RESEARCH ARTICLE

# Encounters between Antarctic limpets, *Nacella concinna*, and predatory sea stars, *Lysasterias* sp., in laboratory and field experiments

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**Abstract** Antarctic limpets, *Nacella concinna*, from the Admiralty Bay (King George Island, South Shetlands) for at least part of the year (austral winter) co-exist with predatory sea stars *Lysasterias* sp. Our laboratory and field experiments established that the presence of *Lysasterias* sp. or its odour had considerable influence upon their behaviour. Limpets' responses, consisting of shell mushrooming, shell rotation and flight, were distinctly different from their reaction to other stimuli, such as food and conspecific odours, or mechanical stimulation. Moreover, a significant impact of sea star presence on limpets' activity was observed, with limpets fleeing to a distance of 60 cm from the predator. Such reactions allow limpets to lower the incidence of sea star predation, but at the cost of presumptive disrupting of foraging and an additional energy expended for locomotion. A visible difference was noted between two limpet populations, with the rockpool limpets responding only after physical contact with being touched by a sea star, and the subtidal ones responding at a distance of up to 20 cm.

## Introduction

Many marine invertebrates exhibit escape behaviours in response to the presence of gastropod and sea star

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predators, limiting the number of dangerous encounters and reducing the risk of consumption (Phillips 1978; Peckarsky 1980; McClintock 1985; Marko and Palmer 1991; Scheibling and Hamm 1991; McKillup and McKillup 1994). Such behaviour may be mediated by both physical and chemical stimuli (Phillips 1978; Vadas et al. 1986; Marko and Palmer 1991; Mahon et al. 2002), and may have considerable effect on spatial and temporal activity patterns in prey species (Leber 1985; Vadas et al. 1986; Marko and Palmer 1991; Scheibling and Hamm 1991; Sparrevik and Leonardsson 1995; Rochette et al. 1997; Rochette et al. 2001).

Antarctic and sub-Antarctic limpets (Patellidae) are known to display escape responses to predatory sea stars (Walker 1972; Simpson 1976; Blankley and Branch 1984; McClintock 1985; Mahon et al. 2002). Behaviours such as shell mushrooming, shell rotation and flight have been observed in response both to physical contact with a predatory sea star and exposure to crude hydrophilic extracts made from sea star body tissues (McClintock 1985; Mahon et al. 2002). Observations on Chilean intertidal limpets showed that different species have developed contrasting strategies (active escape versus passive defense) when encountering predatory sea stars (Espoz and Castilla 2000). Branch (1979) noticed two types of reaction of limpets *Patella oculus* and *P. granatina* towards predatory sea stars *Marthasterias glacialis* (escape in small individuals and aggressive behaviour in large ones).

The Antarctic limpet *Nacella concinna* (Strebel, 1908) is a characteristic and ecologically important component of the Antarctic benthos and occurs from the intertidal zone down to depths of 110 m (Picken 1980) on rocky bottoms (Berry and Rudge 1973) along

the Antarctic Peninsula and adjacent islands (Picken 1980). It is herbivorous and feeds on benthic microalgae (Shabica 1976; Davenport 1997). At the onset of the austral fall individuals abandon intertidal and subtidal zones and migrate deeper presumably to escape low air temperatures and ice formation in the intertidal zone (Walker 1972). Subtidal *N. concinna* often co-occur with the predatory sea stars such as *Neosmilaster georgianus, Odontaster validus* and/or *Lysasterias* sp. (Mahon et al. 2002; M. Markowska, personal observations). *N. concinna* has previously been shown to display escape behaviour to the sea star *Ne. georgianus*, but no escape response to the sea star *O. validus* (Mahon et al. 2002).

The purpose of present study was to investigate the escape behaviours of *N. concinna* in response to the sympatric predatory sea star *Lysasterias* sp. Moreover, the present study explores the impact of a predator on the spatial dislocation of its limpet prey using both laboratory and fields manipulations. Finally, we compared escape responses of intertidal and subtidal populations of *N. concinna* to determine whether populations exposed to different levels of sea star predator risk respond differently.

## Materials and methods

Limpets were gathered from Admiralty Bay (King George Island, South Shetlands) by hand from rockpools during the low tide and by divers from the subtidal area (5–8 m of depth). Individuals were maintained in well-aerated 10 l non-flow tanks for 1 day prior to experiments. Conditions in these tanks (and all subsequent aquarium experiments) were maintained at 0–0.5°C and 34.2–34.5 PSU. Limpets collected from rockpools were significantly smaller than subtidal individuals (*t* test, $P < 0.005$), ranging from 19.8 to 43.3 mm shell length (mean = 21.2, SE = 0.32 mm, $n = 222$), in comparison to 23.7–47.0 mm (mean = 37.4, SE = 0.49, $n = 191$) for the subtidal ones.

Sea stars *Lysasterias* sp. with a radius of 4.5–6.2 cm (measured from the oral opening to the tip of the longest arm) were caught in baited traps (set at depth of 15 m) from the Admiralty Bay (King George Island, South Shetlands). Animals were maintained in well-aerated tanks (ca. 30 l each). To minimize differences in their feeding status they were fed *Notothenia* sp. muscle meat for a week and then starved for 2 weeks prior to experiments.

Behavioural observations were carried out on limpets placed individually in small aquaria (ca. 1.5 l). Individuals were left there for 15 min, allowing them to

reaffix themselves. Limpets were then exposed to the following stimuli: sea star odour, conspecifics odour, microalgal extract, pure sea water, mechanical stimuli or the presence of a live sea star. Sea star odour was obtained from the aquarium that had held two starved *Lysasterias* sp. for 24 h. Limpet odour was obtained from the aquarium that held a group of 10 adult limpets for 24 h. Microalgal extract was obtained by grinding sympatric microalgae (mainly diatoms) encrusting rocks on which limpets were found grazing. Mechanical stimulation was produced by gently touching the shells of limpets with a glass rod. Sea star stimulation was produced by placing a live starved specimen of *Lysasterias* sp. close to a limpet with one arm tip in contact with its shell. In all experiments, limpet behaviours were monitored for 5 min and their behavioural responses were observed (clamping to substrate, pallial tentacles waving, cephalic tentacles waving, shell mushrooming, shell rotation and flight). Each experiment was replicated 40 times (20 times for rockpool limpets and 20 for subtidal ones). Individual limpets were never used for the same test stimulus more than once. As there was no statistically significant differences between the responses of subtidal and rockpool limpets to any of these stimuluses applied in the laboratory experiments (mean reaction times *t* Student's test, $P < 0.05$; number of limpets displaying each behavioural reaction $\chi^2$ test, $P < 0.005$), both sets of results were pooled together.

Additional behavioural observations of limpets in their natural environment were made by divers by placing a starved specimen of *Lysasterias* sp. close to individual subtidal limpets, with one arm tip touching the shell. Limpet behaviours (see above) were monitored for 5 min. In control experiments limpets—freely grazing with no danger from predatory sea stars—were observed for the same amount of time. Each experiment was replicated 20 times. Again, no animal was used more than once.

The impact of sea star presence on limpet spatial dislocation in the laboratory was examined in $40 \times 60$ cm aquaria, with a group of four limpets placed in the central part of each aquarium. The animals were left there for 5 min, allowing them to reattach themselves. As the aquarium bottom was not covered with microalgae, the animals had no incentive to move or graze, and sat immobile in the place they were put. After that time a sea star was placed in the aquarium, about 30 cm from the limpets. Almost instantaneously it began to move towards the gastropods, reaching them in ca. 1.5 min. The sea star was removed from the aquarium after 5 min, and limpets behaviour was observed for further 5 min. Animal positions were noted with the help of a

grid on the bottom of the aquarium. Each experiment was replicated 20 times (10 times for the rockpool limpets, and 10 the subtidal ones) using different individuals each time.

The impact of sea star presence on limpet spatial dislocation in the natural environment was done in both the subtidal area and in rockpools. Observations were made after placing a starved specimen of *Lysasterias* sp. a few cm from naturally occurring groups of feeding limpets (subtidal zone), or resting limpets (rockpools during low tide). The area of rockpools in which experiments were conducted varied from 400 to 3,500 cm², with the number of limpets ranging from 6 to 41. No experiments were done when the water temperature in the rockpool exceeded 2.5°C, as preliminary observations revealed stress symptoms in sea stars under these conditions (their tube feet were extended only partially, they moved sluggish, and attempted to exit the rockpool). In the subtidal zone at 5–8 m depth limpets were distributed unevenly, in clusters from 3 to 10 individuals, at a mean density of 10 ind/m². Maps of locations were made before the experiments and limpets' positions were marked on them. Sea stars were removed after 5 min, and limpets behaviour was monitored for the further 5 min. Each experiment was replicated 10 times each for subtidal and intertidal limpets.

## Results

### Behavioural observations

Limpets showed virtually no behavioural reaction to controls consisting of pure sea water, and sat immobile on the aquarium bottom with pallial tentacles extended outside their shells.

Mechanical stimuli, microalgal extract or conspecifics odour elicited responses from 60% of limpets (Fig. 1). Gastropods touched with a glass rod reacted by instantaneously hiding pallial tentacles and clamping down on the aquarium bottom (Fig. 2). A return to the initial position was observed after $15.5 \pm 1.7$ s (mean $\pm$ SE).

Limpet reaction to microalgal extract consisted of waving the pallial tentacles on the anterior part of the body, shell rising and probing with the cephalic tentacles (Fig. 3). No individual was displayed more than two of these types of behaviour simultaneously. Similar components of behaviour were noticed by divers observing limpets grazing on microalgae in their natural environment. Time from stimulus release to animal reaction was $30 \pm 5.07$ s (mean $\pm$ SE).
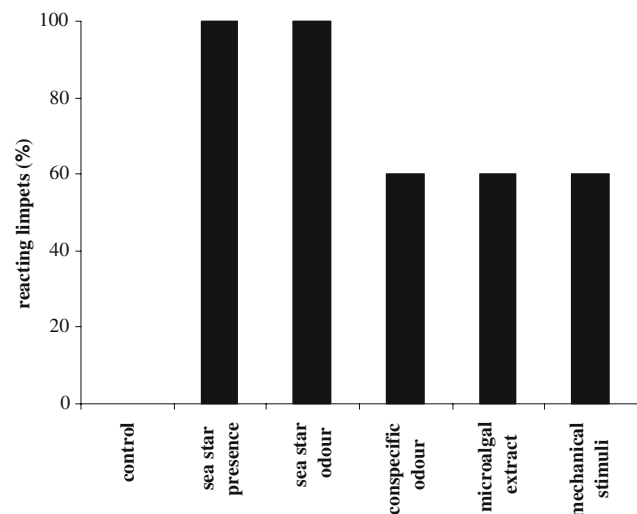


**Fig. 1** Percentage of limpets *N. concinna* reacting to different types of stimuli (*control* pure seawater)
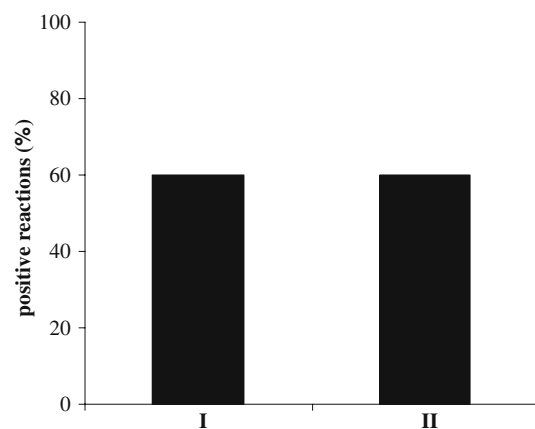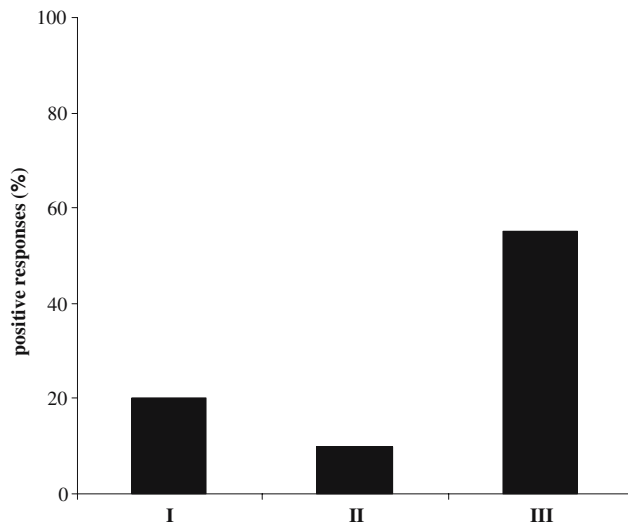


**Fig. 2** Behavioural responses of limpets *N. concinna* to mechanical stimuli. Positive behavioural responses are divided into types: *I* hiding pallial tentacles, *II* clamping down on aquarium bottom

The response of limpets to conspecifics odour consisted of waving pallial and/or cephalic tentacles (Fig. 4). Time from stimulus release to animal reaction was $11.7 \pm 1.7$ s (mean $\pm$ SE).

All limpets reacted to *Lysasterias* sp. "odour" (Fig. 1), displaying such types of behaviour as pallial tentacles waving, cephalic tentacles extension, shell mushrooming, shell rotation, and flight (Fig. 5). From stimulus release to animal reaction took $16.05 \pm 4.58$ s (mean $\pm$ SE). No individuals displayed all types of behaviour simultaneously, but 80% of them displayed more than one type of behaviour. Only 20% of limpets reacted with flight, but as many as 60% of them displayed shell raising and/or rotation.

All limpets reacted to the presence of a live *Lysasterias* sp. (Fig. 1), displaying such behaviour types as shell mushrooming, shell rotation and flight (Fig. 6).
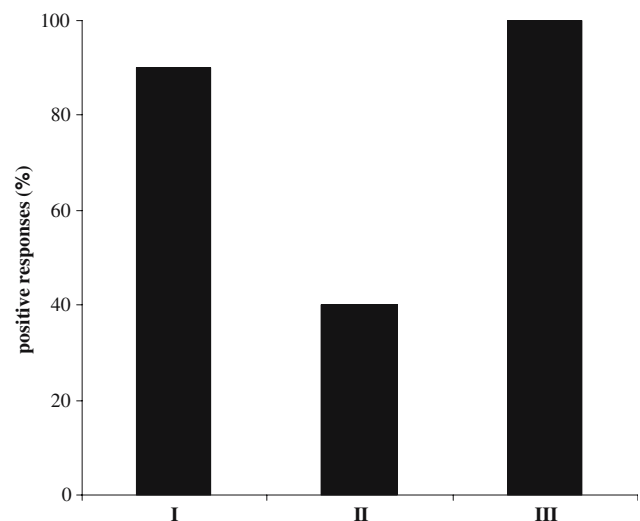
**Fig. 3** Behavioural responses of limpets *N. concinna* to microalgal extract. Positive behavioural responses are divided into types: *I* pallial tentacles waving, *II* shell rising, *III* cephalic tentacles probing
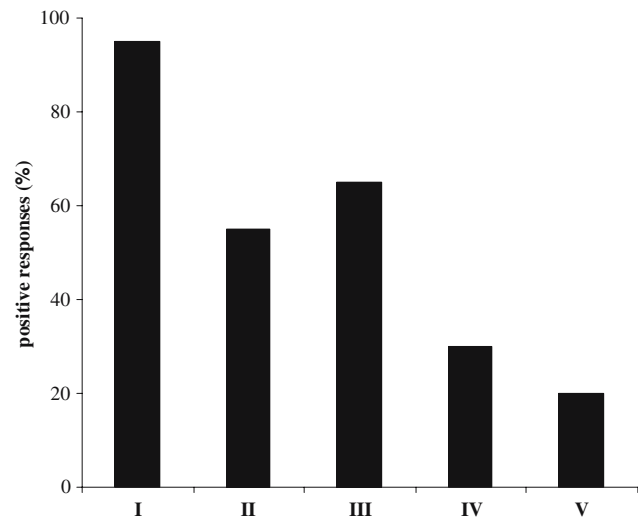


**Fig. 5** Behavioural responses of limpets *N. concinna* to sea star odour. Positive behavioural responses are divided into types: *I* pallial tentacles waving, *II* cephalic tentacles extension, *III* shell mushrooming, *IV* shell rotation, *V* flight
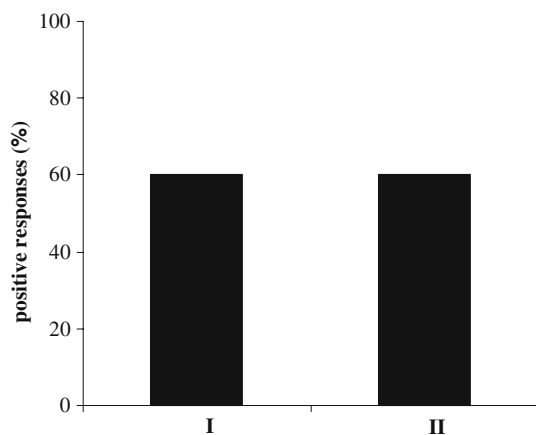


**Fig. 4** Behavioural responses of limpets *N. concinna* to conspecifics' odour. Positive behavioural responses are divided into types: *I* pallial tentacles waving, *II* cephalic tentacles waving



**Fig. 6** Behavioural responses of limpets *N. concinna* to live sea star presence. Positive behavioural responses are divided into types: *I* shell mushrooming, *II* shell rotation, *III* flight

All limpets touched by a live sea star reacted with flight, and—additionally, 90% of them—with mushrooming. Mean time between stimulus and animal reaction was 15.5 ± 3.02 s (mean ± SE).

Observations and manipulations done by divers in subtidal zone showed that all limpets touched by *Lysasterias* sp. responded with instant mushrooming and flight. The height attained by these limpets during mushrooming was twice as great as in the laboratory experiments and was two times higher than limpet shell height.

Position experiments

In the laboratory experiments all limpets from the rockpools or the subtidal sites fled from the presence of

*Lysasterias* sp. Individuals from rockpools reacted only upon being contacted by a sea star, whereas limpets collected from the subtidal site displayed flight when a moving sea star came within a distance of 2–4 cm. As limpets were gathered in a tight group in the aquarium centre, all of them reacted at approximately the same time (there was no statistically significant difference between reaction time of limpets within the group, Student's *t* test, $P < 0.05$).

There was a significant statistical difference between distances covered by fleeing rockpool and subtidal limpets in laboratory during the 10-min experiments

(Mann–Whitney $U$ test, $P < 0.05$), with subtidal limpets escaping much further (by 48%) than rockpool ones (Table 1). Statistically significant difference was observed between flight speeds of rockpool and subtidal limpets with the latter moving faster (Mann–Whitney $U$ test, $P < 0.05$).

Most of limpets' locomotory activity occurred during the first 5 min of experiment, i.e. before the removal of the sea star. During this time period rockpool limpets travelled a mean distance of 10.8 cm (SE = 0.9 cm) and the subtidal ones 17.5 cm (SE = 0.9 cm). This difference was statistically significant (Mann–Whitney $U$ test, $P < 0.05$). After sea star removal, all subtidal limpets and 82.5% of the rockpool ones continued their flight, although distances covered by them ($10.4 \pm 0.9$ cm for subtidal animals and $8.0 \pm 1.8$ cm for the rockpool ones) were significantly shorter than during the first period of observation (Mann–Whitney $U$ test, $P < 0.05$).

In field experiments, the percentage of rockpool limpets reacting to the presence of *Lysasterias* sp. ranged from 20 to 89%. Only individuals contacted by a moving sea star displayed a flight response. Almost 19% of them crawled out of water (one of the individuals travelled several centimetres to the next rockpool). Mean distance covered by escaping animals was 11.2 cm (Table 1), which was significantly less than in the instance of laboratory experiments (Mann–Whitney $U$ test, $P < 0.05$). In field experiments it was not possible to divide distance covered by limpets in two 5 min periods, because the gastropods did not begin to move at the same time. As they were initially dispersed over quite a large area, there was a significant time gap between different limpets being touched by the slowly moving sea star. Nethertheless, it was observed that 70% of escaping limpets continued their flight after the removal of a sea star from the rockpool.

**Table 1** Flight speed and distance covered by limpets *Nacella concinna* fleeing from a starved specimen of the sea star *Lysasterias* sp. in laboratory and field experiments

| | Distance (cm) | | | Flight speed (cm/min) | | |
|---|---|---|---|---|---|---|
| | Mean | SE | Range | Mean | SE | Range |
| Laboratory experiments | | | | | | |
| Subtidal | 27.9 | 2.1 | 6–60 | 3.24 | 0.24 | 0.6–7.2 |
| Rockpool | 18.8 | 1.8 | 2–40 | 2.42 | 0.24 | 0.4–4.8 |
| Field experiments | | | | | | |
| Subtidal | 40.6 | 1.37 | 20–60 | 45.1 | 1.02 | 36–60 |
| Rockpool | 11.2 | 0.64 | 3–35 | 3.9 | 0.69 | 0.2–5.3 |

Data from the laboratory experiments and the field rockpool experiments were calculated for 10 min periods of observation; data for field subtidal experiments for the duration of limpet flight (max. 2 min)

In the subtidal experiments, all limpets reacted to the presence of *Lysasterias* sp. Even individuals as far as 20 cm from the sea star began escaping. Mean distance covered by fleeing animals was 40.6 cm (Table 1), and was significantly greater than in all other experiments (Mann–Whitney $U$ test, $P < 0.05$). Limpets' locomotion ceased after they reached a distance of 40–60 cm from the predator. Due to high speeds attained by them, the whole burst of locomotory activity was exceptionally short, and did not exceed 2 min.

## Discussion

Our experiments indicate that the common Antarctic limpet *N. concinna* discriminates between different chemical and/or physical signals. Alarm signals (sea star contact or odour) elicited the strongest behavioural responses, as all individuals exposed to sea stars reacted in comparison to only 60% of limpets exposed to other stimuli. The behavioural responses to *Lysasterias* sp., i.e., shell mushrooming, shell rotation and flight, were identical to those described for *N. concinna* placed in contact with the predatory sea star *Ne. georgianus* (Mahon et al. 2002). McClintock (1985) noticed similar behaviour in the sub-Antarctic limpet *Nacella edgari* placed a short distance from the predatory sea star *Anasterias perrieri*. Another sub-Antarctic limpet, *N. macqueriesis*, was observed displaying escape behaviour to the sea stars *Anasterias directa* and *A. perrieri* (Simpson 1976). Thus, it can be assumed that escape responses of Antarctic and sub-Antarctic limpets to sea star predators are probably a common occurrence (Mahon et al. 2002).

Mahon et al. (2002) noted, that although *N. concinna* reacted vigorously to the sea star *Ne. georgianus*, it did not display escape responses to *Odontaster validus*, an unselective omnivorous sea star that can act as an active predator, a scavenger or a herbivore. Mahon et al. (2002) suggested that *Ne. georgianus*—a highly mobile sea star with long, narrow arms—may be more adept at feeding on limpets than *O. validus* with its short, web-like arms. Our laboratory observations showed that long arms of *Lysasterias* sp. were flexible and capable of complicated manipulations. Additionally, *Lysasterias* sp. can move at rates that are approximately six times greater than those observed in *O. validus* (A. Kidawa, personal observations). Thus, we can assume that *N. concinna* can assess the relative risks posed by different species of sea stars, and respond to them by fleeing from dangerous species and ignoring others. During our underwater manipulations it was observed that one of the limpets escaping from

*Lysasterias* sp. fled into the arms of a nearby *O. vali-dus*, moving over the sea star without any change of direction (M. Markowska, personal observation). In contrast, when the second sea star encountered was another *Lysasterias* sp., limpets executed a rapid change of direction, and only after this carried on the escape process (M. Markowska, personal observation). A similar phenomenon was also observed by Espoz and Castilla (2000) for the Chilean intertidal limpet *Lottia orbignyi*, which vigorously reacted to the sea star *Heliaster helianthus*, a known limpet consumer, and displayed almost no reaction to *Patiria chilensis* and *Stichaster striatus*, which have never been reported to prey on limpets (Espoz and Castilla 2000).

The signal responsible for *N. concinna* detecting the presence of sea stars is probably chemical in nature. Our observations showed that limpets exposed to sea star odour displayed changes in behaviour similar (although weaker) to those provoked by contact with or the presence of a nearby sea star. Similar results of chemically mediated escape responses to predators were reported earlier for limpets (McClintock 1985; Espoz and Castilla 2000; Mahon et al. 2002) and other marine invertebrates (Marko and Palmer 1991; Vadas et al. 1994; Morton et al. 1995; Moore and Howarth 1996; Rochette and Himmelman 1996). In contrast to previous limpet studies in which sea star homogenates were utilized (Espoz and Castilla 2000; Mahon et al. 2002), we used sea water from the aquarium in which live *Lysasterias* sp. were kept as the danger signal informing limpets of a predator presence. In their natural environment limpets will certainly be more often exposed to the effluents from a live sea star than to a sea star homogenate.

Our underwater observations showed that sea star presence had a visible and clear effect on limpet position, with limpets fleeing a distance of up to 60 cm. In laboratory experiments no instances of limpets climbing aquarium walls were observed. Even when a fleeing limpet reached aquarium wall, it changed direction and travelled parallel to it.

Our data on dispersal distances of escaping rockpool limpets in the laboratory and field experiments were similar to those reported for the Chilean intertidal limpets *L. orbignyi* and *Scurria viridula* (Espoz and Castilla 2000) and much lower than the values measured by us for subtidal *N. concinna*. Speed of Antarctic limpets fleeing from sea stars was previously measured only in the laboratory and ranged from 3.9 cm/min for *N. concinna* (Mahon et al. 2002) to 12 cm/min for *N. edgari* (McClintock 1985). These values and our data for rockpool limpets in laboratory and field experiments, and subtidal limpets in laboratory

experiments are visibly lower than the speed of 45.1 cm/min attained by subtidal limpets in our underwater experiments. Under these conditions, limpets displayed short, very intensive bursts of locomotion rather than rather long, prolonged periods of slower locomotion as observed in laboratory experiments. Significant differences between escape behaviours of subtidal limpets in laboratory and field experiments reveal the importance of underwater observations and manipulations, and underscore the difficulties connected with using laboratory observations to explain ecological processes in the animals' natural environment.

In our behavioural experiments no differences were observed between limpets from rockpool and subtidal populations. On the other hand behavioural experiments in which both limpets and *Lysasterias* sp. could move about freely showed distinct differences in the reaction of these populations, with the rockpool limpets reacting only upon being touched by a sea star (both laboratory and field experiments), and subtidal limpets responding to it from the distance of 2–4 cm (laboratory experiments) or 20 cm (underwater field experiments). Mahon et al. (2002) reported that no reaction of *N. concinna* was observed before physical contact with the predatory sea star *Ne. georgianus*. In contrast, the sub-Antarctic limpet *N. edgari* responded to the predatory sea star *A. perrieri* at a distance of about 6 cm (McClintock 1985). It can putatively be hypothetized that *N. concinna* can distinguish between different species of predatory sea stars, and the dissimilarity of the response is due to difference in perceived threat. This disparity might also have been caused by differences in the experimental methodology (free-moving sea stars versus those manipulated by hand). This explanation implies that the limpets can distinguish between un-stressed and stressed predators, and appropriately modify their reaction. Phillips (1978) noted that the sea urchin, *Strongylocentrotus purpuratus*, has the ability to distinguish between actively foraging and inactive individuals of the predatory sea star *Pycnopodia helianthoides*. In our field observations in rockpools we noticed that on sunny days when water temperature exceeded 8°C, limpets showed virtually no reaction to *Lysasterias* sp. The sea stars placed in such conditions were behaving differently than in lower (1.5–2.5°C) temperatures. Their tube feet were extended only partially, they moved sluggishly, and attempted to exit the rockpool.

Espoz and Castilla (2000) noted that two relatively primitive limpet species displayed strong escape reactions to the predatory sea star *Heliaster helianthus*, whereas two more derived limpet species did not exhibit such behaviours. In the present study, differences in

limpet escape responses to the predator were observed between two populations of the same species. Subtidal limpets came from an environment where they co-exist with different species of sea stars and where the risk of being preyed upon was probably quite significant. Additionally, in subtidal environments the absence or reduction of tidal currents and wave action made chemoreception a more feasible means of detecting the position of predators then in the intertidal zone. In contrast, rockpool limpets were living in the intertidal zone, where the presence of sea stars was only incidental, and the chance of encountering a sea star was almost nonexistent. Moreover, continuous water mixing by waves and tidal currents would also have reduced the effectiveness of distance chemoreception. At the beginning of the Antarctic winter both intertidal and subtidal populations of *N. concinna* migrate deeper (Walker 1972), where the likelihood and danger of encountering a predatory sea star is likely quite high. Therefore, we assume that *N. concinna* can modify its strategy of dealing with the presence of predators, depending on the probability of such encounters, with subtidal limpets, which coexist with predatory sea stars for the entire year, using distance detection and an avoidance strategy, whereas the intertidal ones, which for the part of the year live in the environment devoid of such predators, escaping only when touched by a sea star.

Significant differences between two Antarctic limpet populations living in tidal and subtidal environments were also noticed by other authors. Nolan (1991) observed differences in size, shape and shell morphology between both populations, attributed by him to a combination of behavioural and stress-induced factors. Similar shape differences between both populations were also found by Beaumont and Wei (1991). Additionally, a study of allelic variation, based on the examination of five enzyme loci, revealed no discernible differences between tidal and subtidal population of Antarctic limpets at Signy Island which suggests environmentally induced, phenotypic changes as being responsible for the observed differences (Beaumont and Wei 1991). Such significant morphometric difference between both Antarctic limpet populations suggests that limpets from the tidal population return to their environment when winter is over. Only further underwater behavioural observations during Antarctic winter can solve the issue of plastic versus fixed limpet' behavioural response to predatory sea star presence.

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