

Complex equilibria in the maintenance of boundaries: experiments with mussel beds

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Abstract. Stationary boundaries of sedentary species may belie dynamic processes that form them. Our aim was to test an implication of an evolving body of theory, that such boundaries are manifestations of complex regulatory dynamics.

On rocky shores of British Columbia, large-scale field experiments altered the densities of predatory sea stars (*Pisaster ochraceus*), causing shifts in the location of the lower vertical boundaries of their prey, sea mussels (*Mytilus californianus*). While control mussel beds remained unchanged, experimental reductions of sea star densities caused the downward extension of the lower boundaries, and experimental increases in sea stars densities caused the upward recession of the lower boundary well into the zone presumed to be a spatial refuge from predation. Cleared plots prepared within the initial boundaries were recolonized to varying degrees, depending on predator densities. After 30 months, plots on sea star removal sites showed high densities of adult mussels, control plots showed intermediate densities, and sea star addition plots showed only a sparse cover of alternative prey. Observations by divers at high tide showed that as small prey were depleted progressively from removal, to control, to addition sites, correspondingly larger mussels were attacked, including very large individuals comprising the lower boundary of addition sites.

The findings contradict classic theory of zonation based on static prey refuges and support an alternative theory in which boundaries are maintained by complex, spatially structured equilibria.

Key words: Barkley Sound, British Columbia, Canada; equilibrium; intertidal zonation; *Mytilus* sp.; *Pisaster* sp.; population limitation; predation; refuges; sea mussels; sea stars; size-dependent predation.

INTRODUCTION

Between the highest and lowest reaches of the tides on wave-washed rocky shores occur distinct horizontal zones of barnacles, mussels, algae, and other sedentary organisms (Lewis 1964, Stephenson and Stephenson 1972, Harley 2007). The causes of the vivid zonation patterns are one of the oldest and most intensively studied problems in the ecological literature, because the work bears on the more general problem of the spatial limitation of populations. The accepted explanation maintains that dense populations of sedentary species form in spatial refuges above the reach of natural enemies: superior competitors or predators (Connell 1961, 1970, 1975, Paine 1974, 1976). Below the lower boundary, prey may occasionally be passed over by predators long enough to reach invulnerable sizes, termed an age-size refuge, if the prey species has the

biological capacity to do so. The concept of refuges has been widely applied to communities outside the rocky shore environment (Taylor 1984, Kerfoot and Sih 1987).

The issue of population limitation in this system hinges on the mechanisms of the lower boundary. At relatively low shore levels, durations of tidal submergence and hence time for the settlement of the larvae and food intake by these filter-feeding organisms are prolonged. Episodes of elevated settlement followed by rapid growth (Dehnel 1956, Robles et al. 1995, Garza 2005) generate the potential for explosive changes in mussel biomass and location of the lower boundary. The upper boundary is believed to be set by physical stresses incurred by prolonged periods of tidal emersion at high shore levels. Here settlement and growth rates are low, and the potential for change is less.

That zones represent spatial refuges from predators was established in experimental studies of mussel and barnacle populations on wave-beaten shores of the Pacific Northwest (Connell 1970, Paine 1974). In the case of the mussels (*Mytilus californianus*), predatory sea stars (*Pisaster ochraceus*) are relatively intolerant of physical stresses (temperature or desiccation) during the prolonged tidal exposures high on the shore. Above some critical shore level predation is negligible, and the otherwise vulnerable juvenile mussels accumulate, eventually forming dense beds of adults in the spatial refuge

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from predation. A seminal field experiment provided evidence for the hypothesis (Paine 1974): removal of sea stars from the zone below a mussel bed caused the downward expansion of the mussel zone relative to a reference (control) bed nearby.

The depiction of the lower boundaries as marking the divide between a safe zone and an extirpation zone is a static vision of population limitation: the boundary is set by the tolerance of predators to physical stresses and, consequently, cannot respond to increases in predator density. As an alternative, Robles and Desharnais (2002) proposed that mussel bed boundaries involve dynamic equilibrium processes: the lower boundary arises in an interaction between spatially varying rates of prey production (mussel recruitment and growth) and loss (size-dependent predation). Therefore, boundary location can shift in response to both increases and decreases in predator abundance.

Recent empirical findings (Robles et al. 1995, Robles and Desharnais 2002) argue for dynamic processes. High-tide observations by divers show that sea stars move upward with rising tides, some reaching far above the lower boundaries before retreating with falling tides. The surveys also showed that the average height of foraging sea stars is correlated with site-to-site variation in heights of the lower boundaries. Thus it appears that while tidal exposure constrains sea star foraging, the lower boundary does not delimit an impenetrable refuge, and vertical foraging excursions respond to spatial variation in the zonation of the prey, albeit spatial variation that the predators themselves may influence.

The recent findings also suggest a relationship between size-dependent predation and small-scale variation in sea star densities. As the mussels and other sedentary prey grow larger, they become progressively more resistant to attack (Landenberger 1968, McClintock and Robnett 1986). Consequently, when a broad spectrum of prey is available, the bulk of the diet of foraging sea stars consists of young mussels and the adults of smaller sedentary species (Paine 1976, Robles et al. 1995). Experimental additions (Robles et al. 1995) of small, readily killed mussels along the lower boundary caused rapid increases in sea star abundance; experimental removals of small mussels caused rapid declines in sea star abundance. The lower boundaries, comprised in greatest mass of large mussels, remained intact during the experimentally induced shifts in small prey and predator abundances. Thus, it appeared that sea stars possess a kind of numerical response, moving toward or away from the beds and adjusting local population densities to the size frequencies of mussels at the level of the lower boundary.

If the maintenance of the lower boundary of mussel beds depends on dynamic size-structured processes, then blocking the sea stars' numerical response should alter the boundary. Specifically, sustained reduction of sea star densities should cause the accumulation of juveniles below and eventually the downward extension of the

lower boundary. Sustained augmentation of sea star densities should cause depletion of small prey, greater consumption of large mussels, and the eventual recession upwards of the lower boundary.

The original experimental finding (Paine 1974) that boundaries descend in response to sea star removal is consistent with both the refuge hypothesis and the complex equilibrium hypothesis. The second manipulation is, therefore, crucial: a significant upward recession of the lower boundary following increase of sea star densities would contradict the refuge hypothesis and constitute evidence for equilibrium processes.

METHODS

Study sites.—The experiments were conducted at five locations within a 10-km² area in Barkley Sound, British Columbia, Canada (48°53' N, 125°20' W). The locations were chosen to sample the range of wave exposures over which beds of *M. californianus* occur, from semi-protected sites with surrounding topographies that intercepted a portion of the approaching wave energy, to rocky headlands near the mouth of Barkley Sound and open to oceanic swells. This was done so that the experiments tested the generality of the conclusions over the complete range of wave exposures in which the mussel beds occur (Stephenson and Stephenson 1972, Robles and Desharnais 2002). The wave exposures of the experimental sites were judged by topography and multiple deployments of wave dynamometers (Bell and Denny 1994). Deployments were done in June 2005, after winter storm activity had subsided, when the wave-exposed sites could be reached safely and the dynamometers suffered less damage. Two pairs of dynamometers, 5 m apart at +2.1 m mean lower low water (MLLW; a conventional datum for shore level) and +2.7 m MLLW, were installed on every site. The maximum bottom flow speeds during three 24-h deployments were recorded. Even in the spring, maximum flow speeds ranged from a low of 2.86 ± 0.03 m/s (mean \pm SE) at the least exposed location to 15.00 ± 2.28 m/s at the fully wave-exposed location.

The extreme hydrodynamic forces generated during winter storms sometimes rip gaps in the mussel cover, disrupting boundaries. Both the refuge hypothesis and the alternative view pertain only to the persistent, undisturbed lengths of boundaries. Therefore, we assessed storm damage with observations and photo-mosaic records made in late spring (May–June), a period just after peak storm activity and before the seasonally varying sea star activity resumed sufficiently to affect the beds. At this time, storm-generated gaps in the otherwise continuous cover were easy to recognize, because all mussels were removed from the area of a gap and there was as yet little colonization of the bare rock by early succession species. One of the five locations was omitted from the analysis of boundary location because the entire lower boundary of the addition site and part of the control site mussel bed were obliterated by storms in

late winter to early spring 2006. For the remaining four locations, three of 70 sampling points (positions along the horizontal transects along the lower boundaries) used for the analysis of vertical location and one of 36 intercepts used for the analysis of along the surface coverage were omitted from the final analyses because they fell within storm-generated gaps.

Sea star manipulations.—Each location encompassed three topographically isolated rock benches with mussel beds 5–25 m long. One of three experimental conditions, repeated sea star additions, repeated removals, or no manipulation (control), was assigned by lot to each bench within a location. Sea stars were picked from the removal beds, including buffer zones extending at least 10 m past the ends of the beds. The sea stars from each removal site were translocated to the corresponding addition site. To insure a substantial increase in density, sea stars were also collected from randomly chosen sites away from the experimental locations and translocated to the addition sites. The manipulations were done from August 2004 to June 2007, at intervals no longer than a month, except for unpredictable periods in late fall and winter (December through March), when storm waves posed a risk to experimenters, and the sea stars were inactive (Paine 1974; C. D. Robles, *personal observation*).

A record of sea star densities was maintained. At each site, the number of sea stars in a fixed plot 10 m wide and bounded by the +3.0 m MLLW shore level above and the +1.2 m shore level below was tallied several times in midsummer (July–August) of each year, when the sea stars show peak activity and densities. The vertical range of the fixed plots sampled most of the sea stars active on a site. To estimate densities, a count was divided by the area of the plot, which varied from site to site depending on the slope of the shore. The plot extended well past the section of the lower boundary sampled in the mosaics. Once the manipulations were begun, counts were done just before the manipulation, so that they provide a conservative estimate of the effectiveness of the removals and additions.

Measurements of shifts in the lower boundary.—Changes in boundary location were documented with high-resolution photo-mosaics of the mussel beds. These provided records of the exact placement of sample points along the boundary, as well as the sizes of mussels and associated species in the vicinity of the boundary. By comparing mosaics taken of the same boundary over successive years, a detailed sequence of shifts in location and composition of the boundary could be observed. Digital component images $\sim 1 \times 1.5$ m with a resolution of < 2 mm were taken from the nadir perspective (directly overhead) at 1-m intervals on a transect line along the initial level of the lower boundary of each mussel bed. Details of the method appear in Blakeway et al. (2004).

To measure changes in the shore level (vertical displacement) of the boundaries, markers were placed

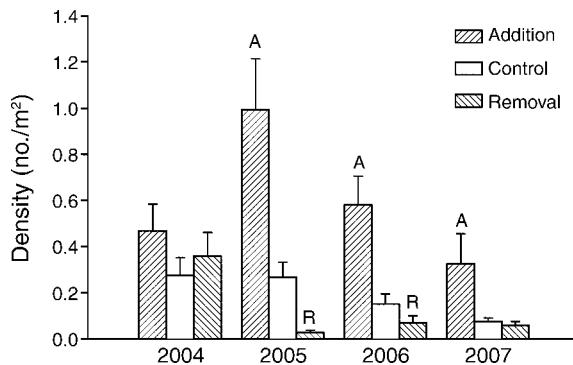


FIG. 1. Experimental changes in sea star (*Pisaster ochraceus*) densities. Densities of sea stars (mean + SE) are grouped by treatment from August 2004, immediately before the manipulations commenced, to July 2007, six weeks after the manipulations ceased. Letters indicate surveys in which mean densities for treatments differed from the control (A, addition vs. control; R, removal vs. control) as determined by Mann-Whitney *U* tests with the Bonferroni correction for procedure-wise error rate. The experiments were conducted at five locations within a 10-km² area in Barkley Sound, British Columbia, Canada.

at 1-m horizontal intervals along the span of the lower boundary. The exact vertical location (height above MLLW) of each marker was estimated with a precision surveying device, Total Station (Topcon, Tokyo, Japan). The constancy of the alongshore placement of the sample markers was confirmed by referring to the photo-mosaics. Estimates of the expansion seaward, or recession landward, of the boundary along the sloping rock shores were made by reference to a fixed baseline. At each site, a permanent horizontal baseline 4–5 m wide was set by installing steel bolts at the end points +3.0 m above MLLW. On a given sample date, transect lines were run vertically down the shore from the end points and center of the baseline past the lower boundary, and the distance along each transect from baseline to lower boundary was recorded. (The layout of sample lines is shown in Fig. 2a, b.) Comparisons of distances between sample dates provided estimates of the landward or seaward shift of the boundary over the sloping rock surface.

Cleared-plot experiment.—To further test the refuge hypothesis, we examined whether mussel bed recovery changed in response to the sea star manipulation. In the three treatments at each of four locations, a 1.25-m square plot was cleared just beyond the horizontal photo-mosaic segment (part of the mussel bed in the buffer zone). The low side of the plot fell along the original line of the lower boundary, so that the cleared area extended well into the otherwise continuous cover of mussels. Clearing the rock surface in the spring of the first year of the experiment duplicated natural gap formation, which occurs winter through spring when storm waves and wave-driven debris batter the shore (Dayton 1971, Paine and Levin 1981, Sousa 1984). The newly denuded rock surface is soon colonized by a

TABLE 1. Repeated-measures ANOVA of the densities of sea stars (*Pisaster ochraceus*) on the experimental sites.

Source	Sum of squares	df	MS	F	P	G-G	H-F
Between-subjects effects							
Treatment	2.441	2	1.221	11.043	0.002		
Error	1.327	12	0.111				
Within-subjects effects							
Time	0.197	2	0.099	3.556	0.044	0.046	0.044
Time × treatment	0.937	4	0.234	8.450	0.001	0.000	0.000
Error	0.665	24	0.028				

Notes: The within-subjects analysis produced significant treatment, time, and time × treatment effects. Abbreviations are: G-G, *P* value for Greenhouse-Geisser epsilon; H-F, *P* value for Huynh-Feldt epsilon. The experiments were conducted at five locations within a 10-km² area in Barkley Sound, British Columbia, Canada.

succession of algae, barnacle species, and the mussels, which eventually displace the other species. At regular intervals, a close-up photograph was taken of a 400-cm² quadrat in the center of each plot. Analyses are reported for the end of the experiment, 30 months after clearing. A comparison of cleared plots on the removal sites with those on the controls indicates the extent to which sea star predation limits the colonization of mussels and other prey in a zone presumed to be a refuge.

Sea star diets and size-dependent predation.—Divers collected sea stars and the prey on which they fed at high tide from the center of each experimental site of the locations used in the boundary analysis. The sizes of sea stars and the identities and sizes of their prey were recorded. Collections for the three sites within a location were made on successive days of an extreme high-tide series (“spring tides”) with the time of collection in a 90-min time window bracketing the predicted time of the peak high tide. Four locations were surveyed; the fifth, a severely storm-damaged location, was not surveyed. Results shown are for collections made in late summer for the year in which the boundary of the addition site within the particular location was observed to recede most rapidly.

Statistical analyses.—To test whether the sea star manipulation did indeed produce the required relative differences in densities, as assessed by the fixed plots, a repeated-measures ANOVA was run with treatments (addition, control, and removals) and time (samples before and after the start of manipulations) as the main effects. Post hoc tests (pairwise applications of the

Mann-Whitney *U* tests, with the Bonferroni correction for procedure-wise error rate) were used to determine which treatment densities differed from controls on a given survey date.

Changes in boundary location after three years of altered sea star densities were evaluated with mixed model two-way ANOVA, with either shift in boundary shore level (vertical difference between 2004 and 2007 levels) or run along the surface (difference in intercepts between 2004 and 2007) as the dependent variable, location as the random independent variable, and treatment as the fixed independent variable. For both shore level and run along the surface, the analysis was done using rank transformed data to meet the assumption of equal sample variances. Post hoc comparisons of the treatments vs. controls were made with Tukey hsd tests. Further explanation of statistical methods appears in Sokal and Rohlf (1981).

To analyze size-dependent predation on mussels, inferences were made using a mixed-model ANCOVA, with treatments as the fixed factor, location the random factor, sea star wet mass the covariate, and the upper quartile of lengths of mussels consumed for each site as the dependent variable. The variances for treatment were equal (Levine’s test, $F_{2,77} = 0.893$, $P = 0.414$). The complete model (including all possible interaction terms) was run and then nonsignificant interactions removed iteratively from three-way to two-way interactions, until the model of minimum sufficient number of terms was obtained (Sokal and Rohlf 1981). In the iterative process, the three-way and two-way interactions involv-

FIG. 2. Photographs of boundary changes on three of the experimental sites. (a, b) Panoramic view to seaward of a removal site (a) immediately before and (b) three years after the start of the experiment. The baseline appears in the foreground, and the transect lines run perpendicular. Orange cones mark the position of the original location of the lower boundary in panel (a). After three years (b) algae and other invertebrates have been replaced by a continuous cover of *Mytilus trossulus*. *Mytilus californianus* settled among its congener, and as they matured the lower boundary of adult *M. californianus* extended downward. (c, d) Sections of photo-mosaics from a sea star (*Pisaster ochraceus*) addition site (c) immediately before and (d) three years after the experiment began. Frames are ~1.3 m wide. The red dots mark the same point on the rock surface. Orange cones in panel (c) mark the initial location of lower boundary. (e–f) Close-ups of lower boundary on a wave-exposed addition site (e) immediately before and (f) three years after the start of the experiment. Examination of the photographic record showed that, over the course of the experiment, small mussels and other prey declined in abundance, the cover of large mussels fragmented, and the lower boundary of continuous mussel cover receded above the frame.



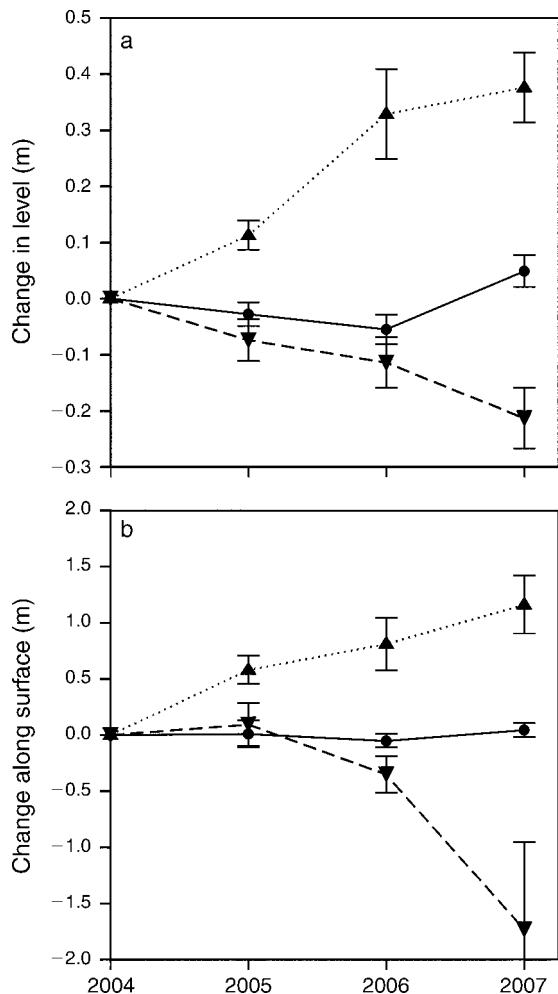


FIG. 3. Shifts in the boundaries of adult mussels (*Mytilus californianus*) after three years of altered sea star (*Pisaster ochraceus*) densities: (a) change in sea level and (b) change in run along the sloping rock surface (<0, distance in seaward movement; >0, distance in landward movement; mean \pm SE). The dotted line represents addition treatment; the solid line is the control; and the dashed line is the removal treatment.

ing the covariate (wet mass) were not significant, confirming the ANCOVA assumption of equal slopes. All analyses were run using SYSTAT 11.0 software (SPSS, Chicago, Illinois, USA).

RESULTS

Sea star densities.—The continual sea star translocations did produce sustained changes in sea star densities. Addition sites averaged threefold more sea stars than the controls. The removal treatment did not eliminate sea stars, but greatly diminished their densities relative to controls (Fig. 1). The repeated-measures ANOVA (Table 1) produced significant treatment, time, and time \times treatment effects. Post hoc tests confirmed that densities of both treatments diverged from controls (Fig. 1).

Shifts in the lower boundary.—Removal sites in the most wave-exposed locations developed dense covers of gooseneck barnacles (*Pollicipes polymerus*) or, in moderately wave-exposed locations, dense covers of the congener *M. trossulus* below the original levels of the lower boundaries (Fig. 2a, b). Juvenile *M. californianus* recruited into the cover of these other prey species and to the bare rock surface and then grew to reproductive sizes, ≥ 4.0 cm long. The statistical analysis was based on covers of adult *M. californianus*. At most sampling points, the lower boundary of adult *M. californianus* was abrupt and its location unambiguous. Where the boundary was more diffuse, its location was defined as the point at which covers dropped below 40%.

The sea star density manipulations caused obvious changes in the vertical level of the lower boundaries: a downward shift on the removal sites, recession upwards on the addition sites, and no significant change on control sites (Fig. 3a). All mussel beds showed these trends, regardless of their location, although the degree to which they were expressed appeared to vary somewhat among locations. The two-way mixed-model ANOVA confirmed a significant treatment effect and nonsignificant trends for location and treatment \times location terms (Table 2). Post hoc tests confirmed that shifts on treatment sites differed from the controls (Table 2).

Because the rock surfaces sloped gradually seaward, the vertical shifts in boundary level correspond to substantial changes in the extent of the beds (Figs. 2a–f and 3b, Table 3). A mussel bed on an addition site, which was the subject of prior studies (Robles et al. 1995) and thus had been observed since 1990 to maintain a stable boundary, was completely eliminated by the sea stars.

Cleared plot experiment.—After 30 months of succession, cleared plots on both control and removal sites were covered predominantly with relatively large prey, which included the mussels, whereas the addition plots supported only sparse covers of small prey (Fig. 4). The number of *M. californianus* of reproductive size (≥ 4 cm long) per 400 cm² were 0.0 \pm 0.0, 10.0 \pm 3.0, and 22.8 \pm 2.9 (mean \pm SE), respectively, for addition, control, and removal sites (Mann-Whitney *U* tests corrected for

TABLE 2. Mixed-model two-way ANOVA of vertical shifts in boundaries, with change from 2004 to 2007 as the dependent variable, location as the random independent variable, and treatment as the fixed independent variable.

Source	Sum of squares	df	MS	F	P
Treatment	13 849.71	2	6924.859	24.833	0.001
Location	787.346	3	262.449	1.650	0.188
Treatment \times location	1673.156	6	278.859	1.753	0.126
Error	8747.950	55	159.054		

Notes: Post hoc pairwise comparisons were significant (Tukey hsd, *P* = 0.001 and 0.001, for addition vs. control and removal vs. control, respectively). Multiple *R*² = 0.65.

TABLE 3. Mixed-model two-way ANOVA of change in extent of adult mussel cover, with change in run along the rock surface as the dependent variable, location as the random independent variable, and treatment as the fixed independent variable.

Source	Sum of squares	df	MS	F	P
Treatment	2208.67	2	1104.335	27.084	0.001
Location	137.876	3	45.959	1.803	0.176
Treatment \times location	244.649	6	40.775	1.600	0.194
Error	560.792	22	25.491		

Notes: Post hoc pairwise comparisons were significant (Tukey hsd, $P = 0.001$ and 0.003 , for addition vs. control and removal vs. control, respectively). Multiple $R^2 = 0.83$.

procedure-wise error rate, $P < 0.05$ for both addition vs. control and removal vs. control). Thus, while a cover of adult mussels became established on control and removal sites, predation prevented the establishment of mussels and severely limited the abundance of other species on addition sites above the original levels of the lower boundaries.

Sea star diets and size-dependent predation.—The records of diet were taken from the years of most rapid boundary recession (2005 or 2006, depending on location). The diet of sea stars foraging at high tide showed a consistent trend. Adult (≥ 4 cm long) *M. californianus* comprised a greater percentage of the total apparent diet on addition sites than controls or removal sites (Fig. 5; χ^2 test of independence = 29.22, $df = 2$, $P = 0.000$).

The analyses also confirmed size-dependent predation on mussels. Pooling the records from all sites revealed a positive relationship between mussel lengths and sea star wet mass (Fig. 6). Paine (1976) found a positive size-dependent relationship in records from many sites differing in the relative abundance and sizes of sea stars and mussels. The divers directly observed sea stars on addition sites successfully attacking the very large mussels comprising the matrix of the lower boundary, but they did not see that behavior on control and removal sites. Examination of Fig. 6 also suggested that

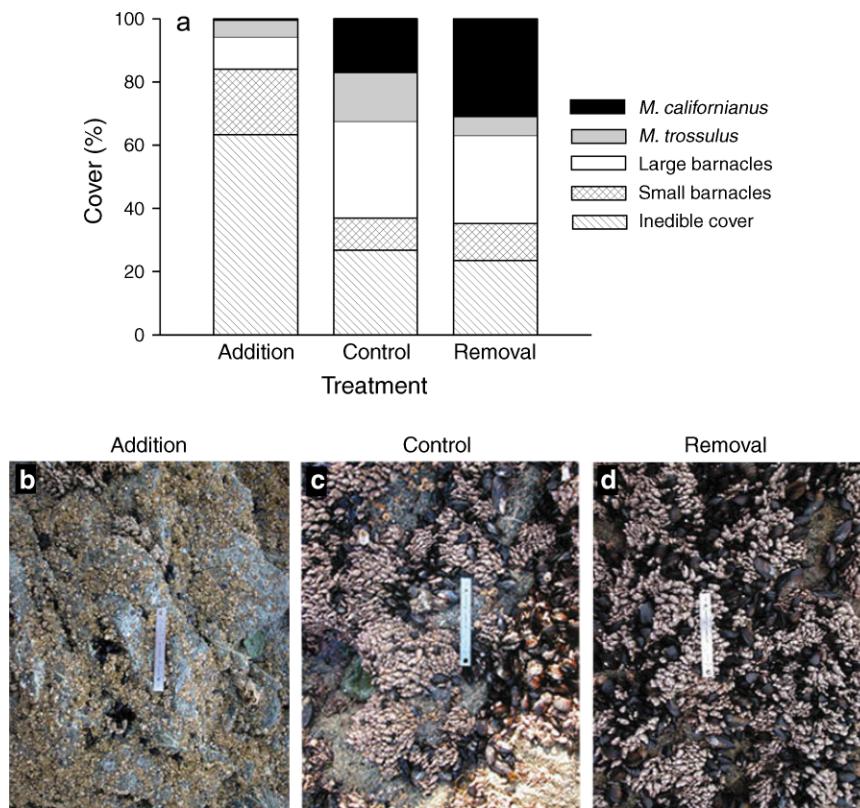


FIG. 4. Results of the cleared-plot experiment, 30 months after clearing. (a) Mean percent covers for the four replicates of the cleared-plot experiment. Inedible cover consists of algae and bare rock; small barnacles consist of acorn barnacles (adult diameters < 2 cm; *Chthamalus fissus* and *Balanus glandula*); large barnacles consist of large acorn and gooseneck barnacles (adults > 2 cm in length at the base of the plates or diameter; *Semibalanus cariosus* and *Pollicipes polymerus*, respectively). *Mytilus trossulus* and *M. californianus* are plotted separately. The means of inedible cover were 63%, 27%, and 24%, respectively, for addition, control, and removal plots (Tukey hsd, $P = 0.013$ and 0.952 , respectively, for addition vs. control and removal vs. control). (b–d) Photographs of the center of cleared plots in one replicate after 30 months. The rule is 15 cm long. A sparse cover of small acorn barnacles (primarily *Balanus glandula* < 1 yr old) appears on the addition plot, and patchy covers of gooseneck barnacles (*Pollicipes polymerus*) and mussels (*M. californianus*) appear on the control and removal plots.

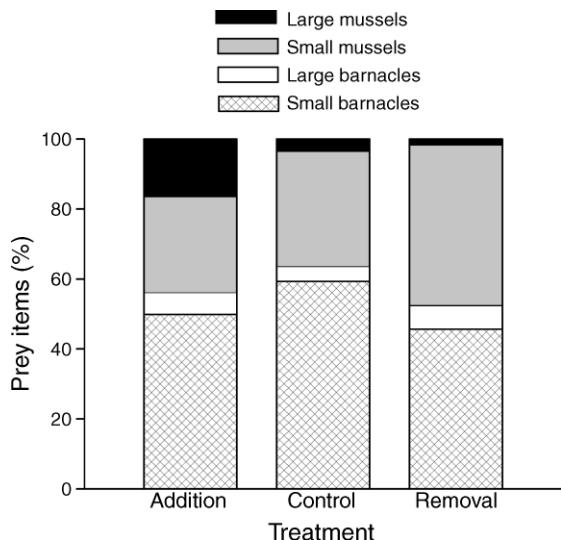


FIG. 5. Mean percentages of each prey species of the total number of prey items taken by sea stars (*Pisaster ochraceus*) at high tide, grouped by treatment. Small barnacles consist of acorn barnacles (adult diameters <2 cm; *Chthamalus fissus* and *Balanus glandula*); large barnacles consist of acorn and gooseneck barnacles (adults >2 cm in length or diameter, *Semibalanus cariosus* and *Pollicipes polymerus*, respectively); small mussels consist of newly recruited *Mytilus trossulus* and *M. californianus* <4 cm long; and large mussels consist of *M. californianus* ≥4 cm long. *Mytilus trossulus* and *M. californianus* recruit together, appear quite similar as recruits, and are both readily consumed in preference to larger *M. californianus*. A total of 1729 prey items were recorded for 342 sea stars.

the maximum sizes of mussels consumed increased from removal to control to addition.

To test whether the maximum sizes consumed increased with experimental sea star densities, we determined the upper quartile of mussel lengths (the largest 25%) consumed on each experimental site and analyzed those records using mixed model ANCOVA with mussel length as the dependent variable, location as the random independent variable, treatment group as the fixed independent variable, and sea star live mass as the covariate (Fig. 7, Table 4). The minimum ANCOVA model showed a significant treatment × location effect. This resulted from differences in the degree rather than the direction of the treatment effect. All four replicates showed the same trend: least squares regression lines for addition sites fell above the lines for controls, which fell above the lines for removals. Consequently, the mixed-model test of treatment effect was significant (Table 4). Post hoc comparisons of addition vs. control and removal vs. control were significant (Tukey hsd, $P = 0.001$ and $P = 0.032$, respectively). We note that prior studies of size-dependent predation used sea star diameter or arm length as measures of sea star size. The inferences of the ANCOVA did not change when either of these measures was substituted as the covariate.

Taken together, photographs of the composition of cover at the original location of the lower boundaries,

the outcome of the cleared plot experiment, the diver observations, and the ANCOVA of size-dependent predation indicate that the progressive depletion of small prey from removal to control to addition sites led to a corresponding increase in the maximum size of mussel consumed. On the addition sites, the sea stars attacked the large mussels forming the matrix of the lower boundary. Mussels >10 cm long were consumed, a size believed highly resistant to predation (Paine 1976).

DISCUSSION

Spatially structured equilibria and population boundaries.—Recent theoretical formulations about the establishment and maintenance of boundaries (Wilson et al. 1996, Wilson and Nisbet 1997, Johnson et al. 1998, Robles and Desharnais 2002, Holt et al. 2005, van de Koppel et al. 2005) range from heuristic models with conceptual parameters to species-specific models parameterized with field measurements. Despite the diversity of approaches and systems, all share a common premise: population boundaries form along lines where spatial gradients in rates of loss (predation, competition, or other risks) exceed the corresponding gain (recruitment and growth) of the population. If risk also depends on size, as is the case with size-dependent predation, then spatial gradients in growth rate and body size interact with the clines in recruitment and mortality rates to determine the exact location of boundaries (e.g., Johnson et al. 1998, Robles and Desharnais 2002). Thus, recent theory suggests that boundaries are

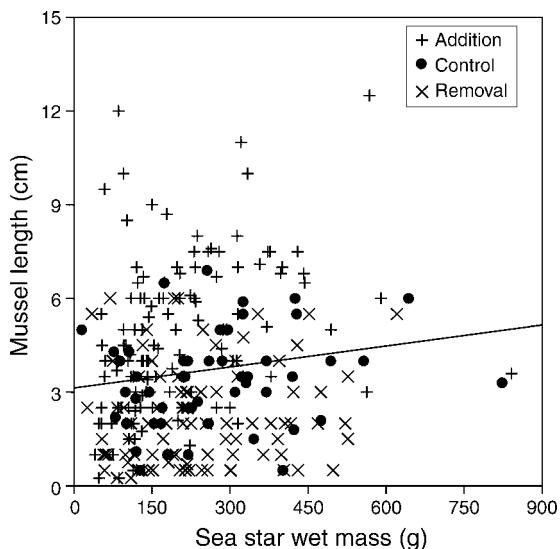


FIG. 6. Linear regression plot of size-dependent predation on mussels. The abscissa represents live wet mass of the sea star (*Pisaster ochraceus*), and the ordinate represents length of the mussel being consumed. The least-squares regression line is shown for data pooled across treatments. Individual records are plotted with respect to treatment group. Regression coefficient = +0.002; $P = 0.029$; squared multiple $R = 0.018$.

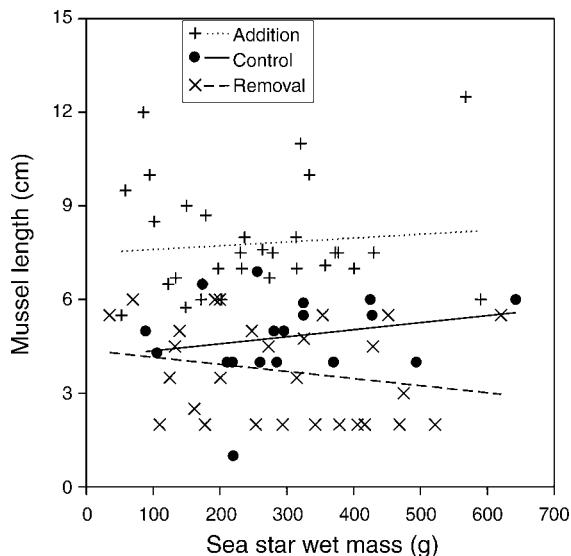


FIG. 7. Linear regression plot of largest mussels consumed in a given treatment group. The abscissa represents live wet masses of the sea stars (*Pisaster ochraceus*), and the ordinate represents the lengths of the mussels in the upper quartile of each site within a treatment group. Individual records are plotted with respect to treatment group. Separate least-squares regression lines are shown for pooled treatments of the four replicates.

manifestations of complex, spatially structured equilibria.

The current work does not constitute validation of a particular model, because it does not examine the specific functional forms of the parameters. The findings do, however, support the general premise of the larger corpus of theory. The maintenance of the lower boundary, and hence the spatial extent of the local mussel population, is fundamentally an equilibrium process. Furthermore, it now seems clear that a definitive theory must include the effects of the tidal gradient on the prey's recruitment, growth, and exposure to aquatic predators, and the predator's flexible responses to the changing size spectrum of prey over the gradient.

The observations made at high tide revealed much about sea star responses to changing prey arrays. First, high-tide diet surveys show that when small prey (barnacles, limpets, and juvenile and small adult mussels) are abundant at lower shore levels they make up by far the greater share of the diet of actively foraging sea stars (Robles et al. 1995). Examination of resting sea stars at low tide often shows few with prey, and, of the feeding stars, a disproportionate number may have larger *M. californianus*, because they take longer to handle and consume (McClintock and Robnett 1986). Second, under natural conditions, site-to-site variation in the vertical excursions of sea stars corresponds to the varying heights of the prey zones (Robles et al. 1995, Robles and Desharnais 2002).

However, the occurrence naturally or by experimental placement of massive recruitment of juvenile mussels below the lower boundary of the mussel beds arrests vertical excursions with the tides. The sea stars remain on these concentrations of preferred prey until they are eliminated, following which excursions up to and beyond the lower boundaries resume (Robles et al. 1995). Lastly, when the natural density adjustments of local sea star populations were blocked experimentally, the relationships between prey zonation and size-dependent predation changed dramatically. Sea stars on the addition sites made longer (higher) vertical excursions, took significantly more large mussels, but continued to consume small prey, which were found within the spaces between the large mussels. Thus, spatial arrays of prey sizes and size-dependent predation are functionally linked in the equilibrium maintenance of boundaries.

Implications for the concept of refuges.—The original statements of the refuge hypothesis (Connell 1975, Paine 1976) proposed that spatial and age-size refuges were separate, alternative mechanisms of prey survival. Low risk of predation accrued solely to the attributes of individual prey within the context of limitations of the predator: a mussel's location above the foraging limit of the sea stars or its chance attainment of an invulnerable size within the range of sea star foraging. Our findings indicate that mussel size and position in the tidal gradient interact as components of a larger spatial process determining risk. The risk of predation to a mussel in the matrix of the lower boundary depends simultaneously on its size, shore level, and the relative abundances of alternative prey at the boundary and lower shore levels. The spatial array of prey in that instant is the product of the interaction of spatially varying prey production and predation. Thus it appears that both the few large mussels one occasionally encounters in the low intertidal zone and the extensive aggregations of mussels higher on the shore result from a unified, spatially conditioned process.

Hypothetical role of the gradient of tidal emersion.—How are we to understand the effect on predation of the gradient of tidal emersion? As part of their normal foraging excursions, the sea stars retreat to lower shore

TABLE 4. Minimum ANCOVA model for analysis of upper quartiles of mussel lengths in sea star diet at a given site, with length quartile as the dependent variable, location as the random independent variable, and treatment as the fixed independent variable.

Source	Sum of squares	df	MS	F	P
Treatment	291.022	2	145.511	9.929	0.012
Location	5.377	3	1.792	1.204	0.315
Wet mass	0.266	1	0.266	0.179	0.674
Treatment × location	87.930	6	14.655	9.842	0.001
Error	98.277	66	1.489	98.277	

Note: Multiple $R^2 = 0.787$.

levels with the receding tide and cease foraging once exposed. If held continually in cages on shore levels above their natural resting height, they die (Petes et al. 2008). Laboratory studies (Pincebourde et al. 2008) show that acute exposure to aerial temperatures above 35°C kills them, and chronic (continual) exposure \geq 23°C suppresses their feeding and growth. This range of temperatures was found to occur frequently on relatively high shore levels during periods of emersion. Therefore, vertical excursions with the tides appear to be a behavioral adaptation that allows *Pisaster* to sustain survival and growth within a gradient of physical stress (Pincebourde et al. 2008).

Vertical excursions should incur energy costs. While the low-tide resting heights are similar among different sites, the corresponding high-tide heights of foraging sea stars are greater on sites with higher mussel boundaries (Robles et al. 1995, Robles and Desharnais 2002). One would expect that as vertical excursions lengthen, travel times increase, and feeding times are curtailed. Furthermore, McClintock and Robnett (1986) suggest that time/energy costs greatly increase if *Pisaster* attacks mussels larger than preferred sizes. As a relatively dense sea star population depletes smaller prey, increases attacks on larger mussels, and causes the recession of the lower boundary, the energy return for a bout of foraging should diminish.

Pisaster possesses indeterminate growth (sensu Sebens 1987), varying growth rates, including shrinkage, depending on the availability of high-value prey. Surveys (Feder 1970) and translocations of tagged sea stars (Paine 1976; C. D. Robles and C. A. Martinez, unpublished data) indicate that growth rates and mean sizes of *Pisaster* depend directly on site-specific differences in prey availability, including the experimentally altered patterns of zonation described in the present work. Together with the numerical response (alongshore movements with changing prey zonation), the indeterminate growth response appears to influence the densities and size structure of *Pisaster* on the sites of mussel beds (further discussion in Paine 1976, Robles et al. 1995), which should bear on the spatially structured equilibria.

In sum, the evidence suggests that (1) the gradient of tidal emersion vertically constrains sea star foraging indirectly, by attenuating energy gains from progressively higher shore levels; (2) as the vertical array of prey varies among sites over time, the resulting changes in the energy returns of foraging drive the sea stars' numerical response and indeterminate growth response, influencing the density and size structure of the local sea star populations; and therefore, (3) the disposition of spatially structured equilibria within the intertidal landscape ultimately depends on as yet unmeasured relationships of evolutionary energetics.

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