

LETTER

Variable interaction strengths stabilize marine community pattern

Sergio A. Navarrete^{1*} and Eric L. Berlow^{2,3,4}

¹Estación Costera de Investigaciones Marinas and Center for Advanced Studies in Ecology and Biodiversity, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

²White Mountain Research Station, University of California, San Diego, 3000 E. Line St., Bishop, CA 93514, USA

³Sierra Nevada Research Institute, University of California, Merced, 4000 Chilnuala Falls Rd, Yosemite National Park, Wawona, CA 95389, USA

⁴Pacific Ecoinformatics and Computational Ecology Laboratory, 1604 McGee Ave, Berkeley, CA 94703, USA

*Correspondence: E-mail: snavarre@bio.puc.cl

Abstract

High variability in the strength of species interactions is usually considered a source of unstable or unpredictable community patterns. However, recent theoretical work suggests that some types of variance in interaction strength may actually promote stability. Here we provide the first empirical evidence that highly variable, context-dependent species interaction strengths and resilient community patterns can be two sides of the same coin. Field experiments show that a persistent rocky intertidal seascape is remarkably resilient to multiple sources of environmental stochasticity largely because of scale dependent and variable species interaction strengths. Biological interactions exert a stabilizing effect because their intensity varies systematically with changes in both physical sources of mortality of established species, as well as recruitment of new individuals. Strong variation in species interaction strengths with disturbance size and environmental conditions is ubiquitous in nature. Elucidating when this context dependency will be stabilizing is critical to predict community-level responses to anthropogenic disturbances.

Keywords

Community regulation, context dependency, disturbance, food web, patch dynamics, pattern persistence, predator–prey interaction, recruitment, resilience, rocky intertidal, stability.

Ecology Letters (2006) 9: 526–536

INTRODUCTION

Predicting the dynamics of populations and communities requires understanding how species influence one another (Neutel *et al.* 2002; Berlow *et al.* 2004; Bascompte *et al.* 2005). Empirical studies have shown that the strength of the interactions between species can be highly variable over time and space (Berlow 1997; Petraitis & Dudgeon 1999; Leibold *et al.* 2004; Peacor & Werner 2004), and this ‘context dependency’ is often associated with unpredictable population and community dynamics (Yodzis 1988; Lawton 1999; Abrams 2001). Stable ecological patterns, such as monocultures and visually striking zonation of species, are often attributed to special cases of temporally persistent, environmentally robust, strong species interactions, such as clear competitive hierarchies and keystone predation (e.g. Levin & Paine 1974; Paine 1984; Menge *et al.* 1994). However, recent theory posits that stability or resilience at the community level may actually be fostered by particular structures of variance at the population level (Tilman 1996;

Levin 1999; Kondoh 2003; Ives & Cardinale 2004; McCann *et al.* 2005). Here we extend this theory to the strengths of interactions among species and provide the first experimental evidence that variable interaction strengths, rather than impeding stable populations and community patterns, can be a critical source of resilience in the face of stochastic environmental variation.

Evaluating in the field whether a naturally occurring community structure is stable has been burdened with methodological and conceptual problems (Sutherland 1974, 1990; Connell & Sousa 1983; Bertness *et al.* 2004; Paine & Trimble 2004; Petraitis & Dudgeon 2004). Numerous ideas of what is meant by ‘stable’, ‘persistent’ or ‘variable’ community structure have been reviewed several times (Lewontin 1969; Margalef 1969; Connell & Sousa 1983; Sutherland 1990; Beisner *et al.* 2003). We consider a system stable when it returns to a given structure or ‘equilibrium’ state after being perturbed by an external force (Connell & Sousa 1983; Paine & Trimble 2004). This has also been called ‘adjustment stability’ (Margalef 1969) or ‘resiliency’

(Connell & Sousa 1983). Persistence or low temporal variability of a community pattern is often considered an indication of stability, but it could simply result from the absence of disturbance forces or from the longevity of component species (Connell & Sousa 1983). We therefore view 'persistence stability' (sensu Margalef 1969) as the long-term consequence of resilience of a given community pattern.

A thorough evaluation of the stability of a given community pattern requires scale-dependent experimentation (Petrakis & Latham 1999). Many theoretical and empirical studies have shown strong scale-dependent dynamics of physical disturbances, which are commonly driven by changes in the importance of biological processes across different disturbance patch sizes (Levin & Paine 1974; Paine & Levin 1981; Miller 1982). Thus, while systems usually recover quickly from small-scale disturbances (Paine & Levin 1981; Miller 1982), large-scale disturbances can generate alternative community states (Petrakis & Dudgeon 1999; Petrakis & Latham 1999) or facilitate the coexistence of early colonists and increase species diversity at the landscape level (Paine & Levin 1981; Miller 1982).

Here, we focus on empirically determining how species interactions contribute to a system returning to a naturally occurring, remarkably invariant community pattern – one which at first glance would appear to be easily nudged to other potentially stable states.

The experimental system

The mid-rocky intertidal seascape of the west shore of San Juan Island (Washington, USA, 48°27' N, 123°2' W) is dominated by beds of the large and competitively dominant balanoid barnacle, *Semibalanus cariosus* (Fig. 1a) which achieves an effective size escape from predation by whelks, *Nucella canaliculata* and *Nucella ostrina*, the main predators in this system (Connell 1970; Dayton 1971; Berlow & Navarrete 1997). Unlike many other monocultures where primary space is entirely monopolized by one competitively dominant species (Paine 1984; Castilla & Durán 1985; Menge *et al.* 1994), this community is characterized by two attributes. First, the dominant sessile species is strikingly sparse and rarely exceeds 25% cover over the entire mid-intertidal seascape (which includes large bare patches: Fig. 1a,d) or around 50% cover within the actual barnacle beds (Fig. 1b,c). Much of the remaining primary space is bare, and other sessile species, including several species of barnacles, mussels and macroalgae rarely reach more than 5% cover in the midzone (Fig. 1b–d), although seasonal algal blooms can temporarily increase algal canopy to *c.* 20–40% primary and secondary (on barnacle shells) cover (Berlow & Navarrete 1997). Second, the vast majority of bare areas are < 10³ cm² (Fig. 1e).

Together, these attributes create what appears to be a remarkably stable size distribution of bare space (Fig. 1f) – a pattern that has been anecdotally noted for decades (Dayton 1971; Connell 1972; Sebens & Lewis 1985; Berlow & Navarrete 1997) and can loosely be termed 'persistent'. Experiments have documented that predation on barnacles (*Balanus glandula* and young *S. cariosus*) by whelks (*Nucella* spp.), and to a lesser extent grazing of algae and bulldozing of newly settled organisms by limpets, play a major role in maintaining existing bare space (Connell 1970; Dayton 1971; Berlow & Navarrete 1997). In addition, filter feeding by large *S. cariosus* upon invertebrate larvae can significantly reduce barnacle settlement in close proximity to live adults (Navarrete & Wieters 2000).

The almost monotonous seascape at this site appears to be highly resilient to multiple sources of environmental stochasticity and biotic interactions that could easily drive the community to different and potentially stable states. First, every spring (between April and June) the annual pulse of barnacle settlement (primarily *B. glandula* and *S. cariosus* but also *Cbthamallus dalli*) is highly variable among years (Strathmann & Branscomb 1979; Berlow & Navarrete 1997; Navarrete & Wieters 2000). Unusually high settlement of sessile species could swamp predators and easily lead to complete monopolization of space by barnacles. *Semibalanus cariosus* is long-lived (Connell 1972; Sebens & Lewis 1985) and the only one of the three acorn barnacle species that is highly resistant to predation once they reach the adult stage at *c.* 1.5 cm basal diameter (Dayton 1971; Navarrete 1996; Berlow & Navarrete 1997). As such, it can withstand several years of low recruitment (Paine 2002). Similarly, occasional winter freeze events or extreme mid-summer thermal stress (Helmuth *et al.* 2002) can reduce the effectiveness of intertidal predators (Berlow & Navarrete 1997). Thus, like the competitively dominant mussel, *Mytilus californianus*, on the Pacific outer coast of the USA (Paine & Levin 1981), we would expect to find a dense *S. cariosus* monoculture dominating the mid-intertidal zone. Given these conditions it is surprising that, *S. cariosus* cover on the west shore of San Juan Island rarely exceeds 50% within the barnacle 'beds' (Fig. 1b).

Second, stochastic physical disturbances regularly cause extensive barnacle mortality, creating patches of bare rock up to tens of square meters in size (Connell 1970; Dayton 1971). Battering by large (0.5–1 m in diameter) drift logs is the primary source of physical disturbance on San Juan Island (Dayton 1971). Dayton (1971) estimated a 20% probability that any given spot on this shore could be struck by a log within 3 years. Together with the well-documented strong predation on colonizing barnacles (Connell 1970; Dayton 1971; Berlow & Navarrete 1997), frequent large disturbances could lead to a seascape devoid of *S. cariosus* barnacle beds and either dominated by bare space or by fast

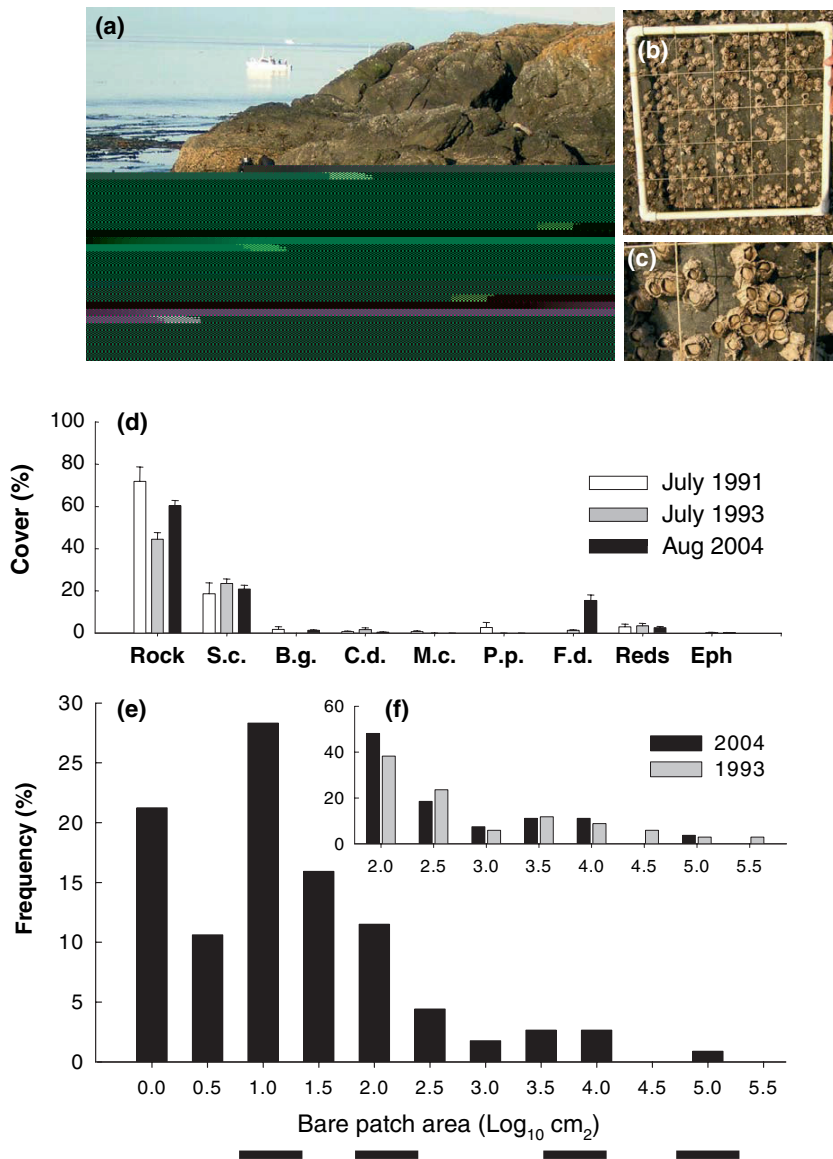


Figure 1 Persistence of community pattern: (a) landscape view of the mid-intertidal zone at Eagle Point, San Juan Island; (b) close up of a 50 × 50-cm quadrat showing the typical spacing among large *Semibalanus cariosus*; (c) close up of a 10 × 10-cm area; (d) cover of sessile species during summers 1991, 1993 and 2004. Bare, bare rock; S.c., *Semibalanus cariosus*; B.g., *Balanus glandula*; C.d., *Chthamalus dalli*; M.c., *Mytilus californianus*; P.p., *Pollicipes polymerus*; F.d., *Fucus distichus*; Reds, red macroalgae; Eph, ephemeral algae. Note that algal cover (F.d., Reds and Eph) includes secondary cover (algae growing on barnacle shells). (e) Size-frequency distribution of bare rock patches observed at Eagle Point in August 2004. The four bars under the panel indicate approximate size of experimental bare patches. (f) (insert) Comparison of size frequency distributions of bare patches in 1993 and 2004, showing only patches larger than 100 cm².

colonizing, disturbance-resistant species such as green algae or small barnacles. Indeed, recruitment of *S. cariosus* tends to be low and more sporadic than other competitively subordinate barnacle species (Berlow & Navarrete 1997; Paine 2002). Thus at first glance, the existing seascape appears precariously balanced between two states: one that is either saturated with a dense *S. cariosus* monoculture, and one that is characterized by fast colonizing, disturbance-resistant species.

To maintain the existing stable size distribution of bare space (Fig. 1f), there must be mechanisms that consistently operate to: (i) prevent large disturbances from dominating (thus driving the seascape towards mostly bare space or fugitive species); and (ii) maintain small bare areas (thus preventing complete monopolization by the dominant).

This stable spatial distribution of bare space would then translate into a sparse monoculture of barnacles. Thus, we tested the hypothesis that the naturally occurring seascape at this site is highly resilient because the strength of predation varies systematically to dampen forces that would otherwise drive the system to other states. We examine two types of driving forces: (i) physical disturbances that generate bare rock; and (ii) stochastic recruitment of all sessile species. We predicted that: (i) if small bare spaces are to persist in the face of annual recruitment of sessile species, then predation must be strong enough to prevent small perturbations from filling in too rapidly; and (ii) if large perturbations are to be muted, then predation on new recruits must be weak enough to facilitate re-colonization by sessile species to pre-disturbance conditions within a year. These predictions are

opposite to those in the model systems envisioned by Levin & Paine (1974); Miller (1982) and Petraitis & Latham (1999). Note also that these predictions extend to the relative abundance of species and that the term 'resilience' is reserved for the 'seascape' pattern (Fig. 1a,d–f) and not for the dynamics within individual patches.

MATERIALS AND METHODS

Field surveys

Cover of sessile species and density of mobile organisms were quantified in July 1991, July 1993 and August 2004 in the mid-intertidal zone in 50×50 -cm quadrats laid continuously along two to four 25- to 40-m transects parallel to the water mark. Cover was estimated visually with the aid of a 5×5 -cm grid (Dethier *et al.* 1993). To determine the size distribution of bare patches, in July 1993 we quantified the cover of sessile species in 165, 10×10 -cm quadrats laid continuously in the centre of a 20-m transect parallel to the water mark. The maximum diameter of a bare patch was estimated by the number of continuous quadrats with 100% bare rock, and areas of bare patches were obtained by assuming an approximately circular shape with a radius half the size of the total number of continuous bare rock quadrats. In this year, the quadrat size used in the field implied that only bare patches larger than $\approx 100 \text{ cm}^2$ could be considered. On the same rocky benches in 2004 we quantified bare rock patch sizes using 2950 continuous 1×1 -cm quadrats along the centre of a 30-m transect parallel to the water mark. Thus, bare patches as small as $\approx 1 \text{ cm}^2$ were identified on this year. In addition to identifying bare patches, we measured the density of 'recruit', 'juvenile' and 'adult' barnacles. We define recruits as those individuals smaller than 2 mm which have settled roughly within the previous 2 months. After this time they were considered juveniles. We could only consistently distinguish among barnacle species once they had reached the 'juvenile' stage.

Experimental manipulations

While we are interested in the resilience of the community at the 'seascape' level, which includes both the sparse barnacle beds and the bare rock patches (Fig. 1a), we could not perform replicated predator exclusions over this spatial scale. Therefore, our approach was to follow the dynamics of experimentally created disturbances that encompassed the size range of patches observed in the field. To control for potentially confounding initial differences among naturally existing patches of varying size, we selected relatively homogeneous areas of the rocky shore with established barnacle beds (e.g. Fig. 1b) and manually cleared the rock to generate replicated experimental disturbances. Thus, the

initial pre-disturbance cover of adult barnacles, and our reference level to evaluate recovery or change following a disturbance (hereafter 'ambient' condition), was ≈ 40 – 50% for all disturbance sizes. Four sizes of bare rock patches were experimentally created: 'micro-scale' ($\approx 1 \text{ cm}^2$), 'small-scale' (10^2 cm^2), 'intermediate-scale' (10^4 cm^2) and 'large-scale' ($\approx 10^5 \text{ cm}^2$). The micro-scale treatment corresponded to the typical spacing among large barnacles (e.g. Fig. 1b,c). The other disturbances were approximately square (with fuzzy edges as the surrounding barnacle beds are sparse).

To quantify consumer interaction strength and community responses at the different disturbance sizes, we manipulated the presence of mobile consumers in paired 10×10 -cm plots at each scale of experimentally created bare rock. Consumers (whelks: *N. ostrina*, *N. canaliculata*; and limpets: primarily *Tectura scutum* and *Lottia pelta*) were excluded using $10 \times 10 \times 6$ cm stainless-steel mesh cages. Spatially paired with each 'exclusion' treatment was one unmanipulated 10×10 cm 'control' plot (marked with screws) and one 10×10 cm 'roof' of the same mesh used for the exclusion cages. The mesh roofs allowed access to mobile consumers and served to evaluate potential artefacts introduced by the cage. Roofs and control plots did not differ significantly (Fig. 2). For all disturbance sizes, all three predator treatments (exclusions, roofs and control plots) were thus spatially aggregated in blocks. The replicate blocks were at least ≈ 1 m apart, haphazardly distributed over ≈ 30 m of coastline. All treatments (i.e. combinations of predation and disturbance sizes) were replicated four to five times. Some replicates were lost towards the end of the experiment due to battering by logs. The entire experiment was initiated once in March 1993 and again in March 1994, 2 years of dramatically different barnacle recruitment. Thus, all disturbance sizes were re-cleared to bare rock and new cages were deployed in March 1994. In this system, all surviving settlers have grown to become young adults by late-summer or early fall. At this point the system has naturally returned to the pre-settlement condition and remains as such until the next spring settlement pulse (Connell 1970; Dayton 1971).

Experimental plots with and without predators were photographed periodically and cover of new sessile species that settled onto the rock surface, after the start of the experiment, was estimated from the photos using a 10×10 -cm quadrat with 81 regularly spaced intersection points. These 10×10 -cm plots were the experimental units in which predator treatment trajectories were measured. For the micro-scale disturbance size, experimental plots were larger than the cleared rock areas – thus, the 10×10 -cm plots included ≈ 40 – 50% adult *S. cariosus* and 50 – 60% cleared bare rock, corresponding to the small bare rock spaces observed within existing barnacle beds (Fig. 1c,e). The cover of the pre-existing adult *S. cariosus* was removed

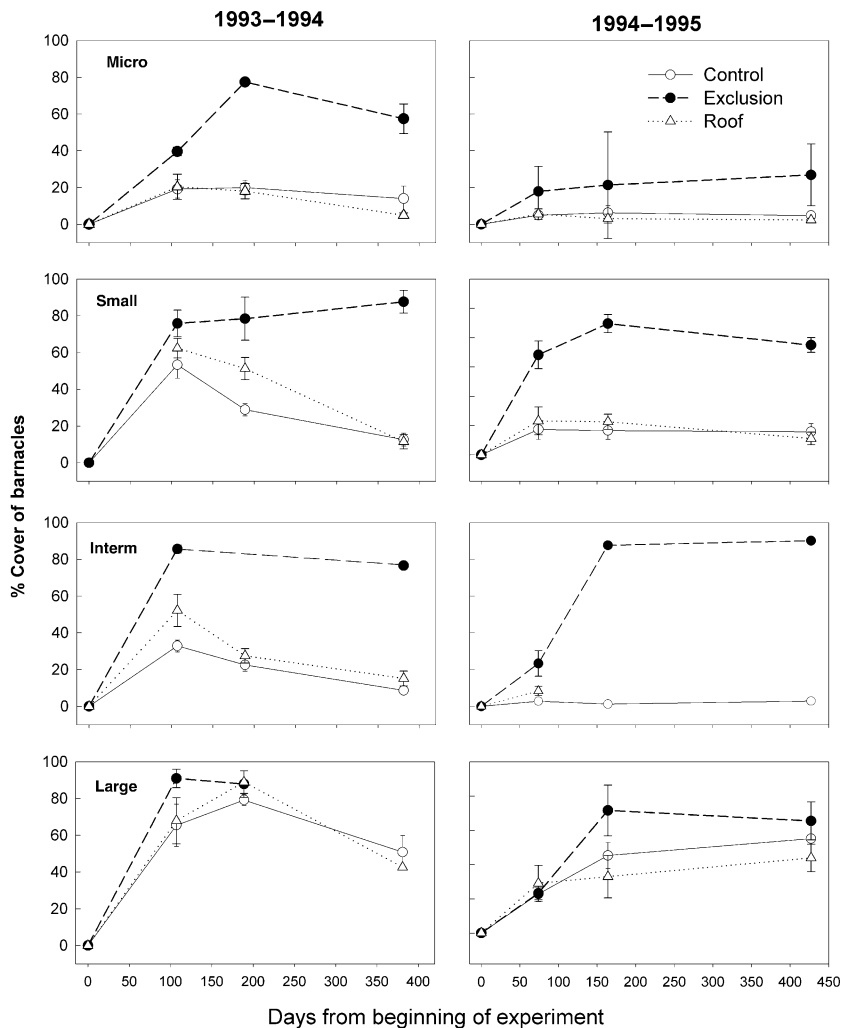


Figure 2 Results of predator exclusion experiments at the mid-intertidal zone of Eagle Point in the San Juan Island. The average (\pm SE) cover of new barnacles (all species pooled) in predator exclusion plots (solid circles), control plots with all predators at natural densities (open circles) and manipulation controls (roofs, open triangles) is shown for experiments conducted in 1993–1994 (left panels) and 1994–1995 (right panels), and for each spatial scale of experimentally cleared bare space: ‘micro’ (1 cm²), ‘small’ (100 cm²), ‘intermediate’ (10 000 cm²) and ‘large’ (100 000 cm²).

from the cover counts to estimate cover of new species in the cleared rock portions of these plots. For the small-scale disturbance size, the cleared area was identical to that of the 10 \times 10-cm experimental plots. The intermediate- and large-scale disturbance sizes were large enough to each include all three predator treatment plots (exclusion, roof and control). In these cases the 10 \times 10-cm plots were positioned near the centre of the cleared areas to avoid edge effects. Within the largest disturbance scale (\approx 10⁵ cm²) we deployed two sets of each predator treatment and averaged these subplots prior to analysis to give one measure of predator effects for each large disturbance patch. For the small- and micro-scale disturbances, the treatments were spatially aggregated (blocks) on the same scale as those in the larger disturbance sizes.

The strength of predation was quantified at each disturbance scale as the standardized difference in total new barnacle cover (including all barnacle sizes) after roughly 1 year between exclusions (E) and paired controls

(C), standardized as $(C - E)/E$. This measure of predation strength is similar to the one proposed by Paine (1992), but it quantifies ‘per population’ or total predation effect of predators on prey (Navarrete & Menge 1996; Berlow *et al.* 1999) instead of ‘per capita’ interaction strength. Predation strength is -1 when predators completely eliminate prey. As interaction strength was calculated from paired exclusion and control treatments, a one-way analysis of variance followed by multiple comparison Tukey tests was conducted to compare interaction strengths among disturbance sizes for each year. Using the same index of predation strength, we quantified the strength of consumption of barnacle larvae because of filter feeding by large barnacles by comparing the cover of newly recruited barnacles to predator exclusion plots in the micro-scale disturbance treatment (which contained pre-existing adult barnacles) to new barnacle cover in the small-scale disturbance treatment (which were cleared of large barnacles). In this manner we could estimate the effect of existing large barnacles on new

recruits in the absence of all mobile consumers. Previous studies have shown that filtration of settling larvae is not effective beyond few centimetres from the adults (Navarrete & Wieters 2000), and therefore, we assumed that the effect of filtration was near zero in all larger-scale disturbances.

The consumer interaction strengths calculated here include the total effects of predators on their prey, and variation in this effect can be due to changes in both predator density and per capita feeding rates (Berlow *et al.* 1999; Navarrete & Castilla 2003). Because the relative abundance of all species was very similar across the study site and among years, we made the simplifying assumption that variation in consumer interaction strengths among disturbance sizes or among years was not mediated by changes in other species abundances (Laska & Wootton 1998; Abrams 2001). The clear exception was the modification of predation strength by the presence of large adult *S. cariosus* that either facilitate mobile consumers by providing a structural refuge or pre-empt them by filtering settlers. To facilitate different interpretations of how predator importance varied among disturbance scales and years, we also present the temporal trends in barnacle cover in all treatments.

To help evaluate the consistency with which large-scale disturbances recover to pre-disturbance conditions, we took advantage of a previous experiment in 1992, where we had manually cleared four large-scale patches and followed their recovery through time (Berlow & Navarrete 1997). We did not perform predator exclusions in those patches.

RESULTS

Field surveys supported observations of a temporally invariant community structure. Over a 13-year span, the same species dominated the seascape and their relative abundances remained virtually unchanged; indeed, covers of the nine most abundant taxa found in the field were highly correlated among years (Pearson $r > 0.98$, $P < 0.0001$, for all pair comparisons between summers 1991, 1993 and 2004). Similarly, patch size distribution remained virtually invariant between 1993 and 2004 (Pearson $r = 0.96$, $P < 0.0001$). Bare patches of $\approx 100 \text{ cm}^2$ were the most common. Published accounts and personal observations suggest that the community pattern in the years we sampled is typical for this site (Dayton 1971; Connell 1972; Sebens & Lewis 1985; B.A. Menge and J. Lubchenco, personal communication). The mean (\pm SE) densities of *Nucella* spp. were 72.7 ± 18.5 , 66.4 ± 8.3 , 82.3 ± 42.3 and 117.6 ± 35.2 individuals m^{-2} for 1991, 1993, 1994 and 2004 respectively. Mean (\pm SE) densities of limpets were 36.4 ± 15.3 , 55.2 ± 7.6 and 50.0 ± 15.4 individuals m^{-2} for 1991, 1993 and 1994 respectively (no data available for 2004). Adult *S. cariosus* in this system were on average (\pm SE) $2.5 \pm 0.5 \text{ cm}$ basal diameter and $1.8 \pm 0.6 \text{ cm}$ height ($n =$

119), and reach an average of $1.1 \pm 0.03 \text{ cm}$ basal diameter ($n = 61$) in 1 year. At this size whelk predation is reduced enough to be ineffective in controlling *S. cariosus* abundance (Navarrete 1996).

In the first year (1993), spring total barnacle recruitment was more than 16 times higher than during the second experimental run in 1994 (1080 recruits 100 cm^{-2} in 1993 vs. 67 recruits 100 cm^{-2} in 1994). The species composition of recruits was mixed. In 1993, the proportions of *S. cariosus*, *B. glandula* and *C. dalli*, respectively, were 44%, 54% and 2% ($n = 4058$ individuals counted in $2 \times 2\text{-cm}$ area from randomly selected exclusion plots). During this 'high recruitment year', barnacle cover in predator exclusions increased rapidly at all disturbance scales (Fig. 2). In contrast, barnacle cover initially increased in controls and manipulation-control plots, but after few months predators were able to reduce barnacle cover to $<10\%$, except in large-scale disturbances (Fig. 2). Accordingly, the strength of predation was similarly high (-0.7 to -0.8) at most disturbance scales except the 'large-scale' patches, where the strength was not significantly different from zero and was significantly different from all other disturbance sizes (ANOVA and Tukey test, $P < 0.0001$, Fig. 3). After ≈ 1 year, *S. cariosus* barnacles in large-scale patches had reached $> 1 \text{ cm}$ in diameter, allowing predators to venture again into the patches and consume the smaller barnacles (mostly *B. glandula*), apparently causing the late decrease in total barnacle cover in control and roof plots (Fig. 2). As predation on settling larvae by adult barnacles can saturate at high settlement densities (Navarrete & Wieters 2000), the effect of barnacle filtration in micro-scale patches was nearly nil on the high recruitment year (hatched bars in Fig. 3).

Total barnacle recruitment in spring 1994 was much lower than the previous year and about average for the area (Berlow & Navarrete 1997). Again, the species composition of recruits was well mixed and slightly different than 1993, with 28% *S. cariosus*, 59% *B. glandula* and 13% *C. dalli* ($n = 2259$). As in the previous year, barnacle cover in control plots was maintained below 10% in 'micro', 'small' and 'intermediate' size disturbances, but not in 'large-scale' disturbances, where barnacle cover reached $\approx 55\%$ by the end of 1 year (Fig. 2). Consequently, predation strength was not significantly different from zero in the 'large-scale' disturbances (Fig. 3), while it was strong at 'small-' and 'intermediate-scale' disturbances (-0.78 and -0.99 respectively). However, in contrast to 1993, predation was weak and highly variable among blocks at the 'micro-scale' disturbance (Fig. 3; mean = -0.27 , SE = 0.35) because mean barnacle cover in predator exclusions never reached more than 27% (Fig. 2). We interpret this as the effect of consumption of settling larvae by large *S. cariosus*, which essentially pre-empted the effect of whelks and limpets in 'micro-scale' disturbances (hatched bar in Fig. 3). Thus,

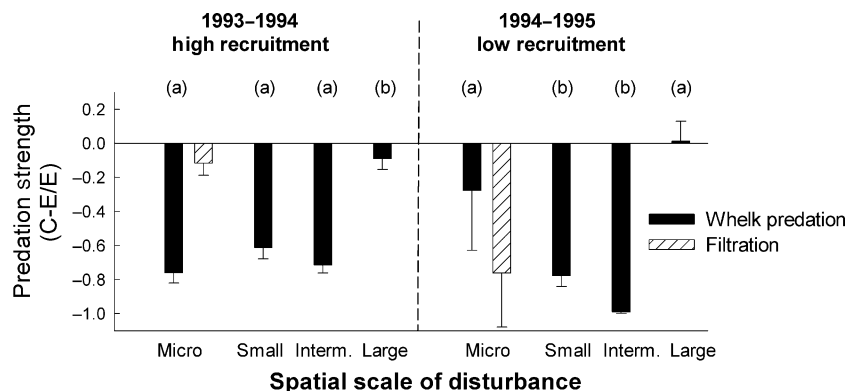


Figure 3 Results from replicated predator exclusion experiments showing the strength of predation (mean \pm SE) by whelks on new barnacles across the four spatial scales of experimental disturbances (black bars) and by large barnacles on settling larvae in the micro-scale disturbances (hatched bars). The experiment was repeated a year of high barnacle recruitment (1993–1994) and a year of low barnacle recruitment (1994–1995). Letters above bars indicate groups that differ significantly (different letter) according to a Tukey test. See Fig. 2 legend for the experimental disturbance sizes.

population predation strength was then low at both the ‘micro’- and ‘large-scale’ disturbances and high at ‘small’ and ‘intermediate-scale’ disturbances (Fig. 3; ANOVA and Tukey tests $P < 0.01$).

The time trajectories of experimentally created ‘large’ bare rock patches on three different years, without manipulating consumers, show that they consistently return to ambient, or pre-disturbance conditions within roughly 1 year (Fig. 4a). Thus, the resultant composition of large-scale disturbances in terms of barnacle cover and bare rock was similar to ambient conditions and very different from smaller-scale disturbances, which show low recovery rates and remained mostly bare (Fig. 4b,c).

DISCUSSION

Our study provides the first empirical evidence that large spatial and temporal variability in the strength of trophic interactions – a ubiquitous ecological phenomenon usually considered to be a source of unstable or unpredictable community dynamics – can confer resilience to a surprisingly invariant community pattern. In particular, our results show that the strength of predation and grazing on sessile species varies inversely with the size of physical disturbance and that, among years, they depend strongly on large interannual variation in recruitment rates. We argue that this variation in interaction strength helps to maintain the landscape-level pattern of species relative abundances and bare rock, and confers resilience to a community pattern that would otherwise easily be driven to another potentially stable states. The primary mechanisms for this stabilizing effect include: (i) the strength of predation within patches varies inversely with the spatial scale of mortality due to physical disturbance; (ii) in small, but not large disturbances,

multiple sources of predation on small barnacles buffer against temporal variation in recruitment and consumer effectiveness; and (iii) the dominant sessile species can recruit to new disturbances within 1 year and reach a size refuge from predators, but cannot close small disturbances by encroaching from the perimeter. As a result of these processes, and contrary to other natural and theoretical systems (Levin & Paine 1974; Paine & Levin 1981; Petraitis & Dudgeon 1999; Petraitis & Latham 1999), large disturbances quickly revert to the pre-disturbance condition, while smaller bare rock patches persist despite annual recruitment of new barnacles.

On years of average to low barnacle recruitment, established large barnacles can filter out nearly all new settling larvae, helping to maintain ‘micro-scale’ spaces of bare rock. On these years, predation by whelks or bulldozing by limpets appears ‘redundant’ in the maintenance of these ‘micro-scale’ patches, as shown by Berlow & Navarrete (1997) in experiments conducted between 1991 and 1992. However, during occasional years of high barnacle recruitment (e.g. 1993), filtering by large barnacles is ineffective and predation becomes critical for maintaining the bare rock. Conversely, acute environmental stresses, such as high temperatures during summer low tides (Helmuth *et al.* 2002) or freezing temperatures in winter could dramatically reduce whelk and limpet foraging rates or even cause massive whelk mortality (Connell 1972). Consumption of settling larvae by adult barnacles would then provide a buffer against consumer mortality or reduced foraging efficiency and promote the persistence of bare rock patches within the large barnacle beds. Thus, patches $\leq 10^4$ cm², where the effects of filter feeding and/or predation are consistently intense, remain bare for long periods of time.

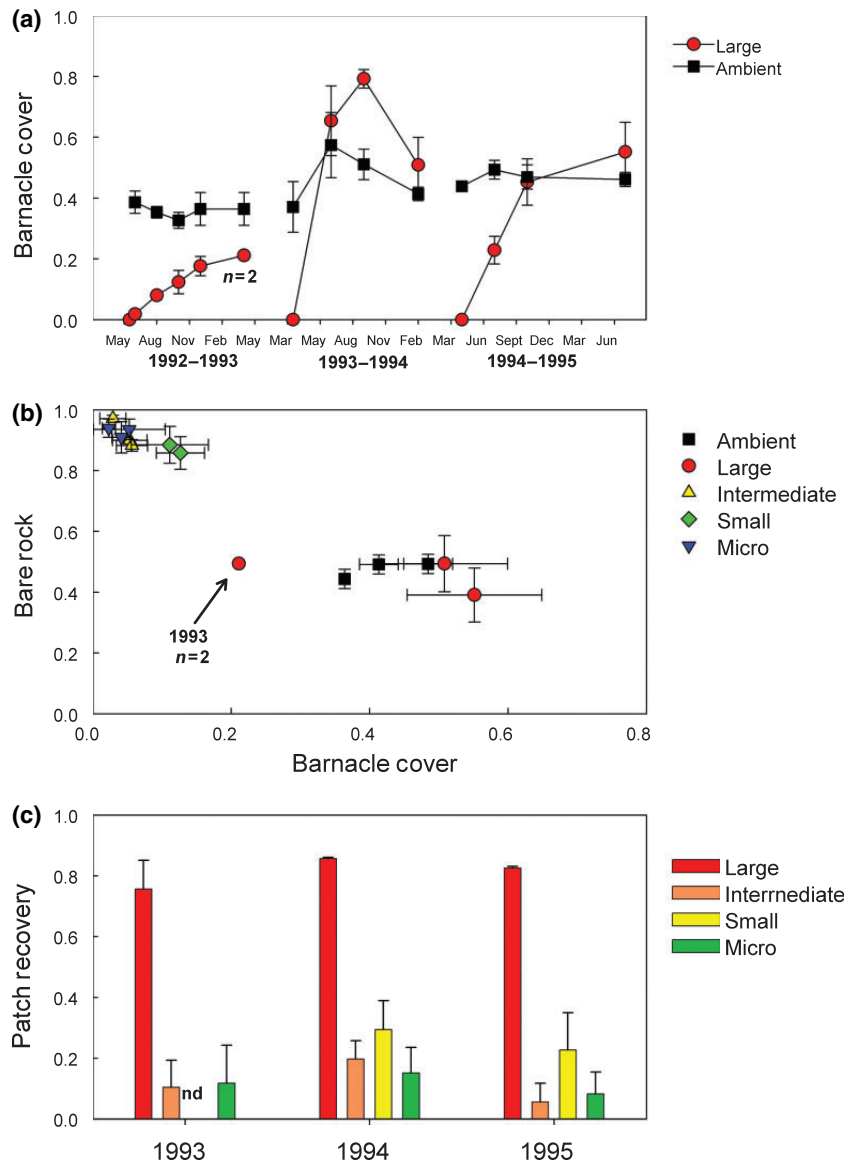


Figure 4 (a) Time trajectories for new barnacle cover in large-scale bare patches experimentally cleared in May 1992, March 1993 and March 1994 and in paired undisturbed areas (ambient). (b) Mean (\pm SE) bivariate composition of bare rock and barnacle cover in experimental disturbances and paired control areas (ambient) at the end of 1 year. The three data points per patch size correspond to three different years. (c) Recovery of patches to ambient (pre-disturbance) barnacle and bare rock cover after 1 year calculated as the bivariate vector distance to ambient levels.

On the other hand, larger disturbances that eliminate adult barnacles from extensive areas consistently return to pre-disturbance levels in both barnacle and bare rock distribution because of unimpeded settlement of all sessile species and reduced predation on newly recruited barnacles (Fig. 4a,b). Weak predation in large-scale disturbances is likely due to the effects of patch size on whelk foraging behaviour both at the population and individual levels: (i) fewer whelks (*c.* 75% less – Berlow & Navarrete 1997) venture out into the middle of large bare patches; and (ii) those that do feed less due to more stressful conditions. Beds of large barnacles provide refuge from desiccation and thermal stresses for whelks and limpets, which remain nestled among the large barnacles during spring and summer low tides (Berlow & Navarrete 1997). The persistence of

small bare spaces and rapid recovery of large bare patches confer stability (resilience and persistence) at the seascape level (Fig. 5) and maintain the relative abundance of species remarkably invariant over time.

Two mechanisms seem to prevent complete monopolization by barnacles in large disturbances. First, all barnacle species recruit to the large patches in relatively mixed sets, with a general predominance of *B. glandula* over *S. cariosus* (in 1991 and 1992 there was virtually no recruitment of *S. cariosus*, Berlow & Navarrete 1997). In about a year, the newly settled *S. cariosus* have reached over 1 cm in diameter (see also Dayton 1971). Predators can then venture into these areas and eat or bulldoze away all small, susceptible barnacles, particularly *B. glandula* and *C. dalli*, leaving most *S. cariosus* that have essentially escaped predation by virtue of

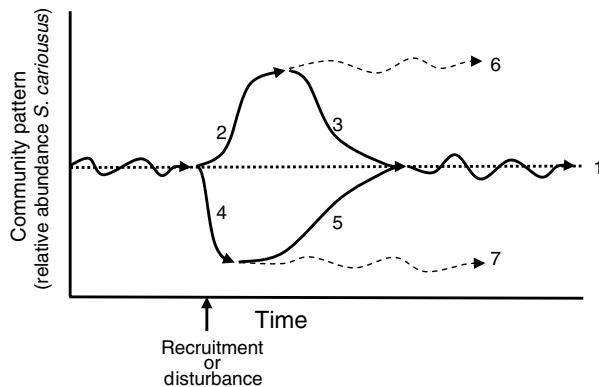


Figure 5 Persistence and resilience of the stable community pattern found on the mid-intertidal rocky shores of San Juan Island. The centre dotted line (1) represents the existing, temporally persistent community pattern. Annual recruitment of three barnacle species each spring can disrupt the system away from this state, increasing the overall barnacle cover and changing the relative abundance of species (2). Predation by whelks and limpets quickly restores small patches of bare space within one season (3). Physical disturbances that create large bare rock patches rapidly drive the community away from the original state, and drastically reduce overall barnacle cover (4). However, the large disturbances quickly return to initial conditions because consumers are ineffective in these areas (5). The upper and lower dashed lines represent hypothetical community patterns that would exist if predators were continually removed (6) or if predators had uniformly strong effects in all disturbance sizes (7). Note that the temporal variability of the existing stable community pattern (1) is not necessarily lower than the two hypothetical community patterns (6 and 7), which are unstable in this community.

their size. Second, if *S. cariosus* completely dominates the barnacle set on a given year and forms a temporarily dense monoculture, random natural mortality of individuals or occasional predation creates micro-scale bare patches that will tend to be maintained over time by the filtration activity of surrounding adults. Consumers can then seek refuge in the micro-scale bare spaces and ensure their persistence.

The pattern found at Eagle Point clearly differs from the sometimes dense stands of *S. cariosus* observed at other places, especially on the outer coast of Washington and Oregon. We believe the main causes of this difference are: (i) recruitment of barnacles (and other species) is consistently higher on the outer coast of Washington and Oregon than on San Juan Island. Persistent heavy barnacle settlement and recruitment is more likely to swamp consumers and eliminates the possibility for maintenance of micro-scale patches by filtration of larvae; (ii) physical stress (temperature and desiccation) is highest in the San Juan Island than anywhere on the open coast of Washington, Oregon or California (Helmuth *et al.* 2002). Thus, on the outer coast, whelk and limpet foraging in large

disturbances does not rely on refuge provided by large adult barnacles (Berlow 1997); (iii) for reasons not yet fully understood, but probably related to recruitment limitation, the mussel *M. californianus*, a dominant competitor for space on the open coast, is not abundant on San Juan Island. Among-site differences in structure and persistence of *S. cariosus* beds suggest that the negative density dependence, which maintains a stable intermediate cover at Eagle Point depends critically on barnacle settlement rates and the potential for adult barnacles to serve as physical refuges for consumers. These results are consistent with studies that have demonstrated regime shifts in density-dependent interactions mediated by thresholds of prey productivity and/or consumer foraging ability (e.g. Ruesink 1998).

Thus, besides recruitment, at least three environmental gradients are likely to regulate the stabilizing influence of variable trophic interactions in rocky intertidal systems: (i) regional and upshore gradients of thermal/desiccation stress, which diminishes foraging efficiency of predators outside thermal refuges; (ii) regional or horizontal gradients of wave action, which can both increase the productivity of basal species and diminish foraging efficiency of predators outside of structural refuges; and (iii) regional gradients in upwelling, which can influence basal species recruitment and growth rates.

We can visualize the long-term 'seascape-level' community pattern or existing 'equilibrium' as the dotted line (1) in Fig. 5. This community pattern is defined as the spatial distribution and relative abundance of sessile species. In this case, the equilibrium pattern consists of *c.* 25% cover *S. cariosus* (averaged over the mid-intertidal 'seascape' and around 50% within barnacle beds) and returns to this state after perturbed. Spring recruitment of three barnacle species disrupts the system away from this state by increasing the overall barnacle cover and changing the relative abundance of species (2). Predation by whelks and limpets quickly restores small patches to bare space (3). Large physical disturbances rapidly drive the community away from the existing state, drastically reducing the overall barnacle cover (4). However, these large disturbances return to initial conditions because predation and bulldozing of settlers and recruits are ineffective in these areas, until the juvenile *S. cariosus* again provide refuge (5). The upper dashed line represents a hypothetical community pattern that could exist if predation was uniformly weak across all patch sizes (6). By contrast, if predation was uniformly strong at all disturbance sizes, they would maintain the seascape virtually devoid of *S. cariosus* (7). The temporal variability of the states that could exist if predation was either uniformly weak (6) or strong (7) are not necessarily greater (or lower) than the existing stable community pattern (1). The variable predation we observed contributes to the remarkable stability of the naturally occurring community structure at Eagle Point (1) by

preventing it from being driven to two other potentially stable states (6 or 7). If all consumers were to become extinct, the new community might be very stable and resilient, but as we show here that community would exhibit radically different structure and dynamics.

The absence of an alternative, self-maintaining stable state in this system contrasts with theoretical models and empirical results showing that large-scale disturbances can push a community into an alternate stable state (Petraitis & Dudgeon 1999; Petraitis & Latham 1999). One precondition for this phenomenon (not present in our system), is that small patches facilitate the existing dominant while large patches facilitate an alternative dominant species that modifies the environment. Our results also contrast with other systems where large disturbances recover more slowly than small ones and develop a distinctly different species assemblage than the surrounding matrix (e.g. Paine & Levin 1981; Miller 1982). In those cases, small disturbances favour the existing dominant (e.g. via encroachment from the edge) and large disturbances are a refuge for early colonizing 'fugitive' species due to the reduced strength of competition (Paine & Levin 1981; Miller 1982).

Our results suggest that multiple community states or mosaics of patches in various stages of succession are but a subset of possible community dynamics that result when the strength of species interactions are a strong function of disturbance size. In addition to facilitating 'switches' in community structure or disrupting equilibrium conditions, systematic variance in interaction strengths may also underlie some of the most temporally stable and resilient patterns in nature. The conditions that promote the latter appear to include a combination of the variance structure and species traits: (i) mortality of the dominant species due to biotic interactions is negatively correlated with environmentally induced mortality and positively correlated with its recruitment or productivity; (ii) there is no strong trade-off between the ability to colonize large disturbances and either the ability to compete for space or escape from predation; (iii) there is size-dependent variation in the relationship between the dominant species and its consumers (from prey to refuge provider). Thus, the stabilizing effect of species interactions in these community depends critically not just on the variability in interaction strengths (Kokkoris *et al.* 2002), but also how this variation correlates with external sources of mortality, prey recruitment and competitive hierarchies.

Conservation agencies are now integrating the concept of community resilience into their management strategies, but most of this work focuses on how resilience is related to physical tolerances of individuals or populations of foundation species. Our results suggest that special attention should be given to the way biological interactions vary with the intensity and extent of disturbances as they can help

buffer a community in the face of changing environmental conditions. Indeed, a better understanding of the relationship between variability in interaction strengths and community stability (Ives & Cardinale 2004; McCann *et al.* 2005) will be critical to assess the resilience of ecological communities to global change.

ACKNOWLEDGEMENTS

We are in debt to a number of friends who helped us in different aspects of this project, including B. Broitman, T. Miller, C. Nedham, Zahna Neskowi, J. Panek, E. A. Wieters, and the kind woman who owns Eagle Pt. Comments and suggestions by Jonathan Chase, Neo Martínez, Bruce A. Menge, Robert T. Paine, Evie A. Wieters and four anonymous referees substantially improved this manuscript. S.A.N. was supported by a Fondap-Fondecyt 1501-0001 grant to CASEB, Fondecyt no. 1040787 and the continuous support from the Andrew Mellon Foundation for which we are most grateful. E.L.B. was also supported by NSF grant no. 0342332 and an Alexander von Humboldt Foundation research fellowship.

REFERENCES

- Abrams, P.A. (2001). Describing and quantifying interspecific interactions: a commentary on recent approaches. *Oikos*, 94, 209–218.
- Bascompte, J., Melian, C.J. & Sala, E. (2005). Interaction strength combinations and the overfishing of a marine food web. *Proc. Natl Acad. Sci. USA*, 102, 5443–5447.
- Beisner, B.E., Haydon, D.T. & Cuddington, K. (2003). Alternative stable states in ecology. *Front. Ecol. Env.*, 1, 376–382.
- Berlow, E.L. (1997). From canalization to contingency: historical effects in a successional rocky intertidal community. *Ecol. Monogr.*, 67, 435–460.
- Berlow, E.L. & Navarrete, S.A. (1997). Spatial and temporal variation in community organization: lessons from repeating field experiments. *J. Exp. Mar. Biol. Ecol.*, 214, 195–229.
- Berlow, E.L., Navarrete, S.A., Briggs, C.J., Power, M.E. & Menge, B.A. (1999). Quantifying variation in the strengths of species interactions. *Ecology*, 80, 2206–2224.
- Berlow, E.L., Neutel, A.-M., Cohen, J.E., de Ruiter, P.C., Ebenman, B., Emmerson, M. *et al.* (2004). Interaction strengths in food webs: issues and opportunities. *J. Anim. Ecol.*, 73, 585–598.
- Bertness, M.D., Trussell, G.C., Ewanchuck, P.J. & Silliman, B.R. (2004). Do alternate stable community states exist in the Gulf of Maine rocky intertidal zone? Reply. *Ecology*, 85, 1165–1167.
- Castilla, J.C. & Durán, L.R. (1985). Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). *Oikos*, 45, 391–399.
- Connell, J.H. (1970). A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of Thais. *Ecol. Monogr.*, 40, 49–78.
- Connell, J.H. (1972). Community interactions on marine rocky intertidal shores. *Annu. Rev. Ecol. Syst.*, 3, 169–172.

- Connell, J.H. & Sousa, W.P. (1983). On the evidence needed to judge ecological stability or persistence. *Am. Nat.*, 121, 789–824.
- Dayton, P.K. (1971). Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.*, 41, 351–389.
- Dethier, M.N., Graham, E.S., Cohen, S. & Tear, L.M. (1993). Visual versus random-point percent cover estimations – objective is not always better. *Mar. Ecol. Prog. Ser.*, 96, 93–100.
- Helmuth, B., Harley, C.D.G., Halpin, P.M., O'Donnell, M., Hofmann, G.E. & Blanchette, C.A. (2002). Climate change and latitudinal patterns of intertidal thermal stress. *Science*, 298, 1015–1017.
- Ives, A.R. & Cardinale, B.J. (2004). Food-web interactions govern the resistance of communities after non-random extinctions. *Nature*, 429, 174–177.
- Kokkoris, G.D., Jansen, V.A.A., Loreau, M. & Troumbis, A.Y. (2002). Variability in interaction strength and implications for biodiversity. *J. Anim. Ecol.*, 71, 362–371.
- Kondoh, M. (2003). Foraging adaptation and the relationship between food-web complexity and stability. *Science*, 299, 1388–1391.
- Laska, M.S. & Wootton, J.T. (1998). Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology*, 79, 461–476.
- Lawton, J.H. (1999). Are there general laws in ecology? *Oikos*, 84, 177–192.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J., Hoopes, M. *et al.* (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.*, 7, 601–613.
- Levin, S.A. (1999). *Fragile Dominion: Complexity and the Commons*. Perseus Books, Reading, MA.
- Levin, S.A. & Paine, R.T. (1974). Disturbance, patch formation, and community structure. *Proc. Natl Acad. Sci. USA*, 71, 2744–2747.
- Lewontin, R. (1969). The meaning of stability. In: *Diversity and Stability in Ecological Systems*. Brookhaven Symp. Biol., 22. Brookhaven National Laboratory, Brookhaven, New York, pp. 13–24.
- Margalef, R. (1969). Diversity and stability: a practical proposal and a model of interdependence. In: *Diversity and Stability in Ecological Systems*. Brookhaven Symp. Biol., 22. Brookhaven National Laboratory, Brookhave, NY, pp. 25–37.
- McCann, K.S., Rasmussen, J.B. & Umbanhowar, J. (2005). The dynamics of spatially coupled food webs. *Ecol. Lett.*, 8, 513–523.
- Menge, B.A., Berlow, E.L., Blanchette, C., Navarrete, S.A. & Yamada, S. (1994). The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecol. Monogr.*, 64, 249–286.
- Miller, T.E. (1982). Community diversity and interactions between the size and frequency of disturbance. *Am. Nat.*, 120, 533–536.
- Navarrete, S.A. (1996). Variable predation: effects of whelks on a mid intertidal successional community. *Ecol. Monogr.*, 66, 301–321.
- Navarrete, S.A. & Castilla, J.C. (2003). Experimental determination of predation intensity in an intertidal predator guild: dominant versus subordinate prey. *Oikos*, 100, 251–262.
- Navarrete, S.A. & Menge, B.A. (1996). Keystone predation: interactive effects of two predators on their main prey. *Ecol. Monogr.*, 66, 409–429.
- Navarrete, S.A. & Wieters, E.A. (2000). Variation in barnacle recruitment over small scales: larval predation by adults and maintenance of community pattern. *J. Exp. Mar. Biol. Ecol.*, 253, 131–148.
- Neutel, A.-M., Heesterbeek, J.A.P. & De Ruiter, P.C. (2002). Stability in real food webs: weak links in long loops. *Science*, 296, 1120–1123.
- Paine, R.T. (1984). Ecological determinism in the competition for space. *Ecology*, 65, 1339–1348.
- Paine, R.T. (1992). Food-web analysis through field measurement of per capita interaction strength. *Nature*, 355, 73–75.
- Paine, R.T. (2002). Advances in ecological understanding: by Kuhnian revolution or conceptual evolution? *Ecology*, 83, 1553–1559.
- Paine, R.T. & Levin, S.A. (1981). Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.*, 51, 145–178.
- Paine, R.T. & Trimble, A.C. (2004). Abrupt community change on a rocky shore – biological mechanisms contributing to the potential formation of an alternative state. *Ecol. Lett.*, 7, 441–445.
- Peacor, S.D. & Werner, E.E. (2004). How dependent are species-pair interaction strengths on other species in the food web? *Ecology*, 85, 2754–2763.
- Petraitis, P.S. & Dudgeon, D. (1999). Experimental evidence for the origin of alternative communities on rocky intertidal shores. *Ecology*, 80, 429–442.
- Petraitis, P.S. & Latham, R.E. (1999). The importance of scale in testing the origins of alternative community states. *Ecology*, 80, 429–442.
- Petraitis, P.S. & Dudgeon, S.R. (2004). Do alternate stable community states exist in the Gulf of Maine rocky intertidal zone? Comment. *Ecology*, 85, 1160–1165.
- Ruesink, J.L. (1998). Variation in per capita interaction strength: thresholds due to nonlinear dynamics and nonequilibrium conditions. *Proc. Natl Acad. Sci. USA*, 95, 6843–6847.
- Sebens, K.P. & Lewis, J.R. (1985). Rare events and population structure of the barnacle *Semibalanus cariosus* (Pallas, 1778). *J. Exp. Mar. Biol. Ecol.*, 87, 55–65.
- Strathmann, R.R. & Branscomb, E.S. (1979). Adequacy of cues to favorable sites used by settling larvae two intertidal barnacles. In: *Reproductive Ecology of Marine Invertebrates* (ed. Stancyk, S.E.). University of South Carolina Press, Columbia, SC, pp. 77–89.
- Sutherland, J.P. (1974). Multiple stable points in natural communities. *Am. Nat.*, 108, 859–873.
- Sutherland, J.P. (1990). Perturbations, resistance, and alternative views of the existence of multiple stable points in nature. *Am. Nat.*, 136, 270–275.
- Tilman, D. (1996). Biodiversity: population versus ecosystem stability. *Ecology*, 77, 350–363.
- Yodzis, P. (1988). The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology*, 69, 508–515.

Editor, Jonathan Chase

Manuscript received 17 October 2005

First decision made 22 November 2005

Manuscript accepted 16 January 2006