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Notes and Comments

Impact of Supply-Side Ecology on Consumer-Mediated Coexistence: Evidence from a Meta-Analysis

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ABSTRACT: Studies of marine nearshore hard substrates have demonstrated that consumers and abiotic disturbances can remove biomass, clearing space for species that are competitively subordinate and subsequently increasing diversity. However, studies often examine the impact of these space-opening forces on diversity in isolation from other potentially interacting factors. In marine systems, space can be closed by recruitment decoupled from local populations. Therefore, we investigated how recruitment influences the impacts of consumers on diversity with a meta-analysis of 27 experiments of community development involving sessile species on marine hard substrates. These studies allowed quantification of recruitment rates, consumer pressure, and species richness of primary space occupants. This meta-analysis demonstrated that consumers generally increase diversity at high levels of recruitment but decrease diversity at low levels of recruitment. Therefore, species diversity of sessile species is controlled by the interaction between forces that open (predation and herbivory) and close (recruitment) space.

Keywords: diversity, marine, meta-analysis, recruitment, rocky intertidal, succession.

Mechanisms that remove biomass of space-occupying organisms can maintain diversity in communities by opening up space for organisms that would otherwise be excluded through competition (Paine 1966; Dayton 1971; Connell 1978; Sousa 1979). Abiotic mechanisms include disturbance such as cyclones, waves, floods, and boulder turning (Connell 1978; Sousa 1979; Reice et al. 1990; Death and Winterbourn 1995; Connell et al. 1997). Biotic mechanisms include activities of mobile organisms, especially of consumers (Paine 1966; Paine and Vadas 1969; Platt 1975; Lubchenco 1978; Menge et al. 1994). However, the effect of disturbance on sessile species diversity can vary with the local rate of space closure (Huston 1979, 1994). In marine systems, space can be closed by recruitment decoupled from local populations and opened by disturbances or consumers (Menge 2000). We examined the relationship between space-closing mechanisms, space-opening mechanisms, and diversity, specifically investigating how the impact of consumers on sessile prey species diversity changed depending on the local rate of recruitment. In this note, we propose and test the hypothesis that effects of consumers on diversity are context dependent. Specifically, we expect consumer impacts on diversity to be most positive when competitive exclusion would otherwise occur, due to high recruitment.

A variety of conceptual models have been developed to explore how diversity may be influenced by processes that alter biomass of sessile organisms (Connell 1978; Huston 1979, 1994; Dial and Roughgarden 1998). All indicate that strong competition tends to reduce diversity. Two main factors—productivity and recruitment—have been suggested to increase biomass of space occupants and intensify competition, whereas disturbance has long been suggested to reduce competition. Alternatively, competition for space is expected to be weak under low-biomass conditions, and additional biomass removal could remove species. Diversity is expected to show a unimodal relationship with disturbance (Paine and Vadas 1969; Grime 1973*a*, 1973*b*; Connell 1978) and with recruitment (Roughgarden 1986; Dial and Roughgarden 1998). Both biomass-enhancing and biomass-reducing factors were included in Huston's (1994) model of species diversity, which predicts highest diversity along a range of conditions where production is countered by biomass removal by disturbance (Kondoh 2001) or consumers (Worm et al. 2002). Finally, Menge and Sutherland (1976, 1987) considered the separate effects on diversity of environmental stress (abiotic distur-

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bance) and consumers. Although they predicted that the relative importance of these two biomass-removing processes would vary, both were expected to reduce competition, leading to higher species diversity, until environmental stress created conditions that most species could not tolerate. These authors also included recruitment as a biomass-enhancing factor, which at high levels would lead to competitive exclusion if not for disturbance or consumers (Menge and Sutherland 1976, 1987).

These conceptual models have motivated substantial research that has allowed these hypotheses to be tested both within and across studies (e.g., Proulx and Mazumder 1998; Smith and Witman 1999). Previous across-study synthesis generally supports Huston's (1994) model because consumers reduce diversity at low nutrient levels but increase diversity in areas with high nutrient levels (Proulx and Mazumder 1998; Worm et al. 2002). However, the intermediate disturbance hypothesis was not well supported by across-study synthesis. Studies examining diversity across a gradient of disturbance do not regularly reveal unimodal relationships, perhaps due to the difficulty of defining an "intermediate" level of disturbance (Mackey and Currie 2002). Alternatively, the relationship between productivity and diversity is often unimodal but is highly variable (Mittlebach et al. 2001) and is likely dependent on scale (Chase and Leibold 2002). However, the interactive effects of recruitment and consumers on diversity have not yet been explored through data synthesis.

In marine systems, while previous studies have recognized the importance of biomass removal or of recruitment, a synthesis would greatly improve understanding of context-dependent impacts of consumers on diversity. Diversity often varies among shorelines with similar disturbance regimes (Menge 1992; Connolly and Roughgarden 1998), and it is well known that consumers also influence local diversity (Paine 1966). Similarly, diversity also varies with recruitment. Depending on the community studied, increased recruitment has been observed to increase (Smith and Witman 1999) or decrease diversity (Robles 1997). Low recruitment is often cited as a cause for low diversity in certain nearshore communities (Wethey 1985; Robles 1997; Smith and Witman 1999). Recruitment is variable at a variety of temporal and spatial extents and resolutions (Gaines and Roughgarden 1985; Roughgarden et al. 1988; Sutherland 1990; Minchinton and Scheibling 1991; Robles 1997; Connolly and Roughgarden 1998; Connolly et al. 2001). Therefore, observed differences in diversity in marine systems could be caused in part by recruitment patterns. Finally, previous studies have observed that the impacts of disturbance or consumers on diversity can be influenced by recruitment (Dayton 1971; Underwood et al. 1983; Gaines and Roughgarden 1985; Robles 1997; Shurin 2001).

We hypothesized that rates of prey propagule supply and consumers interact to influence species coexistence in nearshore communities of space-occupying organisms. Specifically, consumers should primarily reduce diversity under low-recruitment conditions whereas diversity should increase with consumers (and eventually decline if consumers are very abundant) under high-recruitment conditions (fig. 1*A*). At intermediate levels of recruitment, the impacts of consumers on diversity may be unpredictable (fig. 1*B*). These predictions are based on mechanisms suggested by Huston (1979, 1994)—that local diversity is highest when space closure (and subsequent competitive exclusion) is prevented by sufficient but not excessive biomass removal even though there are inherent complexities and feedbacks in predator-prey dynamics (e.g., Menge 1992; Ruesink 1998).

To test for predictable effects of consumers under low- versus high-recruitment conditions, we performed a meta-analysis of studies of community development involving sessile species on marine hard substrates. We focused on cases where taxa were recorded at two or more levels of consumers (with and without consumers, many or few consumers) and where we could estimate recruitment based on the rate of early-successional loss of bare space. We calculated the effect of consumers on Shannon-Weiner diversity (H') for a given level of recruitment. This review addresses a small but important portion of factors suggested to influence local diversity through their effects on biomass.

Methods

We used meta-analysis to quantify the impacts of recruitment and consumers on species coexistence on marine hard substrates. Meta-analysis uses variance and sample size to weight the effect of interest, allowing proper synthesis of data from previous studies (Hedges and Olkin 1985; Osenberg et al. 1999). This type of analysis is ideal for testing whether ecological patterns are context dependent or consistent across studies (e.g., Osenberg et al. 2003). We used meta-analysis to examine whether the local recruitment of a study influences how consumers impact diversity. We searched the literature for previous studies that manipulated consumers, and for each study we calculated the effect of consumers on Shannon-Weiner diversity using Hedges's d as our effect size (Hedges and Olkin 1985). Subsequently, we examined whether the level of recruitment influenced the effect size across all studies.

We calculated the average Shannon-Weiner diversity (H') of the diversity of sessile species on the plot or plate of experimental (with consumers) and control (without consumers) treatments at the end of the experiment,

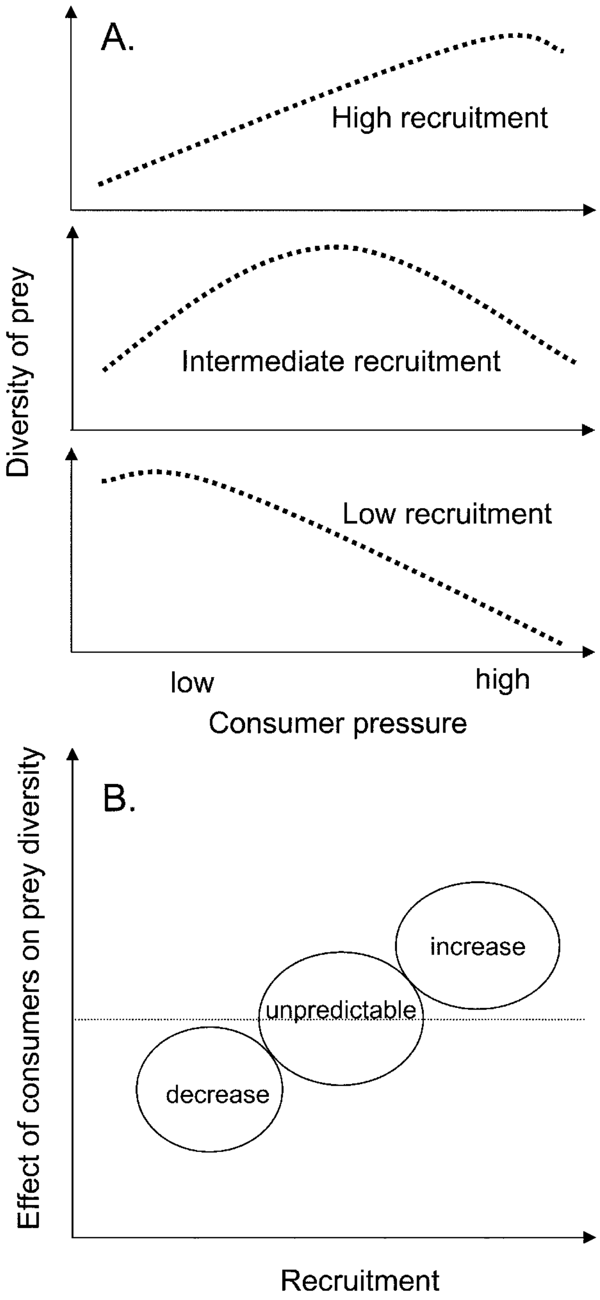

Figure 1: *A*, Predicted relationship between consumers and diversity of their sessile prey at different levels of recruitment (modified from Huston 1994). Consumers include both herbivores and predators. Higher consumer pressure represents higher biomass removal of prey, which could be driven by an increase in number, species, or biomass of consumers. *B*, Predicted relationship between the level of recruitment and the impact of increased consumption on sessile prey diversity. The dashed line corresponds to no change in diversity with more consumers. We investigated the relationship between recruitment, consumers, and diversity by comparing diversity at low and high consumer pressure at various recruitment levels.

$$H' = -\sum (p_i \times \ln p_i),$$

where p is the cover of i species relative to total cover (not including bare space). We used proportional cover data that were presented in text, graphs, or tables. We chose the Shannon-Weiner index because it incorporates richness as well as evenness, it has power to distinguish diversity between sites, and its variance can be easily estimated (Magurran 1988). Because species richness in these studies was generally low, with only 2.6 species on average in each plot or plate, H' primarily reflects richness rather than evenness. However, because these studies were not explicitly investigating diversity, it is possible that researchers did not present data on rare or nontarget species; thus, our calculation of diversity should be considered a conservative estimate.

We estimated the variance of H' ($\mathrm{Var}_{H'}$) following Magurran (1988):

$$\mathrm{Var}_{H'} = \frac{\sum p_i(\ln p_i)^2 - (\sum p_i \times \ln p_i)^2}{N_{\mathrm{ind}}} + \frac{S-1}{2N_{\mathrm{ind}}^2},$$

where S is the species richness and N_{ind} is the number of individuals sampled. Because studies presented proportional cover data rather than the true number of individuals sampled, we estimated the number of individuals sampled as

$$N_{\mathrm{ind}} = n \times R \times \sum p_i,$$

where n is the number of replicates in the experiment and R is the number of points in the community composition sampling protocol (studies either used a grid with R squares or a series of point estimates with R points to record proportion cover) multiplied by the total observed cover. Thus, the meta-analysis attributed a larger (in magnitude) effect size to studies that had more points in the sampling protocol, although R was relatively consistent (94 ± 9.1; average ± SE).

We used Hedges's d as our effect size (Hedges and Olkin 1985), calculated as

$$d = \frac{(H'^{\mathrm{E}} - H'^{\mathrm{C}})}{\mathrm{SD}_{\mathrm{pooled}}} J,$$

where

$$J = 1 - \frac{3}{4(n^{\mathrm{C}} + n^{\mathrm{E}} - 2) - 1},$$

and the pooled standard deviation ($\mathrm{SD}_{\mathrm{pooled}}$) is

$$\mathrm{SD}_{\text{pooled}} = \sqrt{\frac{(n^{\mathrm{E}}-1)(\mathrm{SD}^{\mathrm{E}})^2 + (n^{\mathrm{C}}-1)(\mathrm{SD}^{\mathrm{C}})^2}{n^{\mathrm{E}}+n^{\mathrm{C}}-2}},$$

where n is the number of replicates of the experimental (with consumers, n^{E}) or control (without consumers, n^{C}) treatments of each study and SD is the standard deviation of the experimental (E) or control (C) treatments. We calculated SD from the previously calculated $\mathrm{Var}_{H'}$. Thus, a negative effect size (d) indicates that consumers decreased diversity, while an effect size of 0 represents a scenario where consumers did not alter diversity, and a positive effect size indicates that increased consumer pressure increased diversity. The larger the absolute value of the effect size, the larger the effect.

We searched the literature for studies for our meta-analysis that followed succession on marine hard substrates as well as manipulated consumer densities. We searched the following databases: BIOSIS, Zoological Abstracts, and Aquatic and Fisheries Abstracts. Search terms included: "marine" or "ocean" or "estuar*," "succession" or "recruitment," "clearing" or "cleared" or "fouling" or "settl*." Several hundred articles contained these terms, and we read abstracts to narrow the search further. We supplemented our formal literature search with other articles of which we were also aware. We excluded studies from our analyses if we were unable to interpret or calculate variance or effect size.

The studies we included met the following three criteria. First, the studies focused on space occupants on hard substrates in marine intertidal and subtidal areas. Second, studies included experimental manipulations of consumers. These manipulations were achieved by adding or removing slow-moving consumers such as limpets or by excluding suites of mobile consumers with fences and cages. Third, all studied areas began with bare substrate, and community structure (species-specific cover) was recorded at least twice thereafter. Bare substrate was achieved by either clearing areas of preexisting organisms or setting out new substrate for organisms to colonize. Initial loss of bare space in reduced consumer plots was used as a surrogate for recruitment. This initial loss of bare space was calculated between the start of the study and the first measurable cover, normalized to a monthly rate. Our metric of recruitment includes arrival of propagules but is also affected by factors such as local dispersal, leaning by neighboring individuals, and somatic growth (e.g., Paine and Levin 1981; Sousa 1984). The initial rate of space closure on settling tiles has been previously used as an index of settlement rate (Kiirikki and Lehvo 1997; Worm et al. 2001). We did not use the number of propagules settling through time as our recruitment index because most studies did not report these data.

To determine whether change in percentage cover is an adequate index of recruitment, we compared percentage cover to the number of recruits in one study that included 17 cases with both types of data (Dayton 1971). Number of individuals recruiting was positively and significantly related to monthly cover change, suggesting that recruitment can contribute to space limitation and eventual competitive exclusion ($\ln[\%\ \text{cover mo}^{-1}] = 2.22 \times \ln[\text{propagules d}^{-1}] - 1.26$; $P = .024$, $r^2 = 0.296$, $F = 6.305$, $\text{df} = 1, 16$). Worm et al. (2001) also report a strong relationship between the number of algal recruits and algal cover ($r^2 = 0.51$).

We found 17 articles that described studies that fulfilled our stringent criteria and allowed us to calculate effect size and variance (table 1). Of these, nine performed experiments several times or at several locations. If studies performed more than one experiment at several times at the same location, we calculated the cumulative average effect size and recruitment of that study with weighted averages (Hedges and Olkin 1985; Gurevitch and Hedges 1993; Rosenberg et al. 2000). We combined experiments within each study over time because recruitment is a highly pulsed event that is temporally variable (e.g., Minchinton and Scheibling 1991; Robles 1997). We considered experiments that were performed at different tidal heights to be at the same site. In other words, if a study performed the same experiments at the same site but at different tidal heights, we regarded these experiments as coming from the same site. However, because recruitment is spatially variable (e.g., Connolly et al. 2001), we considered each experiment that was performed at a different location to be a separate experiment. Thus, there is a single calculation of effect size, recruitment, and variance for each set of experiments that was performed at a site, for a total of 27 experiments.

We used MetaWin (Rosenberg et al. 2000) to analyze how the effect size varied as a function of recruitment. We considered recruitment both as a linear (ln transformed to improve normality) and a categorical variable. Because we predicted a priori that effects would be different across studies (Gurevitch and Hedges 1993), we used mixed-effects models to compare the effect of consumers on diversity (d) as a function of recruitment. MetaWin weights effect sizes based on the inverse of the variance and calculates 95% confidence interval (CI) of the slope of the weighted least squares regression and the effect size for each category. We divided studies into two categories of recruitment (high and low) that represent settlement rates of greater than 13% mo^{-1} ($n = 14$) and less than 13% mo^{-1} ($n = 13$), respectively.

Results

The average study lasted 16.9 ± 2.6 (SE) mo, and initial recovery from bare space occurred at an average rate of

Table 1: Studies included in the review

Citation	Number of locations	Consumer excluded	Location	Average experiment length (mo)	Recruitment (% mo^{-1})
Barkai and Branch 1988	2	General (lobster)	South Africa	6	5–38
Benedetti-Cecchi 2000	1	Limpet	Mediterranean Sea	48	5
Berlow 1997	1	Snail	U.S.A. (Oregon)	28.3	12
Berlow and Navarrete 1997	1	Mixed	U.S.A. (Washington)	18	6
Bertness et al. 2002	2	Mixed	U.S.A. (Maine)	42	5–33
Dayton 1971	6	Mixed	U.S.A. (Washington)	7.8	2–6
Farrell 1991	1	Limpet	U.S.A. (Oregon)	29	4
Jernakoff 1983	1	Mixed	Australia	17	14
Kim 1997	1	Limpet	Canada (British Columbia)	36	5
Liu 1993	1	Limpet	Hong Kong	7	82
Menge 1976	3	General (snail)	U.S.A. (Massachusetts and Maine)	9	19–97
Mook 1983	1	Fish	U.S.A. (Florida)	15	73
Otsuka and Dauer 1982	1	General	U.S.A. (Virginia)	20	100
Russ 1980	1	General (fish)	Australia	7	14
Sousa 1984	1	Limpet	U.S.A. (California)	36	33
Sutherland 1974	1	Fish	U.S.A. (North Carolina)	9	45
Worm et al. 2001	2	General	Baltic Sea (Germany)	9	32–33

13.9% ± 1.27% mo^{-1} (back transformed from ln-transformed data, SE). Across all studies, the effect of consumers on diversity was slightly positive, d averaging 1.30, but was quite variable, and overall effects were significantly heterogeneous (Rosenberg et al. 2000; $Q_{total} = 143.46$; $P < .000001$).

This synthesis of multiple studies matched our prediction that consumers are more likely to increase diversity at high levels of recruitment than at low levels of recruitment (figs. 1*B*, 2) regardless of whether we considered recruitment a continuous or categorical variable. If recruitment was treated as a continuous variable, consumers increased diversity more (a more positive effect size) at higher levels of recruitment ($d = 7.06 \times \ln[\%\ \text{cover}\ mo^{-1}] - 19.2$; $Q = 22.3$, $P < .00001$). Consumers increased diversity more when local recruitment was higher; in studies with recruitment levels above 13% mo^{-1}, consumers increased diversity: $d = 5.57$ ($n = 14$; CI: 1.27 to 9.87). Alternatively, in studies with low levels of recruitment, less than 13% mo^{-1}, consumers generally decreased diversity: $d = -6.70$ ($n = 13$; CI: -12.56 to -0.83). In other words, categorical recruitment was significantly related to the effect size ($Q_{between} = 15.41$, $P = .035$). We observed a similar but statistically weaker relationship between recruitment and effect size even when we combined all of the experiments of a study into a single data point.

Discussion

Our review of community succession on marine hard substrates demonstrates that processes that open (predation and herbivory) and close (recruitment) space both influence species diversity (fig. 2). At high rates of prey recruitment, consumers tended to increase species diversity, occurring in 86% of the studies with recruitment >13% mo^{-1}. This observation is consistent with consumers preventing competitive exclusion and dominance of space by a few species. Alternatively, at low levels of recruitment, consumers tended to decrease species diversity, occurring in 69% of the studies that had recruitment levels <13% mo^{-1}. In low recruitment plots, space may not be limiting even in undisturbed treatments, and increased biomass removal mainly decreases diversity.

These results suggest that diversity on marine hard substrates reflects two opposing local forces that close space or open space. Recruitment delivers propagules, contributing to the rate at which space is closed. In opposition, consumers can remove biomass of settled organisms (and perhaps entire species at the extreme) and open up space for colonization (Paine 1966; Connell 1978). In principle, diversity could be highest along a range of conditions (low consumer pressure/low recruitment to high consumer pressure/high recruitment) where consumers prevent competitive exclusion.

These patterns emerged despite a variety of methodologies and communities examined in studies we reviewed (table 1). For example, the composition of the prey community varied between studies. The plates or patches that were used in these studies were various sizes, which can influence future succession (Paine and Levin 1981; Sousa 1984). Different studies excluded different consumers us-

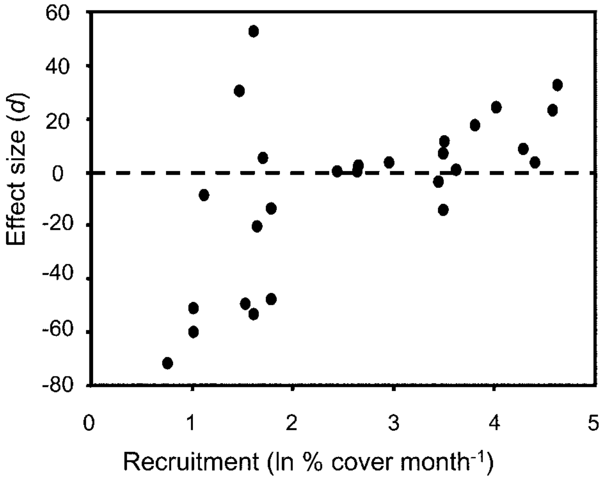

Figure 2: The relationship between recruitment and the impact of consumers on diversity. When *d* was positive, the plots with more consumers had higher diversity. Alternatively, when *d* was negative, then the plots with more consumers had lower diversity than the plots with few consumers. The dashed line through $d = 0$ represents plots where there was no effect of consumers on diversity.

ing a variety of techniques and occurred in locations with different levels of diversity. However, similar consumer systems occurred at a wide range of recruitment levels and thus did not drive the observed pattern (table 1). All of these factors undoubtedly added to the unexplained variance of the results.

Our analyses did not examine the underlying mechanisms of the relationship between recruitment and the impacts of consumers on diversity. Several possible mechanisms exist. First, increased recruitment increases the delivery of larvae of competitively dominant species. At high levels of recruitment, there are more propagules of the competitive dominant species than at lower recruitment, and diversity will decrease unless countered by increased biomass removal (Dial and Roughgarden 1998).

Second, recruitment covaries with food delivery that enhances postrecruitment growth. The initial rate of space closure, which we used to indicate recruitment, undoubtedly also reflects some postsettlement growth. It is not possible from these data sets to distinguish the contributions of recruitment and growth to space closure. If postrecruitment growth is primarily responsible for changes in cover, then these results support Huston's dynamic equilibrium model (Huston 1979, 1994; Kondoh 2001; Worm et al. 2002) for marine systems that vary in secondary as well as primary productivity. Both of these mechanisms above suggest that rapid competitive exclusion occurs at locations with high propagule or food delivery in the absence of consumers.

The studies in this note were not specifically designed to test the interaction of recruitment and consumers on diversity. Thus, the gradient in recruitment was available only by comparing across studies. Explicit tests of the model (fig. 1) would involve simultaneous manipulation of propagule delivery and consumer abundance (e.g., Lotze et al. 2000; Shurin 2001; Worm et al. 2001) while measuring diversity. Our results support those of Shurin (2001), who demonstrated that predators can decrease zooplankton diversity in systems without dispersal, while in systems with dispersal predators increase or have no impact on diversity.

Ecologists are increasingly challenged to understand and predict context specificity of species interactions. In this review of succession on marine hard substrates, initial loss of bare space was related to later impacts of consumers on diversity. The local rate of propagule supply may be an important general consideration in predicting how communities respond to consumers.

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Literature Cited

Barkai, A., and G. M. Branch. 1988. The influence of predation and substratal complexity on recruitment to settlement plates: a test of the theory of alternative states. Journal of Experimental Marine Biology and Ecology 124:215–237.

Benedetti-Cecchi, L. 2000. Predicting direct and indirect interactions during succession in a mid-littoral rocky shore assemblage. Ecological Monographs 70:45–72.

Berlow, E. L. 1997. From canalization to contingency: historical effects in a successional rocky intertidal community. Ecological Monographs 67:435–460.

Berlow, E. L., and S. A. Navarrete. 1997. Spatial and temporal variation in rocky intertidal community organization: lessons from repeating field experiments. Journal of Experimental Marine Biology and Ecology 214:195–229.

Bertness, M. D., G. C. Trussell, P. J. Ewanchuk, and B. R. Silliman. 2002. Do alternate stable community states exist in the Gulf of Maine rocky intertidal zone? Ecology 83:3434–3448.

Chase, J. M., and M. A. Leibold. 2002. Spatial scale dictates the productivity-biodiversity relationship. Nature 416: 427–430.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1311.

Connell, J. H., T. P. Hughes, and C. C. Wallace. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecological Monographs 67:461–488.

Connolly, S. R., and J. Roughgarden. 1998. A latitudinal gradient in northeast Pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. American Naturalist 151:311–326.

Connolly, S. R., B. A. Menge, and J. Roughgarden. 2001. A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. Ecology 82: 1799–1813.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41:351–389.

Death, R. G., and M. J. Winterbourn. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. Ecology 76:1446–1460.

Dial, R., and J. Roughgarden. 1998. Theory of marine communities: the intermediate disturbance hypothesis. Ecology 79:1412–1424.

Farrell, T. M. 1991. Models and mechanisms of succession: an example from a rocky intertidal community. Ecological Monographs 61:95–113.

Gaines, S., and J. Roughgarden. 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proceedings of the National Academy of Sciences of the USA 82: 7307–7311.

Grime, J. P. 1973*a*. Competitive exclusion in herbaceous vegetation. Nature 242:344–347.

———. 1973*b*. Control of species density in herbaceous vegetation. Journal of Environmental Management 1: 151–167.

Gurevitch, J., and L. V. Hedges. 1993. Meta-analysis: combining the results of independent experiments. Pages 378–398 *in* S. M. Scheiner, J. Gurevitch, eds. Design and analysis of ecological experiments. Chapman & Hall, New York.

Hedges, L. V., and I. Olkin. 1985. Statistical methods for meta-analysis. Academic Press, Orlando, Fla.

Huston, M. A. 1979. A general hypothesis of species diversity. American Naturalist 113:81–101.

———. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge.

Jernakoff, P. 1983. Factors affecting the recruitment of algae in a midshore region dominated by barnacles. Journal of Experimental Marine Biology and Ecology 67:17–31.

Kiirikki, M., and A. Lehvo. 1997. Life strategies of filamentous algae in the northern Baltic Proper. Sarsia 82: 259–267.

Kim, J. H. 1997. The role of herbivory, and direct and indirect interactions, in algal succession. Journal of Experimental Marine Biology and Ecology 217:119–135.

Kondoh, M. 2001. Unifying the relationships of species richness to productivity and disturbance. Proceedings of the Royal Society of London B 268:269–271.

Liu, J. H. 1993. The effects of physical factors and grazing by limpets on the colonization, growth and composition of intertidal algae on a rocky shore at Cape D'Aguilar, Hong Kong. Asian Marine Biology 10:27–40.

Lotze, H. K., B. Worm, and U. Sommer. 2000. Propagule banks, herbivory and nutrient supply controls population development and dominance patterns in macroalgal blooms. Oikos 89:46–58.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. American Naturalist 112:23–39.

Mackey, R. L., and D. J. Currie. 2002. The diversity-disturbance relationship: is it generally strong and peaked? Ecology 82:3479–3492.

Magurran, A. E. 1988. Ecological diversity and its measures. Princeton University Press, Princeton, N.J.

Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecological Monographs 46:355–393.

———. 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? Ecology 73:755–765.

———. 2000. Recruitment versus postrecruitment processes as determinants of barnacle population abundance. Ecological Monographs 70:265–288.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. American Naturalist 110:351–369.

———. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist 130:730–757.

Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrette, and S. B. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecological Monographs 64:249–286.

Minchinton, T. E., and R. E. Scheibling. 1991. The influence of larval supply and settlement on the population structure of barnacles. Ecology 72:1867–1879.

Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? Ecology 82: 2381–2396.

Mook, D. 1983. Responses of common fouling organisms in the Indian River, Florida, to various predation and disturbance intensities. Estuaries 6:372–379.

Osenberg, C. W., O. Sarnelle, S. D. Cooper, and R. D. Holt. 1999. Resolving ecological questions through meta-analysis: goals, metrics, and models. Ecology 80: 1105–1117.

Osenberg, C. W., C. M. St. Mary, R. J. Schmitt, S. J. Holbrook, P. Chesson, and B. Byrne. 2003. Rethinking ecological interference: density dependence in reef fishes. Ecology Letters 5:715–721.

Otsuka, C. M., and D. M. Dauer. 1982. Fouling community dynamics in Lynnhaven Bay, Virginia. Estuaries 5:10–22.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65–75.

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs 51:145–178.

Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnology and Oceanography 14:710–719.

Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. Ecological Monographs 45: 285–305.

Proulx, M., and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient-poor versus nutrient-rich ecosystems. Ecology 79:2581–2592.

Reice, S. R., R. C. Wissmar, and R. J. Naiman. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. Environmental Management 14:647–659.

Robles, C. D. 1997. Changing recruitment in constant species assemblages: implications for predation theory in intertidal communities. Ecology 78:1400–1414.

Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 2000. MetaWin: statistical software for meta-analysis. Sinauer, Sunderland, Mass.

Roughgarden, J. 1986. A comparison of food-limited and space-limited animal competition communities. Pages 492–516 *in* J. Diamond and T. J. Case, eds. Community ecology. Harper & Row, New York.

Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. Science 241: 1460–1466.

Ruesink, J. L. 1998. Variation in per capita interaction strength: thresholds due to nonlinear dynamics and nonequilibrium conditions. Proceedings of the National Academy of Sciences of the USA 95:6843–6847.

Russ, G. R. 1980. Effects of predation by fishes, competition, and structural complexity of the substratum on the establishment of a marine epifaunal community. Journal of Experimental Marine Biology and Ecology 42:55–69.

Shurin, J. B. 2001. Interactive effects of predation and dispersal on zooplankton communities. Ecology 82: 3404–3416.

Smith, F., and J. D. Witman. 1999. Species diversity in subtidal landscapes: maintenance by physical processes and larval recruitment. Ecology 80:51–69.

Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60:1225–1239.

———. 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. Ecology 65:1918–1935.

Sutherland, J. P. 1974. Multiple stable points in natural communities. American Naturalist 108:859–873.

———. 1990. Recruitment regulates demographic variation in a tropical intertidal barnacle. Ecology 71:955–972.

Underwood, A. J., E. J. Denley, and M. J. Moran. 1983. Experimental analyses of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. Oecologia (Berlin) 56:202–219.

Wethey, D. S. 1985. Catastrophe, extinction, and species diversity: a rocky intertidal example. Ecology 66:445–456.

Worm, B., H. K. Lotze, and U. Sommer. 2001. Algal propagule banks modify competition, consumer and resource control on Baltic rocky shores. Oecologia (Berlin) 128:281–293.

Worm, B., H. K. Lotze, H. Hillebrand, and U. Sommer. 2002. Consumer versus resource control of species diversity and ecosystem functioning. Nature 417:848–851.

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