

Top-down effects on intertidal mussel populations: assessing two predator guilds in a South African marine protected area

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ABSTRACT: Mussels are important ecological engineers and occupiers of intertidal space in many parts of the world, where their populations are shaped by top-down regulation through predation on adults. In South Africa, adult predation is believed to be low, with mussel populations limited by competition or bottom-up supply of recruits. We tested the hypothesis that predation shapes these populations at the recruit rather than the adult stage by measuring predation on recruits at 2 rocky shores 100 m apart in a marine reserve, with no-take regulations. To explore the role of different guilds of predators, we used 7 treatments (fences, roofs, cages plus appropriate controls) to discriminate between the effects of benthic and pelagic predators. Factorial ANOVA showed that both types of predation had strong effects. Juvenile mussels were quickly removed in treatments with a roof (which excluded pelagic predators), a fence (which excluded benthic predators), and unprotected controls exposed to all predators. Treatments that excluded only one guild of predators were significantly different from the full cage, but not different from each other or the fully exposed control treatment. Thus, benthic and pelagic predators had similar effects that were not significantly different, suggesting that interference may occur between predator guilds. Under experimental conditions, the combined pressure of benthic and pelagic predators resulted in high mortality that may have top-down effects on mussel populations through recruit rather than adult predation.

KEY WORDS: Intertidal · Mussels · Predator exclusion experiment · South Africa · Marine protected areas · MPA · Top-down regulation

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INTRODUCTION

While abiotic conditions set a framework of those species that are capable of living in a particular place (McQuaid & Branch 1984), the recent upsurge in biological invasions, particularly in the marine environment (Ruiz et al. 1997, Rilov & Crooks 2009), has highlighted how critical it is that organisms are able to reach and colonise a habitat. Given a suite of species that can reach and survive in a particular marine benthic habitat, the realised community is often strongly shaped by biological interactions including competition for space (Griffiths & Hockey 1987), facilitation (Bruno et al. 2003), and predation (Paine 1969). The

balance among these various forces remains unclear, however (e.g. Stokstad 2009), and it seems likely that it will differ from place to place.

In temperate littoral systems, mussels are ubiquitous habitat-forming animals (Gosling 1992), and in many parts of the world they risk predation below a given tidal height, but find refuge higher on the shore (Kitching et al. 1959, Connell 1972, Robles et al. 2009). Thus, the physical limitations of the predator can set the lower boundary for spatial refuge (Kitching et al. 1959, Muntz et al. 1965, Paine 1974, 1977, Saier 2001). Predation is considered to be important to mussel communities, not only because it is a primary mechanism that accounts for patterns in their distribution and abun-

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dance, but also because the coexistence dynamics between predator and prey (Holt 1977, Power 1992) help to maintain local diversity; for example by preventing habitat monopolisation (Petraitis et al. 1989, Robles & Desharnais 2002). Processes, including predation, that maintain spatial patterns in mussel populations largely work on early life stages, and occasionally large individuals can be found beyond the general lower limits of distribution. Refuge in size can occur when mussels are able to reach a size beyond the feeding capabilities of the predator. This may occur when predator densities are low (Paine 1974) due to environmental stressors or stochastic population fluctuations. Escape from predation can also occur in topographically complex habitats where the settlement site is not accessible to the predator (e.g. rock crevices; Menge & Lubchenco 1981).

Juvenile mussels are often highly susceptible to predation and their small, thin shells make them a preferred prey of many predators (Harger 1970, 1972, Elnor 1978). For example, Landenberger (1968) showed that small (<13 mm) mussels were preferentially selected as prey in laboratory experiments by the predatory starfish *Pisaster* spp. Thus, Dare (1976) found 74% mortality in 25 mm, and 98% mortality in 50 mm shell length mussels, and the classic work by Paine (1974) showed that removal of *Pisaster ochraceus* resulted in a downshore shift in the distribution of *Mytilus californianus*, along with an increase in the abundance of small mussels (<13 mm).

Intertidal predators of mussels can be pelagic, benthic, or terrestrial. During high tide, intertidal and subtidal predators include seastars (Paine 1969, 1974, Dolmer 1998), lobsters (Pollock 1979, Robles 1997, Robles et al. 2009), gastropods (Dye 1991, Gutiérrez & Gallardo 1999), crabs (Menge et al. 1986, Caro et al. 2008), fish (Rilov & Schiel 2006a), and octopuses (Boyle & Rodhouse 2005). During low tide, terrestrial species can gain access to mussel beds. These include birds (Siegfried 1977, Frank 1982, Kurle et al. 2008), mammals (Navarrete & Castilla 1993, Stapp & Polis 2003), and insects (Robles & Cubit 1982), but generally only birds exert strong predation pressure (Goss-Custard 1980). Thus, predation is known to be a key biological effect controlling mussel populations in both northern (e.g. the starfish *Pisaster ochraceus* in California [Paine 1969] and birds on the Aleutian Islands [Kurle et al. 2008]) and southern (e.g. the gastropod *Concholepas concholepas* in Chile; Palmer 1984, Dye 1991) temperate regions.

All of these predators have different effects on mussel populations and their presence is strongly affected by the local habitat availability (e.g. adjacent subtidal reefs; Rilov & Schiel 2006a,b) and hydrodynamics (Menge 1978). The effects of biological interactions

such as predation are generally studied at rather small scales (Kurle et al. 2008), and, because interactions between predator and prey can differ in time and space, generalisation from small to large scales can create important errors in interpretation (Edwards et al. 1982). Recent studies have emphasised the variability that may exist within geographic regions. In New Zealand, Menge et al. (1999) found that the rates of grazing, predation, prey recruitment, and mussel growth were significantly different between the east and west coasts. They postulated that this was due to the different oceanographic conditions between the coasts, particularly the effects of upwelling. Their study mainly focused on benthic predators such as whelks and sea stars. The effects of more mobile fish and crab predators on the 2 coasts of New Zealand were examined by Rilov & Schiel (2006a,b) who found that these varied with prey size and neighbouring habitats.

The situation appears to be quite different in South Africa, where predation can be a critical determinant of subtidal community structure, even driving the existence of alternative stable states (Penney & Griffiths 1984, Barkai & McQuaid 1988). In contrast, predation on intertidal mussels is believed to be a relatively minor cause of mussel mortality, compared to competition for space (Griffiths & Hockey 1987), but studies of mussel predators there have focussed on adult mussels (e.g. Griffiths & Seiderer 1980, C. L. Griffiths 1981, R. J. Griffiths 1981, McQuaid 1994).

There is a very strong biogeographic trend in mussel recruitment around the coast of South Africa (Harris et al. 1998), and along much of the coast mussel populations are believed to be recruitment-limited (McQuaid & Phillips 2006, McQuaid & Lindsay 2007, Bownes & McQuaid 2009). In such situations it is likely that predation on earlier life stages may be critical to population regulation (G. Rilov et al. unpubl. data), even if predation on adults is limited. Here we examine predation of mussel recruits in South Africa under field conditions, distinguishing the effects of different types of predation (benthic or pelagic) by using manipulative experimentation. Because the study was conducted in a marine reserve where fishing is prohibited, we predicted that the effects of pelagic predators would be particularly strong and exceed those of benthic predators.

MATERIALS AND METHODS

Study site. Field work was conducted in Tsitsikamma National Park on the south coast of South Africa (34° 01' 18" S, 23° 53' 44" E; Fig. 1). The shore is steeply shelving and moderately wave-exposed. The substratum consists of low-relief rock (shale) and partially

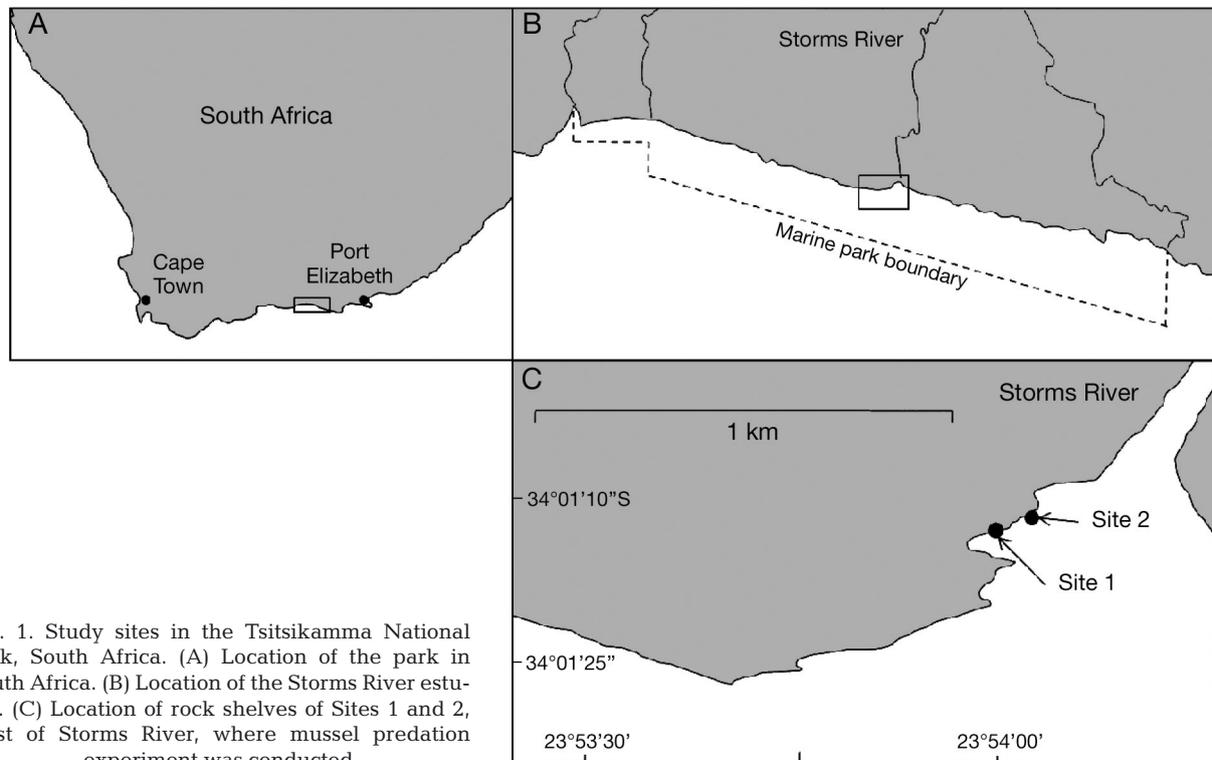


Fig. 1. Study sites in the Tsitsikamma National Park, South Africa. (A) Location of the park in South Africa. (B) Location of the Storms River estuary. (C) Location of rock shelves of Sites 1 and 2, west of Storms River, where mussel predation experiment was conducted

unconsolidated sediments with steep, rocky ridges extending from the shore line (Martin & Flemming 1986).

The Tsitsikamma National Park, established in 1964, includes the oldest marine reserve in the country (extending 72 km alongshore and 5 km offshore; Fig. 1), within which no offshore or onshore fishing is permitted (Tinley et al. 1996). The 2 sites used (Site 1 and Site 2; Fig. 1) are relatively sheltered from wave action by a rocky headland approximately 600 m to the south.

Collection and mounting. Juvenile mussels (a mix of the invasive species *Mytilus galloprovincialis* and the indigenous *Perna perna*) were collected from Plettenberg Bay, 50 km west of the study site, during spring low tides in July 2009. Although this introduces the possibility of species-specific differences in vulnerability to predators, we believe that this is unlikely to have affected the results, as care was taken to ensure that species proportions were similar among treatments and sites. Mussels were transported to a field laboratory 3 km away in a bucket with seawater-dampened paper toweling to reduce desiccation.

Sorting and mounting of mussels occurred immediately after collection. Mussels of ~2 to 15 mm were used for the experiment and were kept in aerated seawater during sorting. Small and medium mussels were haphazardly selected, dried with paper toweling, and 25 individuals were attached in a circular pattern onto

individual experimental tiles using Pratley's Steel Quickset epoxy as described by Lopez et al (2010). The tiles were $5 \times 5 \times 1$ cm pieces of plastic that had been scoured on the application side and covered with a layer of epoxy approximately 2 mm thick. One valve of each mussel was applied to the epoxy leaving the other valve free to allow gaping, feeding, and secretion of byssal threads for natural attachment. Tiles with attached mussels were allowed to air dry and set for 30 min, and then returned to aerated seawater. Tiles with mussels were attached to the shore using a screw through a pre-drilled hole in the centre during low tides on 20 July 2009 at Site 1 and the next day at Site 2.

Experimental design and treatments. To separate the effects of different types of predators, tiles with mussels were exposed to 3 types of caged treatments, replicated 5 times within each of the 2 sites. To permit only benthic predators, a roof treatment was used to exclude predators that would come from above such as birds and fish (Fig. 2C). To prevent benthic predation and allow only predation from above, a fence treatment was used (Fig. 2A). The third treatment was a full cage to eliminate all predation and to account for other causes of mortality (handling-induced mortality, detachment caused by wave action, desiccation, etc.; Fig. 2B). Procedural controls were used for each of the treatments to account for any artefacts of treatment. Procedural controls consisted of identical treatments

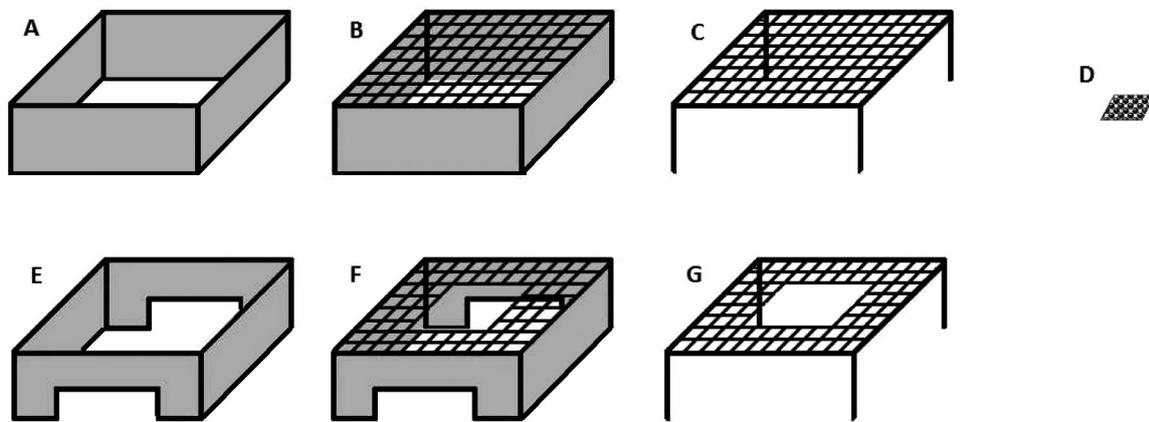


Fig. 2. Treatments used for the experimental exclusion of mussel predators. (A) Fence with no roof for exclusion of benthic predators. (B) Full cage for complete predator exclusion. (C) Roof for pelagic predator exclusion. (D) Control (unprotected tile). (E) Procedural control fence. (F) Procedural control full cage. (G) Procedural control roof. Tiles were screwed to the substratum in the centre of each treatment. Grey area indicates plastic side fencing

with large holes in the mesh of the sides or roof (Fig. 2E,F,G). Procedural controls were replicated 3 times within each site. Five control tiles were used at each site and were completely unprotected (Fig. 2D).

The cage frames were square (15×15 cm), 5 cm high, made of 6 mm steel rods. The sides were made of soft green plastic mesh with 0.25 cm^2 mesh size. The side mesh was wrapped around the bottom of the frames bending towards the centre of the cage floor to prevent animals from crawling underneath. The roofs were made of steel, 1.2 cm^2 mesh size. The procedural controls for fences had holes of 6×3 cm centred on each of 2 sides, reaching the substratum. The roof of the procedural controls had holes 7×7 cm in the centre. Roofs and fences were attached to frames with plastic cable ties.

The location of each cage, within the mussel zone where the 2 species of mussel co-exist, was scrubbed clean; cages and tiles were attached to the substratum using 60×8 mm plastic anchors with a brass screw at each corner. Control sites were drilled with 4 holes with anchors and screws representing the corners of an absent cage. Treatments were allocated to plots haphazardly within the mussel beds.

Sampling. Because of limited mortality during tile preparation (<5%), the living mussels on each tile were counted on deployment to standardise starting densities. Surviving mussels were then counted each day for 13 d during daytime low tides. Mussels were considered alive if still intact and attached to a tile. Individuals were counted as dead when (1) completely missing, (2) only one valve remained, or (3) gaping with no tissue between the valves.

Estimates of mussel and predator densities. Mussel cover and the abundance of whelks were estimated from 25 haphazard photographic quadrats of 861 cm^2

(33.5×25.2 cm) using a camera positioned 30 cm above the substratum with an aluminium rod. Fish abundances were estimated by snorkelling (using continuous, consistent fin kicks) along 100 m subtidal transects. Transects were conducted at both sites on 6 d during high tide. All pelagic fish and octopus within the range of visibility (generally 4 to 6 m) were recorded (Thresher & Gunn 1986). Visibility differed among days, but not between sites.

Intertidal line transects were used to determine the abundance of crabs at each site. Sampling was done 6 times, during night-time low tides, as crabs are generally more active during the night (Burrows et al. 1999). One 10 m transect was run perpendicular to the shore at each site. Crabs within 1 m to the right of the tape (measured using a 1 m aluminium rod) were counted, giving a sampling area of 10 m^2 .

Data analysis. Mussel survival data were converted to %, as tiles had different starting numbers. Percentages were arcsine-square-root transformed to conform to the assumptions of normality and homogeneity (Zar 1999). A time-dependent sampling design can lend itself to a repeated measures ANOVA, but there may be problems of (1) increased chance of Type I error because of non-independence, (2) separation of variability in the error from variables, and (3) problems with interpretation when an interaction includes a time factor (Underwood 1997). Factorial ANOVAs were therefore used to assess the effects of site (2 levels) and treatment (7 levels) on survival of mussels, for each day separately. Both site and treatment were fixed, orthogonal factors. Homogeneity of variance was verified by Levene's test. A Fisher's least significant difference (LSD) post hoc test was used to identify which treatment caused statistical differences.

Procedural controls (procedural fence, procedural roof, procedural full cage) were also tested against the control using a factorial ANOVA to check for artefacts of the cages. Adult mussel cover was arcsine-square-root transformed and analysed using 1-way ANOVA, with site as a fixed factor. Fish and octopus abundances were analysed with Wilcoxon's paired signed-ranks non-parametric test to account for differences in visibility from day to day. Crab and whelk abundances were analysed using a Mann-Whitney non-parametric *U*-test. Where variances showed heteroscedasticity, the results were interpreted conservatively or not at all, depending on the alpha level. All statistical tests were completed with StatSoft Statistica 6.

RESULTS

Mussel survival

The main focus of the present study was to test the effect of the primary treatments (fence, roof, and full cage) in relation to the controls. Survival in the procedural controls never differed from that in the control (Table 1) indicating no caging artefacts and allowing to focus on treatment effects (Fig. 3).

At the end of 13 d there was >85% survival of mussels at both sites in treatments that excluded all preda-

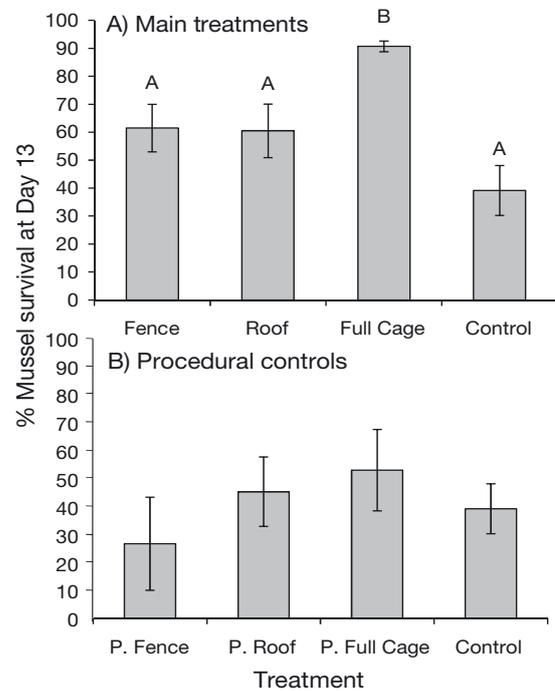


Fig. 3. Mussel survival (mean ± SE across both sites, %) at Day 13 with (A) main treatments (fence, roof, full cage) and control and (B) procedural controls (procedural fence, procedural roof, procedural full cage) and control. Letters in panel A indicate homogeneous subgroups (indicated by Fisher's least significant difference [LSD]; treatments carrying the same letter are not significantly different), there were no significant differences in panel B (see Tables 1 & 2)

Table 1. Factorial 2-way ANOVA of procedural controls (fence, roof, full cage) and control at Site 1 and Site 2 on Days 2, 8, and 13. Data were arcsine-square-root transformed. Significant p-values at $\alpha < 0.05$ are indicated in **bold**

Effect	SS	df	MS	F	p
Day 2					
Site	0.661	1	0.661	11.458	0.002
Treatment	0.405	3	0.135	2.337	0.104
Site × Treatment	0.105	3	0.035	0.606	0.619
Error	1.154	20	0.058		
Fishers's Site					2 < 1
Levene's					0.011
Day 8					
Site	0.535	1	0.535	7.375	0.013
Treatment	0.209	3	0.070	0.961	0.430
Site × Treatment	0.170	3	0.057	0.784	0.517
Error	1.450	20	0.072		
Fishers's Site					2 < 1
Levene's					0.186
Day 13					
Site	0.054	1	0.054	0.451	0.509
Treatment	0.252	3	0.084	0.708	0.560
Site × Treatment	0.087	3	0.029	0.246	0.863
Error	2.370	20	0.119		
Levene's					0.471

tors (full cage; Fig 3). Mussels that were exposed to all predators (control) had <50% survival. The treatments that were exposed to partial predation (roof, fence) showed intermediate survival rates (roof and fence >50%), and constituted one homogeneous group with the control in the post hoc analysis (Fig. 3). ANOVA results show that by Day 1, the effects of site, treatment, and the interaction between site and treatment were significant (Site: $F_{1,32} = 6.489$, $p = 0.015$; Treatment: $F_{3,32} = 9.839$, $p < 0.001$; Site × Treatment: $F_{3,32} = 3.795$, $p = 0.019$). Both the site and interaction effects ceased by Day 9 ($p > 0.20$ for both), while the treatment effect continued through the rest of the experiment (Table 2). After Day 7, the results remained consistent. Mortality was consistently significantly lower in the full cage and equal in treatments with fences, roofs, or no protection (Fig. 4).

Table 2. Mussel survival. ANOVA of main treatments and control on Sites 1 and 2 of Days 1 through 13. Data was arcsine-square-root transformed to reach normality. Significance is at $\alpha < 0.05$ and is indicated in **bold**. Fishers's least significant difference (LSD) is given to identify homogenous groups for significant ANOVA effects. na: post hoc could not identify homogenous groups. FC: full cage; F: fence; R: roof; C: control. Levene's test for homogeneity is given for the interaction

Effect	SS	df	MS	F	p
Day 2					
Site	0.454	1	0.454	16.416	< 0.001
Treatment	1.126	3	0.375	13.577	< 0.001
Site × Treatment	0.425	3	0.142	5.132	< 0.005
Error	0.884	32	0.028		
Fisher's Site					2 < 1
Fisher's Treatment				FC < F = R = C	
Fisher's S × T					na
Levene's					0.080
Day 8					
Site	10.119	1	0.311	6.102	0.019
Treatment	1.424	3	0.475	9.325	< 0.001
Site × Treatment	0.152	3	0.051	0.995	0.408
Error	1.629	32	0.051		
Fisher's Site					2 < 1
Fisher's Treatment				FC < F = R = C	
Levene's					0.335
Day 13					
Site	0.000	1	0.000	0.007	0.933
Treatment	1.913	3	0.638	10.278	< 0.001
Site × Treatment	0.301	3	0.100	1.616	0.205
Error	1.985	32	0.062		
Fisher's Treatment				FC < C = F = R	
Levene's					0.110

Estimates of benthic and pelagic organisms

Both sites were characterised by high levels of bare rock (>30%). On average, mussel cover was around 20%.

Whelks were highly visible and averaged about one per photograph (861 cm²) at both sites, with no significant differences in abundance between sites (Mann-Whitney *U*-test = 984.0, $N_1 = N_2 = 50$, $p = 0.055$). Whelk species include the common dogwhelk *Nucella dubia*, ridged burnupena *Burnupena cincta*, and *Burnupena lagenaria*. No quantification was made of species due to the difficulty of identifying species from the photographs.

Crabs were active and abundant during the night (~25 ind. 10 m⁻²; Fig. 5). Species present were the Cape rock crab *Plagusia chabrus* and Natal rock crab *Grapsus grapsus tenuicrustatus*. There was no difference in abundance between the sites (Mann-Whitney *U*-test = 23.5, $N_1 = N_2 = 7$, $p = 0.898$).

Eight species of fishes were recorded at each site, and only one of these was a regular mussel feeder, the musselcracker *Sparodon durbanensis* (*S. durbanensis* was

only present at Site 2, with one individual being seen on 3 different days). Blacktail *Diplodus sargas capensis*, strepie *Sarpa salpa*, and steentjie *Spondyllosoma emarginatum* were seen in large schools with *S. salpa* reaching schools of more than 300 individuals. The two-tone fingerfin *Chirodactylus brachydactylus* is not a schooling species, but it was regularly seen retreating to crevices. Janbruins *Gymnocrotaphus curvidens*, romans *Chrysolephus laticeps*, and the puffer evileye blassop *Amblyrhynchotes honckenii* were also observed (Fig. 5). The octopus *Octopus vulgaris* was mostly seen at Site 2 and was the only species other than *C. laticeps* that differed significantly in numbers between the sites (Table 3). On 2 days the eagle ray *Myliobatis aquila* was seen in high numbers ($n = 11$, Day 10; $n = 4$, Day 11), but was not present on any other occasions.

DISCUSSION

This was an experimental situation in which mussels would be expected to suffer unrealistically high levels of predation as they were offered to predators almost literally on a plate. Heavy

settlement of mussel spat may result in such carpets of juvenile mussels (C. D. McQuaid pers. obs.), but normally they occur among adults where they are protected from predators and buffered against environmental extremes. Consequently, the levels of mortality recorded here are excessively high, even for caged mussels. The results indicate that mortality of exposed juvenile mussels through predation is rapid and high (ca. 50% in 13 d). We tested the effects of different predator guilds (sensu Simberloff & Dayan 1991), arbitrarily dividing them into benthic (excluded by fences) and pelagic (excluded by roofs) predators. Elsewhere, a particular guild of predators often dominates; for example the starfish *Pisaster ochraceus* in California, the whelk *Concholepas concholepas* in Chile, and fish in New Zealand. In contrast, we found that predation on juvenile mussels was well balanced between benthic and pelagic predators. This was unexpected as the experiments were undertaken in a marine reserve, where fish populations are protected against fishing and are particularly high for this coastline (Roberts & Polunin 1991, Götz et al. 2008), so that higher rates of fish predation were anticipated.

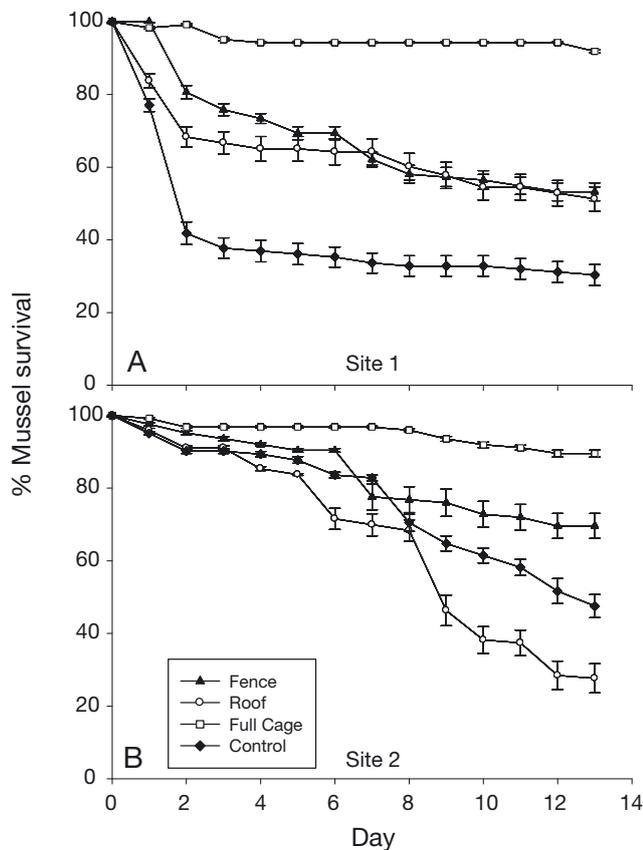


Fig. 4. Mussel survival experiment at 2 sites in Tsitsikamma National Park, South Africa, from July 20 to August 4, 2009. Survival (mean \pm SE) of mussels with full cage (\square), roof (\circ), fence (\blacktriangle), and control (\blacklozenge) treatments were tested to separate benthic and pelagic predation. (A) Site 1, (B) Site 2

Many of the primary mussel predators found in other parts of the world, or even other parts of the country, are not common or even present within the study area. For example, rock lobsters are voracious mussel predators in South Africa (Pollock 1979, Griffiths & Seiderer 1980). The west-coast species *Jasus lalandii* does not extend this far east, while the east-coast rock lobster *Panulirus homarus* does not extend this far west (Berry 1974). A third species of lobster, *P. gilchristi*, is found in the study area, but only in deep waters (Branch et al. 1994). Likewise, predatory starfish, which are significant predators on the west coast (Penney & Griffiths 1984), were not observed. Of the potential predators that were observed, crabs and whelks appear to be relatively unimportant. Two species of crabs (*Plagusia chabrus* and *Grapsus grapsus tenuicrustatus*) were common and occurred at relatively high abundances. Rilov & Schiel (2006a) found ~5 crabs per pot laid out over night, while we recorded 25 per 10 m² transect. Both our species are primarily herbivores but have mixed diets that can include sedentary animals (Griffin 1971, Branch et al. 1994, Edgar 2000). Intraspecific

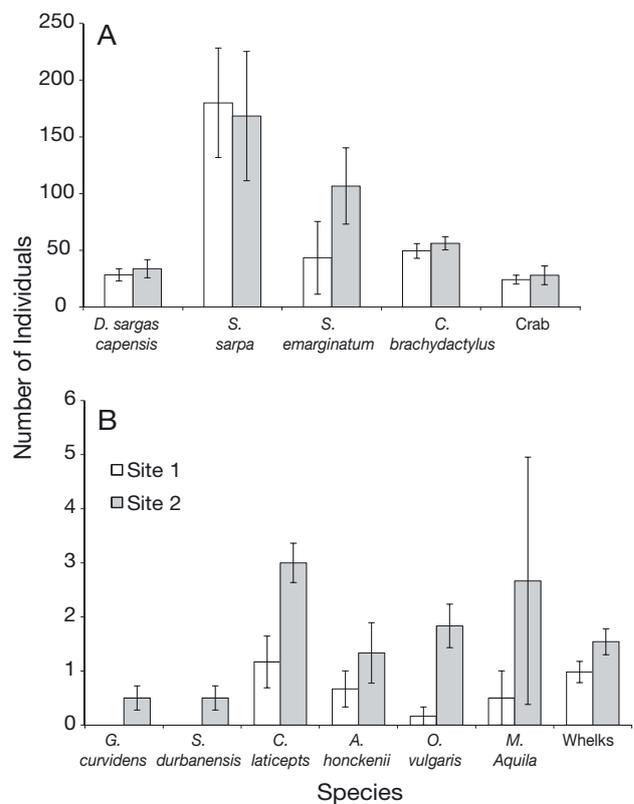


Fig. 5. Mean (\pm SE) number of (A) high abundance blacktail *Diplodus sargas capensis*, strepie *Sarpa salpa*, steentjie *Spondyliosoma emarginatum*, twotone fingerfin *Chirodactylus brachydactylus*, crab *Grapsus grapsus tenuicrustatus* and *Plagusia chabrus*, and (B) low abundance janbruins *Gymnocrotaphus curvidens*, musselcracker *Sparodon durbanensis*, roman *Chrysoblephus laticeps*, evileye blassop *Amblyrhynchotes honckenii*, octopus *Octopus vulgaris*, eagle ray *Myliobatis aquila*, and whelks *Nucella dubia*, *Burnupena cincta*, and *Burnupena lagenaria*. Values for fish and octopus: number of individuals per 15 m swim over 6 different days; for crab: number of individuals per 10 m² over 6 days; for whelks: number of individuals per 861 cm²

Table 3. Wilcoxon signed-ranks test on individual fish species data collected at 2 sites over 6 (n = 6) d. Data were collected on Days 1, 4, 10, 11, 12, and 13 during the daytime high tide. Significant differences (p < 0.05) in abundance between the 2 sites are indicated in **bold**. T: test-statistic for the Wilcoxon signed-ranks test; Z: standard values of the normal distribution

Species	T	Z	p
<i>Diplodus sargas capensis</i>	6.00	0.943	0.345
<i>Sarpa salpa</i>	9.00	0.313	0.753
<i>Spondyliosoma emarginatum</i>	3.50	1.468	0.142
<i>Gymnocrotaphus curvidens</i>	0.00	1.604	0.109
<i>Sparodon durbanensis</i>	0.00	1.604	0.109
<i>Chrysoblephus laticeps</i>	0.00	2.023	0.043
<i>Chirodactylus brachydactylus</i>	4.00	1.363	0.173
<i>Amblyrhynchotes honckenii</i>	1.50	1.278	0.201
<i>Octopus vulgaris</i>	0.00	2.201	0.028

competition at high densities could lead to feeding on juvenile mussels (Smallegange et al. 2006), but this seems unlikely. Whelks are important mussel predators on the west coast of South Africa (Wickens & Griffiths 1985), and *Nucella* spp. are a mussel predator both in Europe (Hughes & Dunkin 1984) and in South Africa (Wickens & Griffiths 1985). Some *Burnupena* spp. are predators of barnacles, mussels, and *Littorina* spp. (McQuaid 1982, 1985, Barkai & McQuaid 1988), but the species found in the present study are believed to be scavengers (Branch et al. 1994). The manner in which mussels were removed often entailed the loss of all individuals within a treatment from one day to the next, while mussel predation by whelks would be slow, with gradual removal of prey. Furthermore, though whelk feeding normally continues during emersion (McQuaid 1985, Burrows & Hughes 1989), whelk predation was never observed during sampling at low tide.

Of the mobile, subtidal species identified during snorkelling, only 2 are known mussel predators, the musselcracker *Sparodon durbanensis* and *Octopus vulgaris*. Rilov & Schiel (2006a,b) found that the effect of fish predation on mussels was significantly higher at sites with a subtidal reef close to the mussel bed than at sites where the adjacent substratum was sandy. Both our sites extended from intertidal rock platforms into the subtidal, offering high structural complexity and suitable habitat for both fish and octopus (Smale & Buchan 1981, Buxton & Clarke 1991). Buxton & Clarke (1991) did not find molluscs to be the main constituent of musselcracker diet, but the frequency of mussels within guts was high at all fish life stages, with an increase in prey size during later life stages. This suggests that mussels used in the present study might have been taken by younger fish. *O. vulgaris* is an important mussel predator on the coast of South Africa (Buchan & Smale 1981, Griffiths & Hockey 1987). A limitation of our study is that the roof treatment may have been ineffective against octopuses. Octopuses can forage by entering crevices only slightly bigger than their beak (Mather 1991), so that small individuals may have been able to fit or reach below the roofs. Smale & Buchan (1981) found that *Perna perna* was the main constituent of the diet of *O. vulgaris*, with mussels making up to 73% of the diet of octopuses and octopus densities of 1 per 12 × 12 m quadrat. Relatively few octopuses were seen during 15 min swims in the present study, but our counts may have been underestimated given the cryptic behaviour of octopuses. Furthermore, remnants of cracked and drilled mussel shells were common (J. G. Plass-Johnson pers. obs.) indicating the possible 'drilling' technique seen with octopuses (McQuaid 1994), or the 'cracking' technique of the Sparidae family (Fernandez & Motta 1997). The

primary predators here seem to have been subtidal, highly mobile, and capable of removing many mussel recruits in a single session. Both octopus and musselcracker could produce the patterns seen here.

The present study explored the effects of different guilds of predators on mussels in a context of potentially high abundances of predators (i.e. within a marine protected area); but while a single species of predator can be critical in other parts of the world, our results indicate the importance of a combined effect of multiple types of predation. Experimental designs and analysis should consider the interactive effects of different predators (Soluk & Collins 1988), as predators will rarely have the additive or linear effects on prey that are often tested (i.e. proportion of mortality from predator A + proportion of mortality from predator B = full mortality). The interaction of predators can limit or facilitate effects on prey causing non-linear relationships (Billick & Case 1994). Sih et al. (1998) explored the complications of studies with multiple predator effects. Interactions (either inter- or intra-specific) among predators can be affected by both predator and prey densities and by their behaviour. Multiple predators can have risk-enhancing or risk-reducing behaviours that cause higher or lower predation on the prey, and this cannot be predicted based on knowledge of each predator separately. Often multiple predator species are able to interfere with each other, resulting in risk reduction for a shared prey species (Peckarsky 1991, Griffen & Byers 2006). In contrast, higher prey densities can reduce predator interactions, changing per capita predation (Abrams & Ginzburg 2000). Predator interactions can also change on different time scales. For example, some predators, such as whelks and octopus, can continue foraging during emersion, at least at night (J. G. Plass-Johnson pers. obs.), while others, such as fish, are constrained by the tide. On a different time scale of days, the quality of the experimental plots as feeding patches would have declined as the number of mussels on the plates was reduced and this is likely to affect predator behaviour and interactions. This may also explain why the expected effects of large fish populations did not occur, though this would need to be tested through direct experimentation.

Due to the restrictions intrinsic to our sampling method, elucidation of the exact predators is not possible, although this does provide a starting point for studies that target organisms feeding specifically on juvenile mussels. Also, it is impossible to extrapolate from the rates of predator-driven mortality observed here to natural rates; but the fact that we found juvenile mussels surviving for over 13 d while completely exposed to predators suggests that natural rates will be low compared to other parts of the world, not only trop-

ical systems (e.g. Menge & Lubchenco 1981), but also in other temperate areas (e.g. Marsh 1986, whose measurements of bird predation included effects on mussel recruits, and Menge et al. 2002, who measured predation on adult mussels (Lopez et al 2010). This accords with the findings for adult mussels in South Africa (Griffiths & Hockey 1987) and adds to the idea that mussel populations are not controlled from the top down by predation, though its effect can be important (the present study and Rilov et al. unpubl. data). This contrasts with other parts of the world and has implications for population regulation in this important habitat engineer. Even weak biological interactions can have powerful effects on community structure (Berlow 1999). Nevertheless, given the high levels of biological diversity and endemism of marine communities in South Africa (Roberts et al. 2002), their age compared to the younger intertidal communities of the north Atlantic, where predation can have a major effect on the utilisation of space (e.g. Menge 1976) and the enormous predation pressure that can be exerted in adjacent subtidal systems in South Africa (Barkai & McQuaid 1988, Barkai et al. 1996), it is surprising that guilds of intertidal predators have not evolved that are capable of exerting stronger top-down influence.

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