although change in cover tended to be greater for *C. bisinuatus* and *G.*



Experimental rocks with inclusion of *A. stellifera*

B.s.	Jul	Aug	Sep	Oct
1	▒	■	■	■
2	■	■	■	■
3	■	■	☐	■
4	☐	☐	☐	▒
5	☐	☐	☐	☐
6	☐	☐	☐	☐

C.b.	Jul	Aug	Sep	Oct
1	■	■	■	■
2	■	■	■	■
3	■	■	■	■
4	■	■	■	▒
5	▒	▒	☐	☐
6	☐	■	☐	☐

G.v.	Jul	Aug	Sep	Oct
1	■	☐	■	☐
2	☐	☐	■	■
3	☐	☐	■	■
4	■	■	■	■
5	■	■	■	■
6	■	■	■	■

H.h.	Jul	Aug	Sep	Oct
1	☐	☐	☐	☐
2	☐	☐	☐	☐
3	☐	☐	■	■
4	■	■	■	▒
5	■	■	■	■
6	■	☐	■	■

B.R.	Jul	Aug	Sep	Oct
1	■	■	■	■
2	■	■	■	■
3	■	■	■	■
4	■	■	■	■
5	■	■	■	■
6	■	■	■	■

■ Present ▒ Less than 5% cover ☐ Absent

Control rocks

B.s.	Jul	Aug	Sep	Oct
1	■	■	■	■
2	☐	■	■	■
3	☐	☐	☐	☐
4	☐	☐	☐	☐
5	☐	☐	☐	☐
6	☐	☐	☐	☐

C.b.	Jul	Aug	Sep	Oct
1	■	■	■	■
2	■	■	■	■
3	☐	■	■	▒
4	☐	▒	☐	☐
5	☐	▒	☐	☐
6	☐	☐	☐	☐

G.v.	Jul	Aug	Sep	Oct
1	☐	☐	☐	☐
2	■	☐	☐	■
3	■	■	■	■
4	■	■	■	■
5	■	■	■	■
6	■	■	■	■

H.h.	Jul	Aug	Sep	Oct
1	☐	☐	☐	☐
2	☐	☐	▒	■
3	■	■	■	■
4	■	■	■	■
5	■	■	■	■
6	☐	☐	■	■

B.R.	Jul	Aug	Sep	Oct
1	■	■	■	■
2	■	■	■	■
3	■	■	■	■
4	■	■	■	■
5	■	■	■	■
6	■	■	■	■

Figure 1. Occurrence of four sessile species on permanent quadrats (100 cm²) along a vertical gradient (1 = higher and 6 = lower, close to sand). (*B.s.*) *Brachidontes solisianus*, (*C.b.*) *Chthamalus bisinuatus*, (*G.v.*) *Gracilaria verrucosa*, (*H.h.*) *Hymeniacidon heliophila*, (B.R.) bare rock.

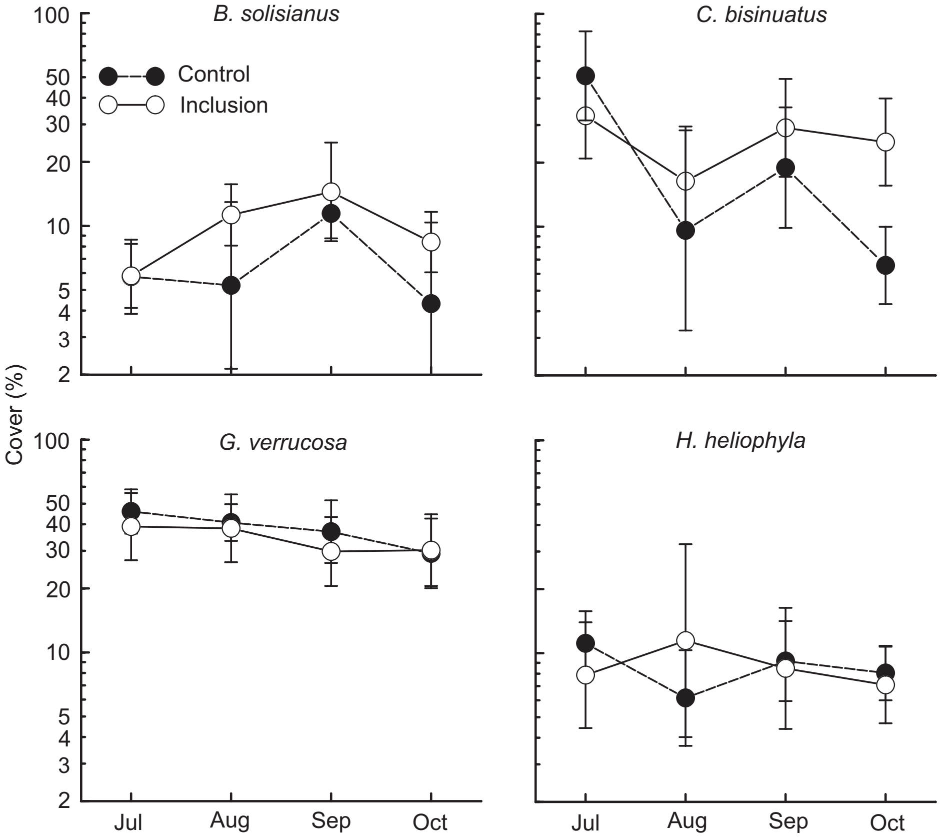


Figure 2. Percent cover (mean ± 95% confidence intervals) of four selected sessile species on permanent quadrats (100 cm²) during an inclusion experiment of *A. stellifera* in Penha, Santa Catarina.

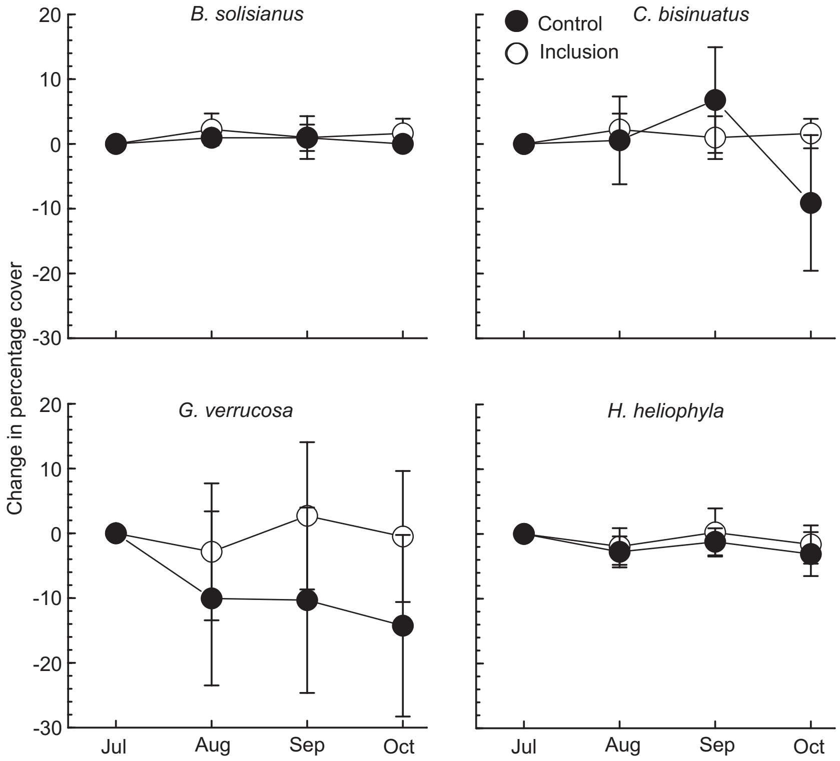


Figure 3. Change in abundance (mean ± 95% confidence intervals) of four selected sessile species on permanent quadrats (100 cm^2) between subsequent months during an inclusion experiment of *A. stellifera* in Penha, Santa Catarina.

verrucosa in the control treatments, its variability did not result in statistically significant differences. Cover in both *B. solisianus* and *H. heliophyla* was relatively constant in both treatments over time (Fig. 3).

Tolerance of *A. stellifera* to variation in salinity and desiccation

All starfish survived all water salinity treatments in the summer and the highest salinity in the winter. In the winter, however, only 57% of the starfish survived the reduced salinity (10 g kg^{-1}) and only 36% righted themselves within 30 minutes.

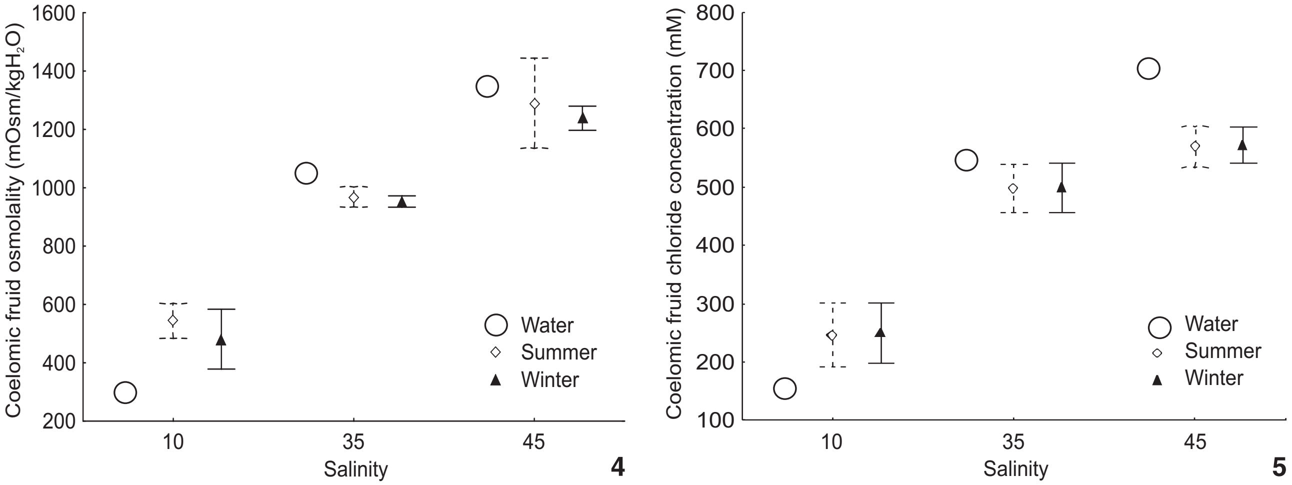
In the desiccation experiment, none of the starfish survived to air exposure under sunshine, during summer (air temperature: 31°C). However, all specimens survived exposure to the air in sunny winter days (air temperature: 27°C) as well as in cloudy days either in summer (air temperature: 29°C) or in winter (air temperature: 23°C).

Osmolality and chloride concentrations of the coelomic fluid was similar (although slightly lower) to that of sea water, both in summer and in winter. However, at 45 g kg^{-1}, coelomic fluid osmolality was not different from that of the water in summer and slightly below in winter. Chloride concentration, on the other hand, was lower, in both seasons. In diluted sea water (salinity 10 g kg^{-1}), the coelomic fluid of *A. stellifera* was maintained hyper-osmotic and hyper-ionic to chloride with respect to ambient sea water, in both seasons (Figs 4 and 5).

DISCUSSION

The rocky intertidal community comprised 32 species (26 of which were sessile), and none showed a trend due to the increase in the number of predatory starfish, *A. stellifera* (Figs 2 and 3). Some species (e.g., *C. bisinuatus* and *B. solisianus*) seemed to vary due to their own dynamics in different ways on different rocks with the result that control treatments were apparently more variable than inclusion treatments (Fig. 3). Thus, the potential regulatory role of this predator was not demonstrated. This result is surprising, considering that we increased the density of predatory starfish by 8-10 times (initial study found an average of four per rock), to attempt to demonstrate how predation might influence the rocky intertidal community. Had we also included an exclusion treatment no trend would have been observed due to naturally low densities.

The population decline of *A. stellifera* in southern Brazil has been substantial in the last decade (R.M. Rocha, pers. obs.), yet experimental densities in this experiment were above natural densities when the species was more common. Thus, the surprising lack of predatory influence on the rocky commu-



Figures 4-5. (4) Osmolality (mOsm/kgH$_2$O, mean ± 95% confidence intervals) of the coelomic fluid of *Asterina stellifera* when exposed to the salinities of 10, 35, and 45, in summer and winter (n = 10 for each group). The single value for water in each group was calculated considering salinity 1 = 30 mOsm/kg H$_2$O (Prosser 1973); (5) chloride concentration (mM, mean ± 95% CI) of the coelomic fluid of *Asterina stellifera* when exposed to the salinities of 10, 35, and 45, in summer and winter (n = 10 for each group). The single value for water in each group was calculated from reference values published for standard sea water (Prosser 1973).

nity may be due to predator limitation due to its narrow tolerance range to desiccation and low salinity levels that may often occur. Also, apparently the potential prey has much greater tolerance as demonstrated by its continued abundance throughout the experiment. Interestingly, in the field, *A. stellifera* was seen exposed to the air (Vidolin *et al.* 2002), but perhaps for shorter time intervals or under less temperature stress than those in this experiment.

Also, the starfish is sensitive to reduced salinity (10g kg^{-1}), especially during winter. Echinoderms are typically osmoconformers and stenohaline, and very permeable to water and ions (review in Stickle & Diehl 1987) and so it is expected that they not be active predators when exposed during low tide. Indeed, no starfish was ever seen consuming prey while exposed during low tide. However, physiological limitation does not completely explain the apparent lack of predatory influence on the community, since predation could certainly increase during high tides.

The osmolality of the coelomic fluid of *A. stellifera* in the higher salinities followed an osmoconformer pattern, as typically described for echinoderms (Stickle & Diehl 1987), though with the maintenance of small osmotic and ionic gradients, but especially of a clear ionic (chloride) gradient, in the concentrated sea water (45g kg^{-1}). Coelomic fluid chloride below sea water concentrations has been reported for echinoids (Vidolin *et al.* 2007). The starfish also displayed a certain capacity to avoid extreme dilution of its extracellular medium when exposed for 3h to very dilute sea water (10 g/kg). Avoidance of change in coelomic fluid osmolality was found in this starfish after air exposure for 1h in the field (Vidolin *et al.* 2002). These results thus indicate a certain physiological capacity to withstand the environmental challenges of tidal pools and even emersion during low tide.

The impact a predator has in a community may be related to its predatory capacity, prey abundance and vulnerability, prey selection and, in rocky coasts, availability of refuges (Barbeau & Scheibling 1994, Gaymer *et al.* 2001a, Wellenreuther & Connell 2002, Wong & Barbeau 2005). Starfish are passive predators, that is, they take prey as they are encountered while foraging, rather than hunting and chasing specific prey. This behavior suggests that it is prey vulnerability rather than predatory capacity of the predator (Wong & Barbeau 2005) that structures a community. This is particularly relevant for starfish that evert their stomach when attacking prey, is the case for *A. stellifera*. In the laboratory, *A. stellifera* mostly preyed on barnacles, mussels, and anemones. After stomach eversion, starfish remained almost motionless for 1 – 3 days. This behavior may be responsible for its weak predatory action observed in the field and may indicate a low metabolic rate. In the field the only movement during low tide was vertical (downward). In Peru, *Heliaster helianthus* (Lamarck, 1816) displays similar behavior in rocky coastal habitat and foraging is reduced after days of intense predation. This starfish is also considered a passive predator, not displaying any horizontal displacement while searching for its preys on the rocky coast (Tokeshi & Romero 1995).

Asterina stellifera, a weak predator in this study, in contrast with other starfish that are important predators in North America and in Australia at similar subtropical latitudes (Paine 1974, Cameron *et al.* 1991, Navarrete & Menge 1996, Gaymer *et al.* 2002, 2004) and may be keystone predators (Menge *et al.*

1994). Starfish are often the most abundant benthic predators of the subtidal and intertidal areas (Cameron *et al.* 1991, Himmelman & Dutil 1991, Gaymer *et al.* 2001a, 2002) where they prey intensively on most macro-invertebrates of both consolidated and unconsolidated substrates (Himmelman & Dutil 1991). They are very abundant and they aggregate on coastal rocks and reefs, thus maximizing the effects of predation (Paine 1971, 1974, Cameron *et al.* 1991, Gaymer *et al.* 2002, 2004).

Asterina stellifera had no apparent effect on the rocky coastal community of Penha, nor did it appear to influence any one prey more than any other. The starfish may have had a small effect on the barnacle *C. bisinuatus* and the alga *G. verrucosa*, yet due to the variability this possible trend will require further study (Fig. 3). Barnacles are prey for starfish, but any effect on *G. verrucosa* might be due to the indirect effects, such as on recruitment (Leonard 1994). Different types of predators, either strong or weak, with high or low rates of predation, can impose important indirect effects, and they may occur independently of any lethal or decimating effects that the predator may cause (Peacor & Werner 1997). Constant presence of the predator may alter the behavior of the prey in response to predation risk (Lima 1998). Thus, we cannot yet rule out, even without high predation rates, that long-term presence of the predator may influence population dynamics of the prey species by modifying their feeding or reproductive behavior.

In addition to the possible weak predation by *A. stellifera*, the possible subtle effect on the barnacle *C. bisinuatus* and not on the mussel *B. solisianus* would be surprising. Bivalves are frequently reported as preferential starfish prey (Paine 1969a, b, 1971, McClintock & Lawrence 1985, Navarrete & Menge 1996, Gaymer *et al.* 2001b). The single study that shows close interaction between asteroids and barnacles was in the Wadden Sea in the Netherlands. Exclusion of the starfish *Asterias rubens* Linnaeus, 1758 from the subtidal region increased recruitment of *Balanus crenatus* Brugière, 1789, while exclusion from the intertidal area did not influence either recruitment or population density of the barnacle *Semibalanus balanoides* (Linnaeus, 1767) (Buschbaum 2002).

In Penha, other predators may also be important for structuring the encrusting community. Herbivores, such as *C. subrugosa*, *F. clenchi*, *T. viridula*, *L. ziczac*, *L. flava*, *L. variegatus*, *A. lixula*, and *Aplysia* sp. were found on both the control and inclusion treatments (and so did not interfere with the experiment). These predators may have maintained the community at lower levels thereby reducing the potential impact of the starfish. In the Wadden Sea foraging by herbivorous gastropods was considered important for the population size of intertidal barnacles (Buschbaum 2002). The role of the so-called "weak predators" may have been mistakenly minimized, especially in stressful environments, such as the intertidal ecosystem. In Oregon, the gastropods *Nucella emarginata* (Deshayes, 1839) and *N. canaliculata* (Duclos, 1832) are weak predators that have a small effect on the mussel bank of *Mytilus trossulus* Gould, 1850, which is usually regulated by the important key predator *P. ochraceus*. When the starfish was excluded, both species of *Nucella* became voracious predators and replaced the starfish in its role in structuring the community (Navarrete & Menge 1996).

Here we found the surprising result that increasing the density of an important community-structuring predator in other regions did not influence community structure in southern Brazil. We suggest that the starfish *Asterina stellifera* may still play a role as a weak predator in this subtropical intertidal community. However, perhaps long-term studies are required to elucidate that role. While density was artificially high, its importance could have been moderated by the other predators in the system. Its currently low and declining density, hence it being considered endangered, also suggests that it has little impact as a potential factor in community structure. Further studies to examine the role of predation in community structure should examine the entire ensemble of predators.

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