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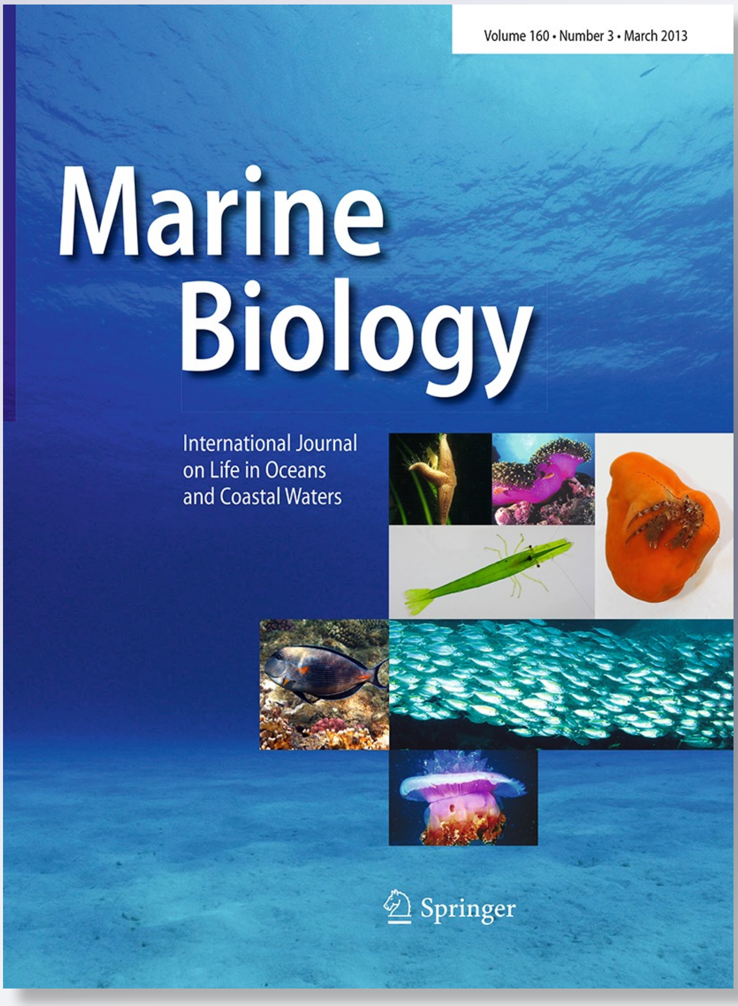

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ORIGINAL PAPER

Predators of juvenile sea urchins and the effect of habitat refuges

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Abstract We evaluated the effects of potential predators from intertidal habitats on *Strongylocentrotus purpuratus* survival using laboratory experiments and assessed abundances of main predatory species along the Pacific coast of North America. The interactive effects of urchins' and predators' sizes in mediating predation were quantified. Habitat complexity (substrate pits, adult spine canopy) was manipulated to examine its effects on predation of most susceptible individuals (<14 mm). *Pachygrapsus crassipes* was identified as a major predator of urchins up to ≈30 mm. A positive effect of predator size on consumption of progressively larger urchins was detected, probably due to a mechanical limitation on crabs' ability to consume large prey. Larger claws of males with respect to females of comparable sizes facilitated the handling of larger prey. Substrate refuges significantly reduced mortality on juvenile urchins. These results show that crab predation may be important in organizing intertidal communities, despite multiple ecological mechanisms promoting sea urchin survival.

Introduction

Early stages of marine invertebrates usually undergo high rates of mortality. Many factors are involved in this inherent feature of juvenile stages, such as delay of metamorphosis, biological or physical disturbance, physiological stress, competition and predation (Hunt and Scheibling 1997). Predation is one of the strongest biological processes affecting community structure and ecosystem organization (Hariston et al. 1960; McClanahan 1998; Duffy and Hay 2001; Guidetti et al. 2005) and is a well-documented cause of early mortality for benthic species (Hunt and Scheibling 1997). It is also a major factor determining the organization of sea urchin populations (Tegner and Dayton 1981; McClanahan and Muthiga 1989; Sala et al. 1998; Shears and Babcock 2002; Hereu et al. 2005; Clemente et al. 2009, 2010), with potential to modulate population density fluctuations that could result from episodic settlement and recruitment (Sala and Zabala 1996; Sala et al. 1998; Clemente et al. 2009).

The purple sea urchin, *Strongylocentrotus purpuratus*, plays a central role in structuring marine benthic communities on the Pacific coasts of North America (Pearse 2007), and pulses of recruitment strongly influence population dynamics and adult abundances (Ebert 1983; Underwood and Fairweather 1989; Hernández et al. 2010).

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Nevertheless, size-selective predation on juvenile sea urchins may be important in limiting recruitment of populations (e.g. Highsmith 1982), as small sizes (<20 mm in test diameter) are the most susceptible to predators. Due to the inherent difficulty of studying early-life stages, this phenomenon has received little attention and much of the research on the influence of predation in controlling sea urchin populations has focussed on interactions between adults and their predators (Tegner and Dayton 1981; McClanahan and Muthiga 1989; Sala et al. 1998; Shears and Babcock 2002; Hereu et al. 2005; Clemente et al. 2009). However, mortality patterns of juveniles cannot necessarily be predicted from those of adults as vulnerability to different sources of mortality often varies with size (Hunt and Scheibling 1997).

The importance of predation on small sea urchins and the subsequent effect on recruitment patterns is generally unknown. However, there are studies of many other factors, such as disease (Scheibling 1984; Pearse and Hines 1987; Lessios 1988), natural settlement and recruitment variability (Ebert 1983; Underwood and Fairweather 1989) and habitat-related variables (Sala et al. 1998; Hereu et al. 2005) that add to the regulation of sea urchin densities. For instance, the impact of predation on benthic communities can be reduced when prey species utilize certain kinds of refuges in the habitat that prevent predator access (Connell 1975; Witman 1985; Ojeda and Dearborn 1991). Spatial heterogeneity and the availability of physical refuges have been identified as major factors determining predation rates upon sea urchin populations (Roberts and Ormond 1987; Hereu et al. 2005), and hence the abundance of certain species (Tegner and Dayton 1981; Carpenter 1984; McClanahan and Kurtis 1991; Andrew 1993, Sala et al. 1998; Hereu et al. 2005). Most juvenile sea urchins typically live cryptically in topographic irregularities of the substratum, such as under rocks or in small cracks or crevices (Bernstein et al. 1981; Harrold and Reed 1985; Keats et al. 1985; Witman 1985; Himmelman 1986; Raymond and Scheibling 1987; Ojeda and Dearborn 1991; Dumont et al. 2006; Scheibling and Robinson 2008). Where the rock is sufficiently soft, individuals of *S. purpuratus* are known to excavate and inhabit small, urchin-sized pits or cavities in the substratum (Ricketts et al. 1985). Predators would probably experience increased difficulties in capturing an individual wedged into a pit (Grupe 2006), so living in this kind of microhabitat may increase sea urchin survival. Moreover, in populations of some species such as *S. purpuratus*, and more importantly in *S. franciscanus*, large individuals are considered extremely important as they provide 'canopy' microhabitat for small juveniles of the species (Tegner and Dayton 1977; Cameron and Schroeter 1980; Nishizaki and Ackerman 2007) and of other taxa (Rogers-Bennett and Pearse 2002) that shelter beneath adult spines. Once urchins settle on to the benthos, they often live during the juvenile phase in association with adults. This nursery association not only offers improved access to food sources to the smaller individuals, but also physical protection from predators and wave dislodgement (Tegner and Dayton 1977; Breen et al. 1985; Nishizaki and Ackerman 2007). Urchins that settle without any kind of physical protection may be more vulnerable to a suite of small invertebrate predators and demersal fish (Rowley 1990; Scheibling 1996; Hereu et al. 2005; Scheibling and Robinson 2008; Clemente et al. 2010; Urriago et al. 2012).

In general, fish and crabs have been recognized as the most common predators of early juveniles of many benthic species, including sea urchins (Hunt and Scheibling 1997; Jennings and Hunt 2010; Urriago et al. 2012), but in most cases their specific identities remain unknown. Connell (1975) proposed that some individuals of a prey species reach an 'escape size' and are less vulnerable to predation, so urchin size *per se* is a mechanism that deters predation. But at the same time, as individuals increase in size they may outgrow substrate refuges or become too large to fit among the spines of adults, thereby increasing predation risk (Bernstein et al. 1981; Keats et al. 1985; Witman 1985; Himmelman 1986). Size-selective predation on small urchins that have outgrown spatial refuges, but have not yet reached escape size may greatly influence population structure and dynamics in some species (Tegner and Dayton 1977, 1981; Andrew and Choat 1982; Tegner and Levin 1983; Scheibling and Hamm, 1991). Additionally, the prey's risk of being eaten will depend on the size structure of the predator population, since, in general, larger predators can handle and consume larger prey (e.g. Elner and Hughes 1978; Hughes and Seed 1981; Sanchez-Salalar et al. 1987; Robles et al. 1990), although they may also lack the mechanical dextrecity to handle small prey efficiently (Sousa 1993).

The objective of this study was to determine the effects of several potential predatory species common in the intertidal habitat (tidepool fish, crabs and starfish) of the Pacific coast of North America on the survival of the sea urchin *S. purpuratus*. We used a series of laboratory experiments to identify sea urchin predators, especially of juvenile stages, and assessed the interactive effects of predator and prey sizes in mediating predation rates and consequently potentially influencing adult population structure. We manipulated the structural complexity of the habitat, in terms of spatial refuges provided by pits in the substrate and by spine canopy of adult individuals, to examine the effects of habitat heterogeneity on the survival of juvenile sea urchins. We predicted that juvenile survival would increase with growing urchin size and decrease with increasing predator size, and that greater structural habitat complexity (shelter in pits and adult canopy) would decrease predation rates. We also conducted field surveys along the Pacific coast of North America to give insight into the patterns of distribution of main predatory crabs within the natural intertidal habitat of the sea urchin.

Materials and methods

Sample collection and handling

All experiments were carried out in the open seawater system of 'Instituto de Investigaciones Oceanológicas', at the 'Universidad Autónoma de Baja California' in Ensenada, Mexico. The experimental system consisted of a fibreglass seawater table (300 × 132 × 55 cm), supplied with filtered seawater at one end and constantly drained in the opposite end, creating a unidirectional current.

Sea urchins (*S. purpuratus*) of 5–30 mm in test diameter were collected from intertidal habitats at several locations around Baja California (Bajamar: 32 01′14.0″N, 116 52′52.6″W and Punta Baja: 29 57′19.4″N, 115 48′33.9″W) in March–April 2009. Individuals were maintained at ambient seawater temperature (10.5–11.5 °C) in the experimental tank and were regularly fed kelp (*Macrocystis pyrifera* and *Egregia menziesii*) prior to the experiments. Potential predators also were collected locally using hand nets and maintained in open seawater tanks to acclimate. All trials were conducted within 2 days of field collections.

Prior to trials, sea urchin test diameter, height and diameter of spines canopy were measured using knife-edge digital callipers (±0.01 mm). Individual predators were also measured and sexed. Predator sizes were recorded as total body length for fish, carapace width and claw lengths for crabs, and arm-to-arm diameter for starfish (±0.01 mm, the longest dimension). To standardize feeding status between individuals, all potential predators were fed small pieces of mussel flesh to ensure they were capable of feeding (Scheibling and Robinson 2008), and then starved for 1 day prior to trials. Replicate runs used different individual predators.

Identifying predators

To identify predators of *S. purpuratus* and assess vulnerability of sea urchins, we exposed individuals (≈5–30 mm in test diameter) to a variety of benthic invertebrates and fish that are commonly found sharing the intertidal habitat (Garth and Abbott 1980; Ricketts et al. 1985). Small juvenile sea urchins of 5–10 mm test diameter were included in the trials since they are considered the most susceptible sizes to predation. Potential predators included eight species: five species of crustaceans, one species of asteroid and two species of demersal fish (Table 1).

We tested the effects of *Pisaster ochraceus,* in completely enclosed (to retain the starfish) mesh cages (50 × 30 × 17 cm and 0.4 × 0.4 cm mesh wide) immersed in flowing seawater in the sea table. A slightly different system was used with intertidal fish *Clinocottus analis* and *C. recalvus*; topless cages (25 × 30 × 17 cm) were suspended from above into the seawater table. Cages were positioned in the sea table so the bottoms were ~12 cm below the surface of the water and the tops of the cage walls were always above the water line, preventing fish and sea urchins from escaping the enclosure.

Table 1 Taxa used in laboratory experiments to identify predators of the sea urchin *S. purpuratus*

Taxon	Species	*n*	Size (mm)	% sea urchins consumed	Size of predated sea urchins (mm)
Crustacea	*Cancer antennarius*	7	43–51	35.71	9.88–32.30
	Cancer magister	2	98–103	25.00	24.94–29.11
	Pachygrapsus crassipes	31	13–39	70.97	5.55–31.76
	Pagurus sp.	10	5–12	0	–
	Taliepus nuttallii	2	16–18	0	–
Asteroidea	*Pisaster ochraceus*	4	21–28	0	–
Chordata	*Clinocottus analis*	6	95–127	0	–
	Clinocottus recalvus	2	90–106	0	–

Number of individuals (*n*) and size ranges of potential predators (carapace length for crabs, arm-tip-to-arm-tip length for *P. ochraceus* and body length for fish), as well percentages and sizes (test diameter, mm) of sea urchins consumed during the course of the experiments are listed

Experiments with crustaceans as potential predators were conducted in PVC cylinders (12 cm diameter × 15 cm height) (Fig. 1a). The tops and bottoms of the cylinders were closed by mesh, so individuals were confined to the enclosures while seawater flowed through the structures. Cylinders were randomly positioned inside the sea table on their sides, allowing water to flow through the mesh following the dominant current created by the water supply at the end of the tank (Fig. 1a).

For each experimental trial, 3 juvenile sea urchins of comparable sizes were placed in each enclosed mesh cages (experiments with asteroids/fish) or the PVC cylinders (experiments with crustaceans), in the sea water table. A single potential predator was added to each container, while respective control treatments without the potential predatory species were conducted for each trial. When a predatory species successfully predated on these small sea urchin sizes, progressively larger urchin sizes were offered to detect any possible urchin escape size. The number of

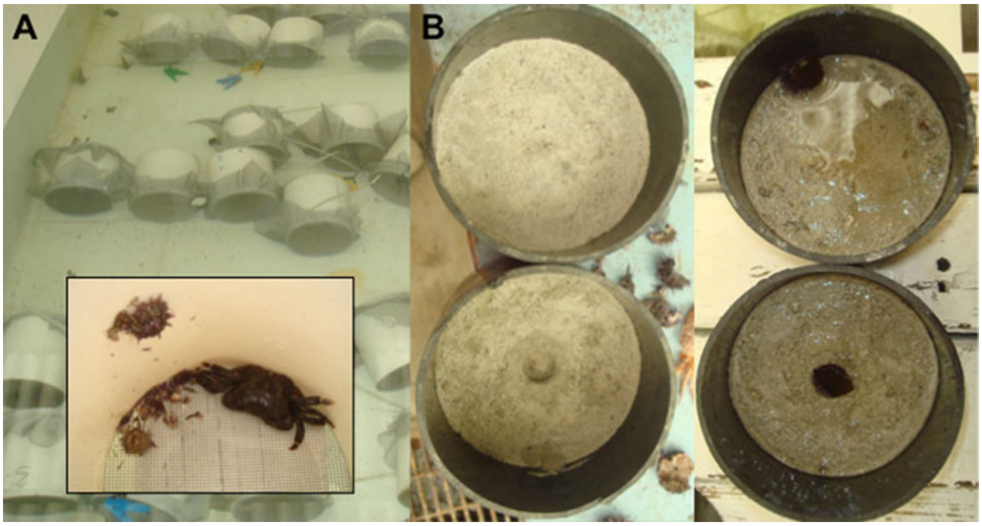

Fig. 1 Experiment settings. **a** Random positioning of PVC cylinders for experimentation with predatory crabs inside the seawater tank, and details of one experimental structure with a running trial with *P. crassipes* showing remains of the sea urchin *S. purpuratus*. **b** Modifications of the PVC cylinders to test the effects of substrate protection on predation of juvenile sea urchins. Pictures show the 'no-pit' treatment, where cylinders were filled with concrete for a flat surface (*top figures*), and the 'pit' treatment had a single small concave cavity moulded in the surface (*bottom figures*), as well as the typical positions of juvenile sea urchins in these respective structures (*right figures*)

replicates used for each predatory species was highly comprised by the availability of the species in the field and are given in Table 1.

Effects of *Pachygrapssus crassipes* and prey sizes on sea urchin survival

The most voracious predator of juveniles obtained in previous experiments, the crab *P. crassipes*, was used to assess the effects of both predator and prey sizes on predation rates. We used a 3 × 6 factorial design with crabs (of known gender) as one factor with three levels (small: 13.5–22.5 mm; medium: 22.5–31.5 mm and large: 31.5–40.5 mm in carapace width) and urchins size as the other factor with 6 size-class levels (5–10; 10–14; 14–18; 18–22; 22–26; 26–30 mm in test diameter), using PVC cylinders as cages. To detect any possible urchin escape size from crab predation, sea urchin prey ranged from early recruits (5–10 mm), which are the smallest sizes that can be found in the field in proportion to true abundance (Ebert 1983), to small-sized adult urchins (26–30 mm). Each replicate had 3 urchins and one predator. 6–9 replicates run for each combination of crab, and sea urchin size class were conducted, as well as respective control trials without the predatory species.

Effects of substrate refuge utilization on predation rate by *Pachygrapssus crassipes*

We tested the effects of substratum refuges on the effects of predation by *P. crassipes* on *S. purpuratus*. Experimental structures were PVC cylinders immersed into the seawater tank, in which structural refuges (Pits) or flat surfaces were provided for the sea urchins (Fig. 1b). To set up the experimental surfaces, cylinders were filled with concrete up to ~5 cm in height. In the 'pit' treatment, single small concave cavity (15 mm in diameter and 10 mm deep) was moulded in the substrate inside each cylinder. In the 'flat surface' treatment, no such cavities were built. A single juvenile sea urchin of 10–14 mm in test diameter (size class consumed by all crab sizes in previous experiments) was added to each experimental container in the pit and non-pit treatments. A ~2-h period was given for individuals to firmly attach to the substratum and was enough for urchins in the pit treatments to occupy their refuges before starting the trials (95 % of individuals were observed within pits before experiment commencement). Then, an individual of the crab *P. crassipes* in three size classes (small, medium and large) was placed in each experimental unit. A total of 5 replicates runs for each crab size class were conducted. Respective control trials without the predatory species were established for pit and non-pit treatments.

Effects of adult canopy protection on predation rate by *Pachygrapssus crassipes*

To test the effects of protection by adult sea urchin spine canopy on crab predation of juvenile *S. purpuratus*, juvenile urchins (10–14 mm in test diameter) were assigned to two treatments in PVC cylinders experimental units. The 'canopy' treatment consisted of introducing a single juvenile sea urchin together with an adult individual (33–39 mm in test diameter). In the 'non-canopy' treatment, no adult urchin was added, and the juvenile was completely exposed to the predator. A ∼2-h period was given to individuals to firmly attach to the substratum and was enough for juvenile and adult urchins to aggregate before starting the experiments. Then, an individual of the crab *P. crassipes* in three size classes (small, medium and large) was added to each experimental container. A total of 5 replicates for each crab size class and refuge treatment were conducted, and respective control trials without the predatory species were established for canopy and non-canopy treatments.

Experimental monitoring

All trials were carefully monitored every 24 h during two consecutive days, identifying surviving juveniles or their remains and determining the number of sea urchins consumed at each daily interval. Sea urchins consumed in the first day were replaced by individuals of the same size classes to maintain the numbers of prey available to predators at each daily interval (3 individuals per day), so a maximum of 6 sea urchins was exposed to each predator during the course of the trials (2 days).

Field surveys of intertidal populations of *Pachigrapssus crassipes* over a latitudinal gradient

Field surveys were carried out at a total of 26 sites along 6 latitudinal regions of the Pacific coasts of North America: Vancouver Island, Oregon, Northern California, Central California, Southern California and Baja California (Online resource 1), covering the whole distribution range of *P. crassipes*. At each study site, at least two middle–low intertidal tidepools that constitute the habitat of the sea urchin *S. purpuratus* were surveyed and their dimensions were measured. Surface area of a pool was estimated based on simple measures of the waterline of the surface and general shape (Ebert 2010). At study site, pools were emptied of sea water, all crabs were collected, carapace width were measured with vernier calipers to the nearest 0.01 cm and then organisms were returned. Densities were scaled to a surface area of 1 m^2, but potentially were overestimated with greatest error for deep pools with small surface areas. However, the same errors have been used in other studies that have attempted to estimate density of organisms in the intertidal (e.g. Sagarin and Gaines 2002).

Data analyses

For experiments that focused on the effects of predator *P. crassipes*, predation rates were calculated as the number of urchins consumed per day. Differences in sea urchin predation rates between urchin sizes and crab sizes were assessed with a distance-based permutational ANOVA (Anderson 2001). A two-way design was conducted where 'Crab Size' was a fixed factor with three levels (small, medium and large) and 'Urchin Size' was a fixed factor with six levels (5–10; 10–14; 14–18; 18–22; 22–26; 26–30 mm). In addition, differences in predation rates between crab sexes were analysed with a one-way distance-based permutational ANOVA. When testing the role of physical protection on predation of juvenile urchins, either in the form of substrate refuges or adult spine canopy protection, urchin predation rates (number of predated individuals day^{-1}) were analysed with two-way distance-based permutational ANOVAs. In each of these models, either 'Refuge' or 'Canopy' were treated as fixed factors with two levels (pit vs. flat; canopy vs. non-canopy, respectively) and 'Crab Size' as a fixed factor with three levels (small, medium and large).

A two-way permutational ANOVA was conducted over densities of *P. crassipes* recorded in the field to test for differences along the latitudinal gradient of the Pacific coast of North American. 'Region' was treated as a fixed factor with six levels, and 'Site' as a random factor nested in 'Region' (26 levels).

All ANOVA analyses were based on Euclidean distances of raw data, with p values obtained using 4999 permutations of the appropriate exchangeable units (Anderson 2001). Significant terms in the full models were examined individually using appropriate *a posteriori* pairwise comparisons, also conducted by permutations. The software PRIMER 6 & PERMANOVA+ was used to perform these procedures.

Correlation analyses were carried out to examine the relationship between the sizes of the predatory crabs, *P. crassipes*, and sea urchin prey sizes. To quantify crab size, we used crabs' carapace width (a standard measure of body size) and claw length (main offensive structures). For sea urchins, we used test diameter and spine canopy diameter as main prey defensive structures. In order to give insight into the potential differences of sea urchin consumption rates among sexes of the predator *P. crassipes*, we also explored the differences in allometry between both sexes, by means of examining the relationship between the length of claw and carapace of individuals used in the experiments. All these procedures were performed with SPSS-15.0 software.

Results

Identifying predators

Of eight potential predators, only three crab species (*Cancer antennarius, C. magister* and *P. crassipes*) consumed juvenile sea urchins (Table 1). Mortality rates resulted in ≥25 % of individuals consumed after 48 h for all crab species (Table 1). *P. crassipes* was a particularly voracious predator, consuming sea urchins of a wide range of sizes (Table 1) and in some trials accounting >90 % of predation of individuals. Sizes (test diameter) of consumed sea urchins depended on the species of predator: *C. antennarius*: 9–32 mm, *C. magister*: 24–29 mm and *P. crassipes*: 5–31 mm (Table 1).

Effects of *Pachygrapsus crassipes* and prey sizes on sea urchin survival

When analysing the effects of *P. crassipes* and prey size over predation rates, the number of consumed sea urchin per day significantly varied with sea urchin size (Table 2A; Fig. 2). *A posteriori* pairwise analyses of significant factor 'urchin size' showed that mortality by crab predation at the two smallest sea urchin size classes (5–10 and 10–14 mm) was significantly higher than at the larger sizes (Table 2B; Fig. 2). No significant effects of crab size or interaction between crab and urchin size were detected (Table 2A), although predation of large juveniles (14–18 and 18–22 mm) and small-sized adult sea urchins (22–26 and 26–30 mm) was only observed for large individuals of *P. crassipes* (Fig. 2). No urchin mortality was recorded at any of the respective controls established at the experiment.

We found a significant positive linear relationship between carapace width of *P. crassipes* and test diameter of their sea urchin prey (Fig. 3a). The relationship was more adjusted when considering the linear relationship between crabs claw length (attacking structure) and the diameter of the spine canopy of preyed sea urchins (defensive structure) (Fig. 3b). Variability in the size of consumed sea urchins (measured either by test or spine canopy diameter) increased progressively as crabs were larger or had longer claws. Crabs measuring >32 mm in carapace width or with claws longer than 16 mm were the only ones able to successfully prey on sea urchins >14 mm in test diameter or >30 mm in spine canopy diameter (Fig. 3a, b).

The length of *P. crassipes* claws was positively and allometrically related to the carapace size (Fig. 4a). However, this allometric relationship varied between sexes, with males having comparatively larger claws than females, especially at larger sizes (Fig. 4a). This sexual dimorphism was reflected in the outcome of the predation experiments, as mortality of *S. purpuratus* differed in response to the sex of their crab predator (1-way ANOVA: $F = 5.01$, $p < 0.05$). Urchin mortality caused by males of *P. crassipes* was significantly higher than mortality due to predation by females (Fig. 4b).

Table 2 (A) Results of the two-way distance-based permutational analyses of variance (ANOVA) assessing differences in the number of predated *S. purpuratus* exposed to the action of the crab *P. crassipes* (number of predated individuals day^{-1}), between size classes of both urchins and crabs, (B) Estimates for pairwise comparisons of significant effects of the factor 'urchin size' are shown

A. Source of variation	*df*	SS	MS	Pseudo-*F*	*P* (perm)
Urchin size (*U*)	5	20.78	4.16	5.51	0.001
Crab size (*C*)	2	3.59	1.80	2.38	0.107
$U \times C$	10	8.07	0.81	1.07	0.398
Residual	71	53.53	0.75		
Total	88	87.78			

B. Pairwise analyses	Urchin size (mm)	*T*	*P* (perm)
	5–10 vs. 10–14	0.08	0.948
	14–18	2.54	0.016
	18–22	3.16	0.010
	22–26	2.54	0.031
	26–30	2.71	0.018
	10–14 vs. 14–18	2.60	0.018
	18–22	3.23	0.002
	22–26	2.63	0.016
	26–30	2.77	0.019
	14–18 vs. 18–22	1.42	0.173
	22–26	0.58	0.590
	26–30	1.20	0.252
	18–22 vs. 22–26	0.64	0.619
	26–30	0.09	0.929
	22–26 vs. 26–30	0.51	0.684

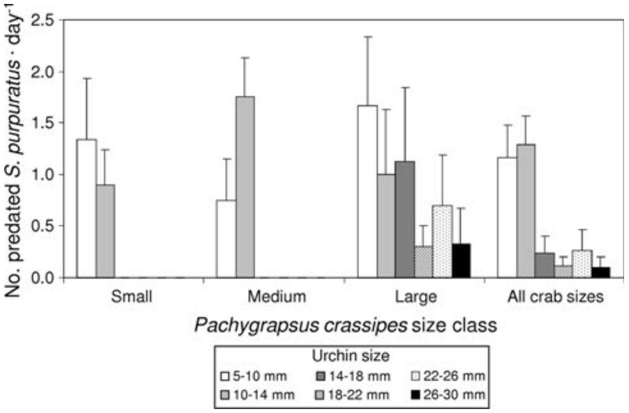

Fig. 2 Predation of *S. purpuratus*. Numbers of predated sea urchins (mean ± SE) in each of the six sea urchin size classes studied by small (13.5–22.5 mm in carapace width), medium (22.5–31.5 mm) and large (31.5–40.5 mm) crabs *P. crassipes* at laboratory experiments

Effects of substrate refuge on predation rate by *Pachygrapssus crassipes*

Predation of *S. purpuratus* measuring 10–14 mm in test diameter, the size class consumed by all sizes of *P.*

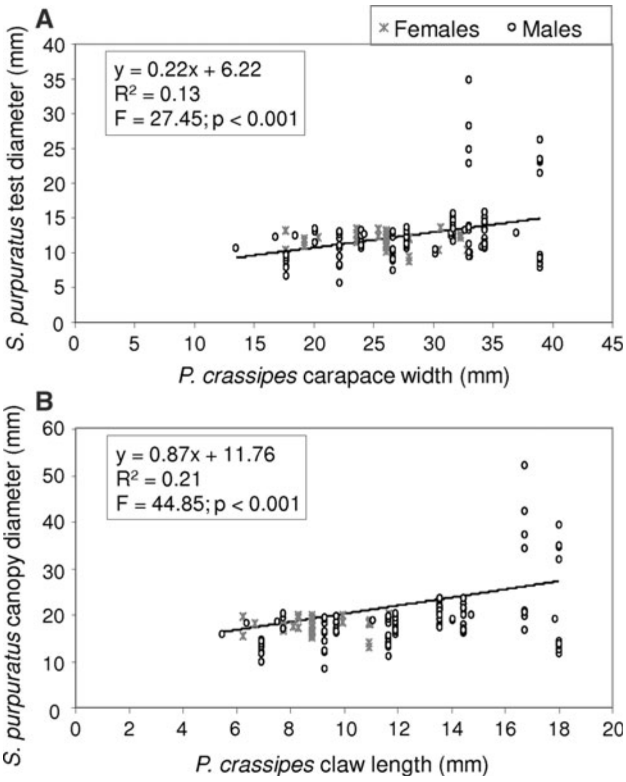

Fig. 3 Predator–prey length correlations. **a** Relationship between carapace width of the predatory crab *P. crassipes*, and the test diameter of sea urchin consumed; and **b** relationship between the lengths of claws, considered crab main offensive structures and the spine canopy diameter or defensive structure of sea urchins

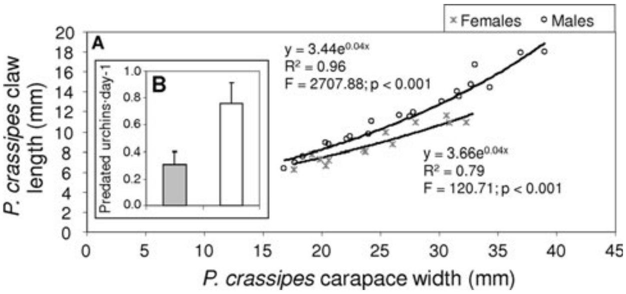

Fig. 4 Sex-dependent claw–allometry relationships and sea urchin predation intensity of *P. crassipes*. **a** Exponential relationships between crab carapace width and claw length of both sexes. **b** Numbers of predated sea urchins (mean ± SE) due to the action of both female (*shaded bar*) and male (*open bar*) crabs at predation experiments in the laboratory

Table 3 Results of the two-way distance-based permutational analyses of variance (ANOVA) assessing differences in the number of predated *S. purpuratus* exposed to the action of crab *P. crassipes* (number of predated individuals day^{-1}) in laboratory experiments, between degrees of spatial refuge utilization by sea urchins (individuals occupying pits vs. exposed urchins) and size classes of predatory crabs

Source of variation	*df*	SS	MS	Pseudo-*F*	*P* (perm)
Refuge (*R*)	1	1.30	1.20	9.29	0.008
Crab size (*C*)	2	0.02	0.01	0.06	0.946
R × *C*	2	0.35	0.17	1.35	0.303
Residual	24	3.10	0.13		
Total	29	4.67			

crassipes in previous experiments, was significantly lower on sea urchins occupying spatial refuges (pits) than on exposed urchins (flat substrate), but no significant effect of crab size was found (Table 3; Fig. 5a). Despite no effect of crab size on pit and exposed urchin mortality, small- and medium-sized crabs were able to dislodge and consume urchins occupying refuges, while large-sized *P. crassipes* did not consume any of the pit urchins in the experiments (Fig. 5a). Observations during the course of the experiments suggested that small- and medium-sized crabs were able to somehow manipulate urchins inside their pits since some of the individuals appeared dead inside their substrate cavity. Remains showed that the individuals were damaged from above, suggesting that claws' of small- or medium-sized *P. crassipes* were small enough to go into the small cavities of the substratum and manipulate their sea urchin prey. There was no urchin mortality in any of the controls (treatments without predators) established for pit and non-pit treatments.

Effects of adult canopy protection on predation rate by *Pachygrapssus crassipes*

Juvenile sea urchins under the spine canopy treatment quickly sought shelter under or near the adult individual when introduced into the experimental units. The outcome of predation experiments showed a marginally non-significant effect of protection by spine canopy of adult *S. purpuratus* over predation of juvenile sea urchins (Table 4A). However, a pattern of increased mortality upon exposed sea urchins was observed, especially with the largest crabs (Fig. 5b). Sea urchin predation significantly varied with the size of the predatory crab *P. crassipes* in the experimental treatments (Table 4A). *A posteriori* pairwise analyses showed that small-sized crabs caused significantly lower urchin mortality than medium- and large-sized individuals regardless of whether or not individuals were protected by the spine canopy of adults (Table 4B; Fig. 5b). No urchin mortality was registered at any of the respective controls.

Intertidal populations of *Pachigrapssus crassipes* over a latitudinal gradient

Populations of *P. crassipes* at middle–low intertidal tidepools inhabited by the sea urchin *S. purpuratus* differed

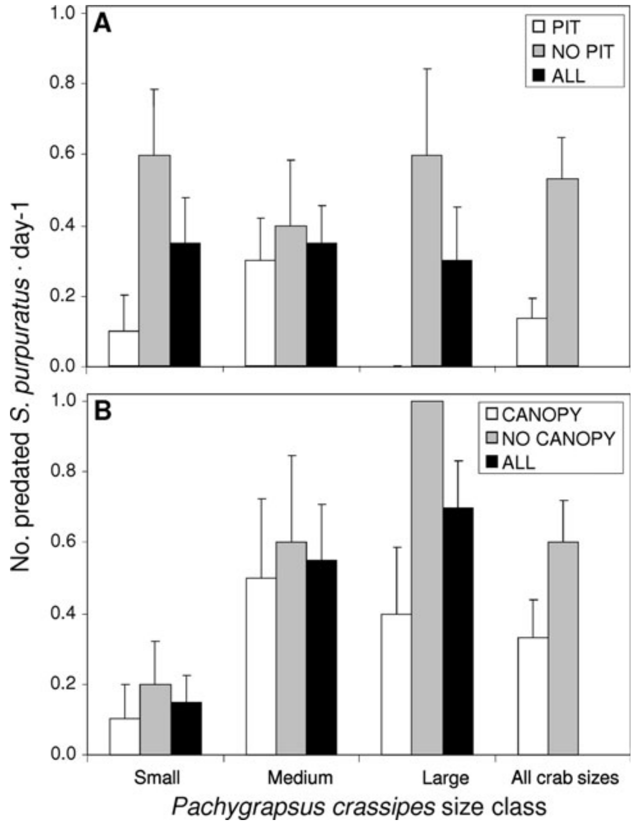

Fig. 5 Effects of physical protection on predation of juvenile *S. purpuratus*. Numbers of predated sea urchins (mean ± SE) by small (13.5–22.5 mm in carapace width), medium (22.5–31.5 mm) and large (31.5–40.5 mm) *P. crassipes* at **a** experiments with juvenile urchins occupying either refuges in the substratum (pits) or flat substrates that exposed the individual to the potential action of the predator (no pit); and **b** trials with juveniles protected by spine canopy of a nearby adult in contrast to trials where no adult sea urchin was added (non-canopy)

Table 4 (A) Results of the two-way distance-based permutational analyses of variance (ANOVA) assessing differences in the number of predated *S. purpuratus* exposed to the action of crab *P. crassipes* (number of predated individuals day^{-1}) in laboratory experiments, between degrees of protection by spine canopy of adult sea urchins and size classes of predatory crabs, (B) Pairwise comparisons of significant factor crab size are included

A. Source of variation	*df*	SS	MS	Pseudo-*F*	*P* (perm)
Canopy (Ca)	1	0.53	5.33	3.76	0.067
Crab size (*C*)	2	1.62	0.81	5.71	0.008
Ca × *C*	2	0.42	0.21	1.47	0.237
Residual	24	3.40	0.14		
Total	29	5.97			

B. Pairwise analyses	Crab size	*T*	*P* (perm)
	Small vs. medium	2.18	0.036
	large	4.49	0.002
	Medium vs. large	0.79	0.446

between regions of the latitudinal distribution of the species (Table 5A). Crab densities were significantly higher on southern regions of central Southern California and Baja California than at northern latitudes (Table 5B; Fig. 6).

Discussion

We have shown that some crustacean decapods can consume the sea urchin *S. purpuratus* in intertidal rocky habitats. Exposure of juvenile sea urchins to a variety of common intertidal invertebrates and fish identified three species of crabs as sea urchin predators: *Cancer antennarius, C. magister* and *P. crassipes*. However, the low abundances of the first two species found in our field sites (pers. obs.) did not allow us to conduct further experiments to study patterns of predation.

In contrast to findings for other sea urchin species (Scheibling and Robison 2008; Urriago et al. 2012), hermit crabs *Pagurus* sp. were not found to consume juveniles of the purple sea urchin. Similarly, we did not observe any predation by the *Pisaster ochraceus*. However, previous studies showed this starfish occasionally feed on a variety

Table 5 (A) Results of the two-way distance-based permutational analyses of variance (ANOVA) assessing differences in the abundance of the predatory crab *P. crassipes* at intertidal habitats, between six regions along the latitudinal gradient of the Pacific coasts of North America and sites studied within each region, (B) Pairwise comparisons of significant factor region are included

A. Source of variation	*df*	SS	MS	Pseudo-*F*	*P* (perm)
Region	5	485.03	97.00	26.14	0.001
Site (region)	20	74.30	3.72	1.11	0.390
Residual	27	90.74	3.36		
Total	52	649.68			

B. Pairwise analyses	Region	*T*	*P* (perm)
Canada vs.	Oregon	<0	ns
	Northern California	0.96	0.383
	Central California	2.04	0.077
	Southern California	4.96	0.116
	Baja California	5.43	0.013
Oregon vs.	Northern California	1.12	0.296
	Central California	2.38	0.033
	Southern California	5.71	0.009
	Baja California	6.61	0.005
Northern California vs.	Central California	2.99	0.013
	Southern California	2.42	0.041
	Baja California	9.72	0.001
Central California vs.	Southern California	0.86	0.382
	Baja California	5.36	0.002
Southern California vs.	Baja California	3.67	0.061

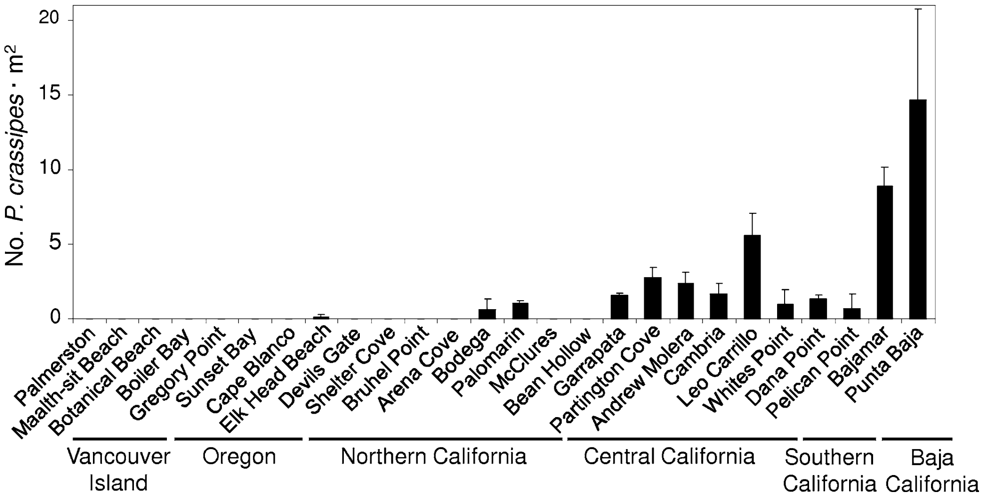

Fig. 6 Population densities of *P. crassipes*. Abundances of the predatory crab (mean ± SE) at intertidal habitats of study sites within each of the six regions surveyed along the latitudinal gradient of the Pacific coasts of North America (Vancouver Island, Oregon, Northern California, Central California, Southern California and Baja California)

of intertidal organisms, including *S. purpuratus* (Feder 1959; Mauzey 1966), and sea urchins are known to show specialized behaviours that can effectively resist starfish attacks (Dayton et al. 1977; Mann et al. 1984; Gaymer and Himmelman 2008; Urriago et al. 2012). Intertidal sculpins, previously recognized as potential predators of early stages of sea urchins (Hunt and Scheibling 1997; Jennings and Hunt 2010), were not observed to damage or consume any juvenile urchins in our experiments. Other studies have also found that sculpins have no effect on survival of juvenile urchins (Scheibling and Hamm 1991; Scheibling and Robinson 2008). However, these preliminary results must be confirmed with further experiments using smaller sea urchin sizes and larger predators than the ones used in the current study, as well as larger sample sizes.

We found that *P. crassipes* was a particularly voracious predator, and inclusion experiments showed that the 'lined shore crab' significantly increased mortality of purple sea urchins of sizes up to ≈30 mm in test diameter, particularly in the absence of spatial refuges of the substratum. This result highlights the potential importance of crabs in structuring intertidal communities in the Pacific coast of North America and contrasts with a previous study by Hiatt (1948) that found that *P. crassipes* fed mainly on cyanobacteria, diatoms and algae and also could scavenge on dead animals and be cannibalistic in North America, making it an omnivore. This conclusion was repeated by Garth and Abbott (1980), while there is also an interesting observation of *P. crassipes* preying on limpets off the coast of California (Chapin 1968). Considering that this decapod constitutes a frequent species inhabiting sedimentary bottoms (Squires 1990) and that it commonly co-occurs with sea urchins on rocky substrata along the midddle–low intertidal tidepools, our finding that the species could act as such an effective predator may be of ecological relevance. This grapsid crab is widely distributed along the eastern Pacific coast of North America, from Charleston, Oregon, (USA) to central Baja California (Mexico) including the Gulf of California (Garth and Abbott 1980; Sousa 1993; Wicksten 2009), covering an important part of the distribution of *S. purpuratus* (Ebert 2010). Current evidence suggests that the species is expanding its distribution northwards. It has been found as far north as Bamfield (Vancouver Island, British Columbia, Canada) since 1997, probably as a result of the interplay of periodically higher sea water temperatures, caused by the increased frequency and intensity of El Niño events, and global warming processes (Cassone and Boulding 2006). Our results support this hypothesis as higher abundances of the crab at middle–low intertidal tidepools of southern regions of its range of distribution were found, probably this is an ecological strategy to cope with higher ambient temperatures and avoid desiccation. With regards to the sea urchins, a previous study by Ebert (2010) found maximum population densities at middle latitudes, between 35 and 37°N, with highest numbers of recruits even further north, between 34 and 38°N. Predator-prey relationships inferred from our results may be influencing to some extent these patterns of abundances of the sea urchin (especially of recruits), despite the interplay of other factors, such as thermal tolerance and larvae supply (Ebert 2010), controls the distribution of *S. purpuratus*. Given the importance of sea urchin grazing activity in structuring benthic communities in this region (Pearse 2007), variability in predator–prey interactions along the distribution of the sea urchin may be a factor with potential to influence urchin mortality, particularly at early stages, and hence influence the organization of populations. Therefore, the finding that *P. crassipes* could be such an effective sea urchin predator should be carefully considered for future ecological studies of intertidal communities of the region.

Inferring predator–prey dynamics from laboratory experiments must be always done with caution. Although various experimental artefacts may differentially affect predators and preys, these studies are extremely useful in identifying factors that can potentially influence the intensity and variability of recruitment of benthic marine invertebrates, such as mortality at juvenile stages. Knowledge of events that occur shortly after settlement is particularly useful to get a more complete understanding of population dynamics. However, monitoring post-settlement mortality in the field is extremely difficult for most species. Under these circumstances, laboratory experiments are particularly relevant.

Our results show that a wide range of sizes of *S. purpuratus* are vulnerable to predation across the array of *P. crassipes* sizes tested. The average and maximum sizes of consumed sea urchins increased with increasing predatory crab size. In fact, juvenile urchins were vulnerable to a suite of crab predators, including *P. crassipes* and two other species (Table 1), and only large adults appeared to reach an escape size refuge from all but the largest crab predators, as found in previous studies (Scheibling 1996). As juveniles grow, they are less likely to be consumed, particularly by small crabs. For many prey species, it has been proposed that after reaching certain size or 'escape size' they become less vulnerable to predation (Connell 1975; Menge and Sutherland 1976). Our results show that *S. purpuratus* generally reaches a size refuge from *P. crassipes* predation at ≈30 mm in test diameter. However, larger individuals were occasionally still vulnerable to the largest crabs, and there was no evidence of an absolutely invulnerable urchin size, especially when considering the other predatory crab, *Cancer magister*.

In addition to the clear effect of crab size, an effect of predatory crab sex was detected over sea urchin consumption. Male crabs ate larger urchins on average than did females of equal size. There is probably a mechanical limitation on the ability of predatory crabs to handle and consume large prey using their claws as offensive structures. Therefore, the largest claws that males of a certain size have with respect to females clearly reduce the difficulties of handling progressively larger prey. The observed sex- and size-mediated predator–prey interactions might then influence predatory relations along the distribution range of the sea urchin, and may be a factor with potential to influence urchin mortality, particularly at early stages.

The outcomes of predation depend not only on prey and predator sizes, but also on the ability of prey to utilize refuges that exclude predators (Connell 1975; Witman 1985). For instance, predation risk for early juveniles commonly varies among microhabitats provided by substrate heterogeneity for many benthic invertebrates (Hunt and Scheibling 1997). Our results showed that small individuals of purple sea urchins (<14 mm in test diameter) are the most strongly affected by crab predation and are susceptible to being eaten regardless of the size and sex of the predator. However, the presence of suitable refuge appeared as a key factor in avoiding predation and reducing urchin mortality in the presence of a crab predator. In the field, topographic irregularities of the substratum such as cracks and crevices, act as important refuges for these small sea urchins (Keats et al. 1985; Witman 1985; Himmelman 1986). In other cases, where the rock is sufficiently friable, sea urchins erode and occupy cavities. These microhabitats can dramatically affect sea urchin survival as well as other aspects of the species' biology (Grupe 2006; Hernández and Russell 2010). Simulation of these pit refugees under laboratory conditions provided suitable shelter habitats similar to those commonly utilized by sea urchins in natural environments (Grupe 2006; Ebert 2007), and showed their effectiveness in protecting sea urchins from *P. crassipes* predation. However, in this case small- and medium-sized crabs appeared able to manipulate individuals inside the pits, given that their claws were small enough to go inside the pits and damage urchin test from above. The fact that overall predation of the most susceptible sea urchin sizes is reduced inside pits suggests that the availability of living space is an important factor affecting the survival of *S. purpuratus* populations and, probably, the distribution and abundance of associated benthic predators. Therefore, the risk of predation faced by *S. purpuratus* depends not only on its size and on the size and sex of its crab predator, but also on the availability of spatial refugees, or alternatively on the presence of substrata friable enough to be eroded.

The occurrence of juvenile sea urchins near or under adults also offers protection from predation in several echinoid species such as *Strongylocentrotus franciscanus* (Tegner and Dayton 1977) and *Dendraster excentricus* (Highsmith 1982). When juveniles become too large to fit under or around the spine canopy of adults, they are forced to shift habitats as their vulnerability to predation naturally decreases with increasing size (Tegner and Dayton 1977; Bernstein et al. 1981; Scheibling and Hamm 1991; Shears and Babcock 2002). However, our laboratory experiments did not fully demonstrate that aggregation of juvenile *S. purpuratus* with conspecific adults was an effective defence against crab predators, despite results indicated that canopy may provide refuge to juvenile sea urchin from predation by large crabs.

Several factors such as physical disturbance and competition also play important roles in determining aspects of the community ecology of rocky subtidal environments (see Sebens 1985; Witman 1985). Future studies should evaluate the influence of these factors and the various causes of mortality on patterns of distribution of sea urchin recruits at different spatial scales. However, our quantification of the dynamics of crab predation on juvenile purple urchins demonstrate the important role predation can play in controlling juvenile sea urchins—the most vulnerable size ranges of the population.

Our results show that predation, particularly by abundant crab predators, and the presence of spatial refuges are relevant controlling forces that play a key role in organizing intertidal benthic communities. These findings are consistent with others that have shown similar controlling factors within marine communities worldwide (Connell 1975, Menge and Sutherland 1976, 1987; Paine 1980; Ojeda and Dearborn 1991; Scheibling and Robinson 2008; Clemente et al. 2010). Additionally, different prey escape mechanisms, such as size, defensive structures (spine canopy) and spatial refuge utilization show important ecological strategies that promote sea urchin survival. These new insights into the patterns of juvenile sea urchin predation by common crab predators, as well as prey mechanisms that increase urchin survival, add to the understanding of sea urchin populations and their key role in rocky intertidal communities and should not be overlooked in future studies of population dynamics.

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