

Variation in recruitment and the establishment of alternative community states

P. S. PETRAITIS^{1,3} AND S. R. DUDGEON²

¹*Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104-6018 USA*

²*Department of Biology, California State University, Northridge, California 91330-8303 USA*

Abstract. Mussel beds and rockweed stands (furoid algae) have been shown to be alternative states on rocky intertidal shores in New England, and here the hypothesis that variation in recruitment provides opportunity for the development of alternative community states was tested. Disturbance by ice scour opens patches for development of alternative states, and in winter 1996–1997, 60 experimental clearings of differing sizes were established on Swan’s Island, Maine, USA. Half of the plots were re-cleared during the winter of 2010–2011. Recruitment data for barnacles, mussels, and furoid algae collected from 1997 to 2012 were used to (1) test for persistence of scale-dependent thresholds, (2) estimate the magnitudes and sources of variation, (3) fit a surface of alternative states as defined by the cusp catastrophe, and (4) test if 1997 recruitment would predict 2010–2011 recruitment in re-scraped plots (i.e., a test of divergence, which is expected in systems with alternative states). For barnacles and mussels, recruitment varied enormously year to year and among sites, but showed consistent patterns over the long-term with respect to clearing size. Average recruitment prior to re-clearing was a good predictor of recruitment afterwards. In contrast, over 50% of the variance in furoid recruitment was unexplained with weak effects among years and locations. Past furoid recruitment was a poor predictor of subsequent recruitment. The cusp analysis indicated that furoid recruitment defines the alternative states. Furoid recruitment was largely unpredictable and suggests long-term, small-scale priority effects drive the development of alternative states. These observations strongly reinforce the notion that long-term and well-replicated experiments are necessary to develop robust tests of ecological theory.

Key words: *algae; alternative stable states; barnacles; cusp catastrophe; Gulf of Maine; mussels; recruitment; rocky shores; spatial variation; temporal variation.*

INTRODUCTION

It is well known that ecological processes may vary over several orders of magnitude both spatially and temporally and this variation can have huge impacts on community structure and composition. Large variation in recruitment rates is especially prevalent in organisms that potentially release very large numbers of gametes or offspring and also are capable of dispersing passively over large distances (Kinlan and Gaines 2003). Year-to-year variation in production of offspring coupled with the vagaries of successful long distance dispersal and post-dispersal mortality drive recruitment variation, and this syndrome is commonly found in fungi, terrestrial vascular plants, marine macroalgae, and marine invertebrates (e.g., Santelices 1990, Åberg 1992, Koenig et al. 1994, Santos and Duarte 1996, Herrera et al. 1998, Martiny et al. 2006, Schwartz et al. 2006, Taylor et al. 2006, Broitman et al. 2008). For marine invertebrates and macroalgae, recruitment rates typically vary over

>5 orders of magnitude in both time and space (Santelices 1990, Broitman et al. 2008).

Variation in recruitment is known to affect not only demography and population dynamics (e.g., Fogarty et al. 1991, Doherty and Fowler 1994, Hairston 1996, Gaillard et al. 2003, Secor 2007), but also species interactions and community level processes (e.g., Janzen 1970, Witman et al. 2003, Navarrete et al. 2005). It has also been suggested that variation in recruitment provides a window of opportunity for the development of alternative community states (Petraitis et al. 2009b). There are several theoretical models (e.g., Drake 1991, Fukami 2001, Chase 2003a, Shurin et al. 2004, Fukami and Nakajima 2011), but few experimental tests or observations, of the links between variation of recruitment and the formation alternative stable states (but see Sutherland 1974, Vanschoenwinkel et al. 2007, 2008, Buschke et al. 2013). Whereas biotic interactions and productivity are known to influence and shape the development of alternative stable states in grasslands, lakes, and ponds (e.g., May 1977, Scheffer et al. 1993, 2001, Chase 2003b, Schröder et al. 2005, Petraitis 2013), the influence of recruitment remains an open question. The tremendous variation in recruitment shown by highly fecund, passively dispersing species plus potential

Manuscript received 5 November 2014; revised 30 April 2015; accepted 26 May 2015. Corresponding Editor: E. D. Grosholz.

³ E-mail: ppetrait@sas.upenn.edu

priority effects suggests that recruitment might be a potential driver of alternative states in ecosystems characterized by species with such life history traits.

We document the long-term and broad spatial scale variation in recruitment by mussels, barnacles, and rockweeds, and examine the effects of this variation on the establishment of mussel beds and rockweed stands as alternative community states on rocky intertidal shores. In the Gulf of Maine, USA, the intertidal zone in sheltered bays is dominated either by stands of the fucoid rockweeds (*Ascophyllum nodosum* and *Fucus vesiculosus*) or patches of mussels (*Mytilus edulis*) interspersed with barnacles (*Semibalanus balanoides*). It has been hypothesized that rockweed stands and mussel beds are alternative states, and the switch between states is driven by winter ice scour creating large clearings and subsequent recruitment into these clearings (Petraitis and Latham 1999, Dudgeon and Petraitis 2001, Petraitis and Dudgeon 2004, 2005). Petraitis et al. (2009b) showed experimentally that large clearings made in rockweed stands could, indeed, switch and become mussel beds. However, what has been lacking is a test of whether variation in recruitment can be a driver of this switch.

To make this linkage, recruitment data from 1997 to 2012 for mussels, barnacles, and one species of rockweed (*A. nodosum*) were collected and used to explore how variation in recruitment could drive the development of alternative states. We first used the recruitment data to estimate the sources and magnitudes of spatial and temporal variation, and to look for long-term patterns using both univariate and multivariate approaches. Our data are unique in that almost no studies exist in which the recruitment of codominant species have been examined at the same time and in the same place (but see Broitman et al. [2008] in which mussels and barnacles were studied together). Our data represent the longest continuous observation of recruitment by mussels, barnacles, and fucoid rockweeds on the eastern shores of North America. Long-term trends were examined because there have been reports of declines in mussel recruitment. In addition, the simultaneous observation of all three species allows us to compare directly the sources and magnitudes of variation for each species in relation to the others and to explicitly assess how differences in life history play out as differences in recruitment.

We then used two approaches to assess how variation in recruitment could drive the formation of alternative states. First, theory of alternative states predicts very small differences in starting conditions can lead to very different outcomes and to alternative states (for reviews of experimental studies, see Schröder et al. 2005 and Petraitis 2013). In other words, history matters, and repeating the experiment should not necessarily give the same results as before (Savage et al. 2000, Chase 2003b). Thus, if rockweed stands and mussel beds are alternative states and if we re-clear our experimental plots, past

recruitment should be a poor predictor of subsequent recruitment. To test this, we re-scraped half of our clearings. Second, if variation in recruitment is a driver, then we hypothesized that long-term averages in recruitment could be used to model and predict alternative states and/or smooth thresholds between states (Fig. 1). It is often thought that smooth logistic-like shifts and sudden discontinuous jumps between alternative states is an either/or proposition, but in fact, both can be incorporated into a single model known as a cusp catastrophe for which the theoretical underpinnings are well understood (see Fig. 1; Zeeman 1976, Gilmore 1981, Petraitis 2013). Linear, logistic, and cusp models were fitted and compared. We found not only can recruitment be used to predict mussel beds and rockweed stands as alternative states, but also there are levels of recruitment at which only one state exists. Indeed, the system contains both smooth shifts between states and alternative states.

METHODS

Descriptions of sites and experimental clearings

Experiments were done on sheltered shores of Swan's Island in the Gulf of Maine, USA (44°10' N, 68°25' W). The shores are dominated by stands of fucoid rockweeds (*Ascophyllum nodosum* and *Fucus vesiculosus*) interspersed with patches of mussels (*Mytilus edulis*) and barnacles (*Semibalanus balanoides*). Winter ice scour events periodically open up areas for colonization by algae and invertebrates. In winter 1996–1997, experimental clearings were established to mimic the effects of ice scour. Experimental clearings along with uncleared control plots were created at three sites within each of four bays for a total of 12 replicate sites. At each site, four circular clearings (1, 2, 4, and 8 m in diameter) were made. In winter 2010–2011, half of the plots were re-scraped to test if past recruitment (1997–2008) can predict subsequent (2011–2012) recruitment. Details about the sites, the size and extent of natural ice scour events, the creation and GPS position of plots, and which plots were re-scraped can be found elsewhere (see Supplement 1; also Petraitis and Dudgeon 1999, 2005, Dudgeon and Petraitis 2001, Petraitis and Vidargas 2006, Petraitis et al. 2008, 2009a).

Collection, standardization, and availability of data

Recruitment data were collected on *A. nodosum*, *S. balanoides*, and *M. edulis* from 1997 to 2012. A complete description of the sampling protocol is provided elsewhere (Petraitis et al. 2009a); see Table A1 in Appendix A for information on identification of fucoids, and sampling dates and intervals. Fucoid recruits were assumed to be *A. nodosum* based on when the recruitment tiles were set out (see Appendix A: Table A1); the terms “fucoid” and “rockweed” are used for *A. nodosum* unless otherwise stated. Data from 1997 to 2007 are available in *Ecological Archives* (Petraitis et al. 2009a); Supplement 2 contains 2008–2012 data, which

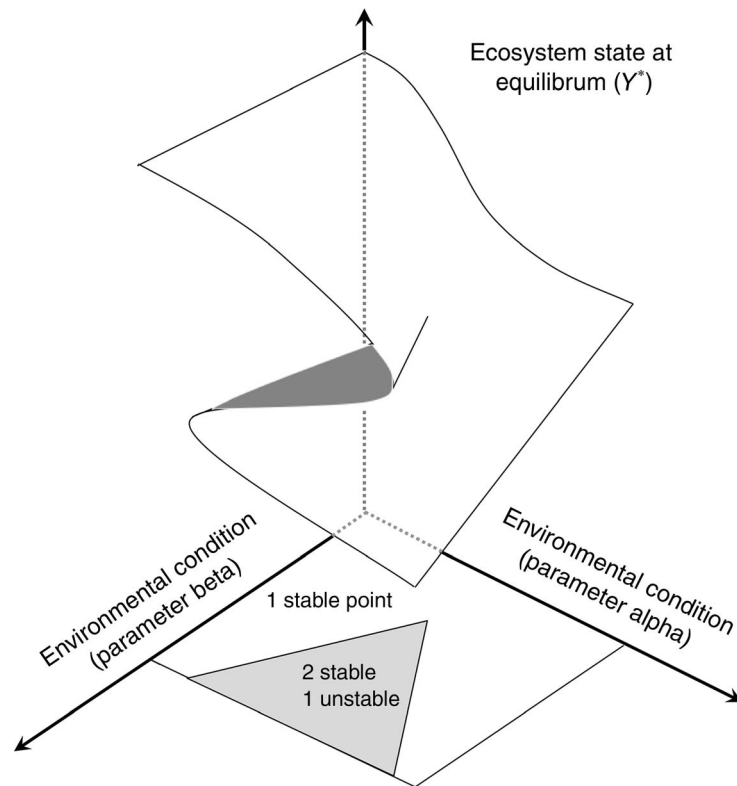


FIG. 1. The equilibrium surface for a cusp catastrophe. Alpha and beta define the parameter space, and Y^* is the equilibrium state of the system. Alpha and beta are model parameters (i.e., fixed values that at which there is one or three equilibrium points). There is a specific combination of alpha and beta at which Y^* forms a kink or cusp and divides (bifurcates) into two folds and three surfaces. The two outermost surfaces define stable equilibrium points; the inner surface, unstable equilibrium points. The folds are where there are discontinuous jumps between stable points. The shaded region on the parameter surface shows areas with multiple stable points. Outside of this area and at all other combinations of alpha and beta, there is only one stable point.

can be appended seamlessly to the 1997–2007 data file. For analyses done here, recruitment rates are standardized because exposure time of recruitment substrates, the length of time that recruitment was assayed, varied from year to year. Data were $\log_{10}(x + 1)$ -transformed for analyses.

Analysis

What are the sources of variation and are there thresholds?—The overall experimental design was a mixed-effects model with clearing size, bays, and years being fully crossed and with sites nested within bays. Size was considered fixed; the main effects of bays, years, sites nested within bays, and all interactions were considered random. The relative contributions of location and time to the variation in recruitment were examined using variance components and Burnham and Anderson's (2002) approach for inferring the best-supported model (see Appendix B for details of Burnham and Anderson's approach). We also tested for the presence of thresholds at specific sizes of clearings using competing models because thresholds were reported previously (Dudgeon and Petraitis 2001).

Data on all three taxa were also examined in a single multivariate analysis to assess if recruitment of the three species covaried. If recruitment of the three species were highly correlated, then it would be unlikely we could disentangle recruitment variation into two independent variables (i.e., alpha and beta in Fig. 1) as required to undertake the cusp analysis. Constrained analysis of proximities (also known as constrained analysis of principal coordinates or CAP) was used for the multivariate analysis and tested using permutation tests. CAP is a constrained multidimensional scaling (MDS); that is CAP is an analog of discriminant analysis as MDS is an analog of PCA.

Analyses were carried out using R (version 2.15.2; R Development Core Team 2012) and used only data collected prior to re-scraping (1997–2008) to avoid confounding effects of re-scraping, which was done in 2010–2011. See Supplement 3 for details about analyses, R scripts, and data files.

Fitting a cusp surface.—Cusp surfaces were fitted using percent cover to define the ecosystem state and average recruitment rates as parameters (Fig. 1). Fitting was done using the R package cusp. The state of the

system (i.e., Y) was defined as a linear combination of percent cover by mussels, barnacles, *A. nodosum*, and *F. vesiculosus* in 2005 because these 2005 data were used in the discriminant analysis that defined mussels and rockweeds as alternative states (Petraitis et al. 2009b). The parameters alpha and beta were defined as linear combinations of the average 1997–2004 recruitment rates for mussels, barnacles, and fucoids. Seven different combinations were tested. Each run of the package cusp fits three models (linear, logistic, and cusp) for a total of 21 models tested. Y is fitted by solving a cubic equation (see Grasman et al. 2009; Appendix A: Table A6). Models were evaluated using Akaike's information criterion corrected for sample sizes, AIC_c . See Supplement 4 for data and R script.

Temporal patterns.—Half of the clearings were re-scraped in winter 2010–2011 to test for divergence and if past recruitment could predict subsequent recruitment. Data from 1997–2008 were used to estimate past recruitment, and data from 2011–2012 were used to estimate subsequent recruitment. Data were analyzed in several ways. We first examined the correlations between recruitment in 1997 and the 2011–2012 averages and then, between the 1997–2008 averages and the 2011–2012 averages. We used two estimates of past recruitment (i.e., data from 1997 only and 1997–2008 averages) because we were concerned that data from a single year could be too idiosyncratic and misleading (see comments of Bourget and Fortin [1995]) and because we wanted to assess if there was a signature of clearing size on the long-term averages. Second, Mantel tests were used to test the concordance in recruitment in individual plots before and after scraping.

Third, we expected to see an interaction between the effect of scraping and the effect of clearing size. We expected plots that were re-scraped would show scale-dependent effects as reported in Dudgeon and Petraitis (2001), but we predicted scale dependence would not be seen in plots that were left intact. We compared competing models using data from 2011 and 2012, which were the years for which we had data from both re-scraped and intact plots. Data files, details of analyses, and R scripts are provided in Supplements 5 and 6.

We also examined the long-term trends in mussel recruitment because the plot of 1997 vs. 2011–2012 averages revealed much lower recruitment in 2011–2012. The average long-term trend was estimated using variance-weighted meta-analysis on the regression coefficients for each plot because of the amount of plot-to-plot variation (Becker and Wu 2007).

RESULTS

Sources of variation in recruitment

Results from the analyses of competing models for rockweeds, barnacles, and mussels are surprisingly similar. All of the best models that are well supported (deltas less than 2.6) contain most of the higher order

interactions. The full model, which contains all possible interactions, is the second best model for mussels and barnacles, and the third best model for rockweed (Appendix A: Table A2).

Examination of variance components shows the sources of variation are quite different for barnacles and mussels vs. fucoids (Fig. 2). Barnacles and mussels show huge year-to-year variation with moderate amounts of variation due to location (i.e., sites and bays) and interactions involving sites nested within bays. In contrast, nearly all of the variation in fucoid recruitment is unexplained or is due to interactions involving years. The unexplained variance for fucoids is not due to variation in zygote supply since all of the experimental clearings are surrounded by extensive stands of *A. nodosum* with virtually 100% cover.

Multivariate analysis in which recruitment rates of all three taxa are combined gives a similar answer. The constrained analysis of proximities (CAP) shows all main effects and all two-way interactions are significant (Appendix A: Table A3). CAP plots show variation among years is far greater than variation among bays or clearings of different sizes (note the differences in the spread of the centroids in Appendix A: Fig. A1). More importantly, recruitment rates for barnacles, mussels, and fucoids do not co-vary (see isoclines in Appendix A: Fig. A1; fucoids are correlated with both axes, barnacles with CAP 1, and mussels with CAP 2).

The best-supported models indicate thresholds in recruitment exist for mussels, barnacles, and fucoids at distinct breaks in clearings of different sizes (Fig. 3; Appendix A: Table A4). Mussel recruitment is greatest in clearings less than 4 m in diameter and barnacle recruitment is lowest in clearings less than 2 m in diameter. Analysis of fucoid recruitment shows nearly equal support for exponential decline and for a threshold between clearings that are 1 and 2 m in diameter.

Recruitment defines a cusp surface

The best-supported cusp model has fucoid recruitment as the parameter alpha and mussel recruitment as beta (Fig. 4; Appendix A: Table A5). No combination of rates provides a better supported model. The ecosystem state (Y) is defined by understory cover by barnacles and canopy cover by rockweeds; understory cover by mussels contributes very little (Appendix A: Table A6). The predicted values clearly show a bimodal distribution of the cover index when plotted against fucoid recruitment (Fig. 4), and the two groups of points are in nearly complete concordance with the assignment previously done using discriminant analysis (Petraitis et al. 2009b).

Temporal patterns

The results of the three separate tests, which were done to examine the predictability of re-scraping, are mixed. On one hand, Mantel tests and models including

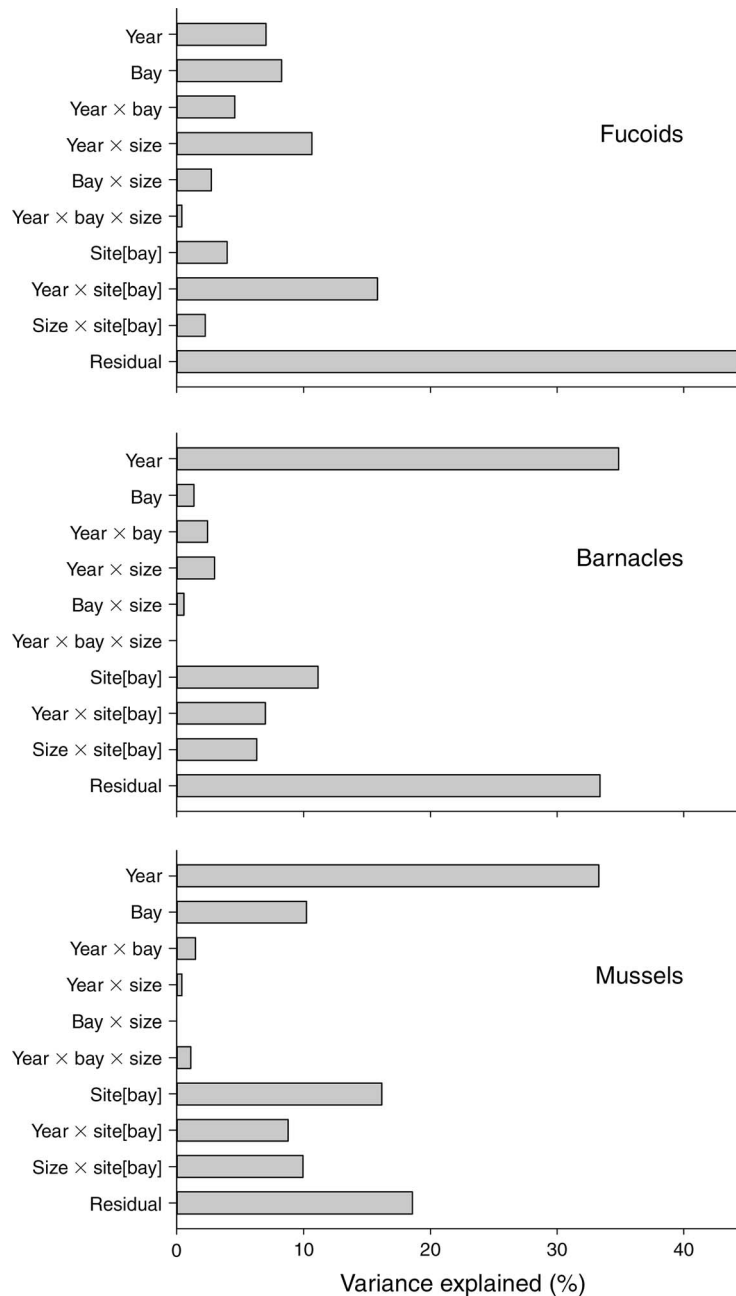


FIG. 2. Variance components for fucoid, barnacle, and mussel recruitment. Components for all terms are provided although the best-supported models for all three species lack the year \times bay \times size interaction (see Appendix A: Table A2). AIC differences (Δ) for the full models are near 2, suggesting good support for these models.

re-scraping as a factor suggest the average of past recruitment predicts recruitment in 2011–2012. All Mantel tests are significant at $P < 0.001$ (Appendix A: Table A7). The best-supported models include the main effect of scraping, but not the interaction of scraping with clearing size as we expected (Appendix A: Table A8). Plots that were re-scraped show less recruitment by rockweeds and more recruitment by barnacles and mussels (Fig. 5). On the other hand, correlations of

recruitment in 1997 explain only moderate fractions of the variation in the 2011–2012 averages: 19.3% for fucoid, 26.4% for barnacles, and 49.0% for mussels (see Appendix A: Fig. A2). There is also a long-term decline in mussel recruitment but not in barnacle or fucoid recruitment (Appendix A: Fig. A3). The average rate of decline for mussels is striking and is 15% per year from 2000 to 2012. This represents a decline of over two orders of magnitude in just over a decade.

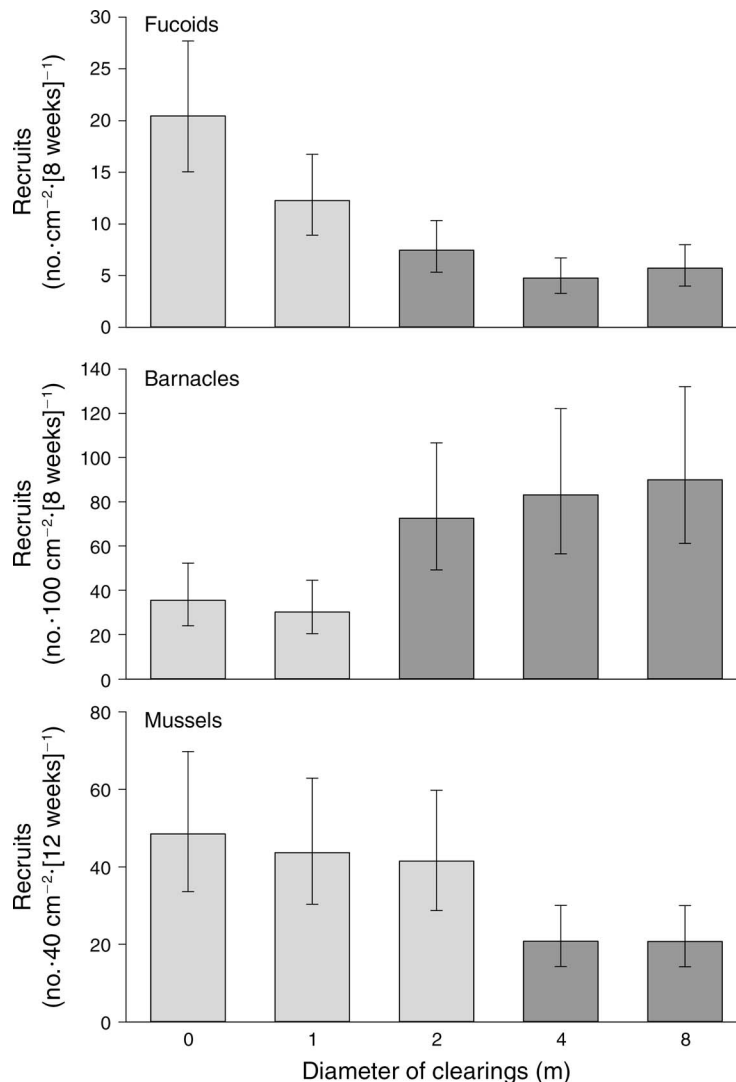


FIG. 3. Average recruitment by fucoids, barnacles, and mussels in clearings of different sizes over the years 1997–2008. On the abscissa, 0 denotes the uncleared control plots. Error bars are 95% confidence limits; averages and confidence limits were calculated by back-transforming log-averages and log-SEs. Shading shows best-supported thresholds.

DISCUSSION

Among the diversity of results from this large data set, we focus on four that stand out from the analyses and their implications. The first involves the specifics of the huge amount variation in recruitment, which is common in marine systems (e.g., see comments of Kinlan and Gaines [2003] and Cornell and Harrison [2013]). The second is the strong consistency of several patterns for barnacles and mussels but less so for fucoids; this includes how well past recruitment predicts subsequent recruitment, the effects of re-scraping, and the long-term signature of clearing size on recruitment rates. Third is the surprising decline in mussels, which has significant implications for establishment of mussel beds as an alternative state. Finally, we address the roles of

variation, consistency, and nonlinearity on the establishment of alternative states.

Variation

One of the most interesting results of this study is the extent to which several sources of variation matter to recruitment of barnacles, mussels, and fucoids. For all three, the best-supported models (among 43 competing models) contained all main effects and nearly all of the interactions between them suggesting recruitment is highly contingent in space and time. Recruitment depends on the bay, the site within a bay, the size of a clearing at a site, and the pattern of recruitment among clearing sizes varies bay to bay. Moreover, the patterns of recruitment among bays, sites, and clearings sizes, as

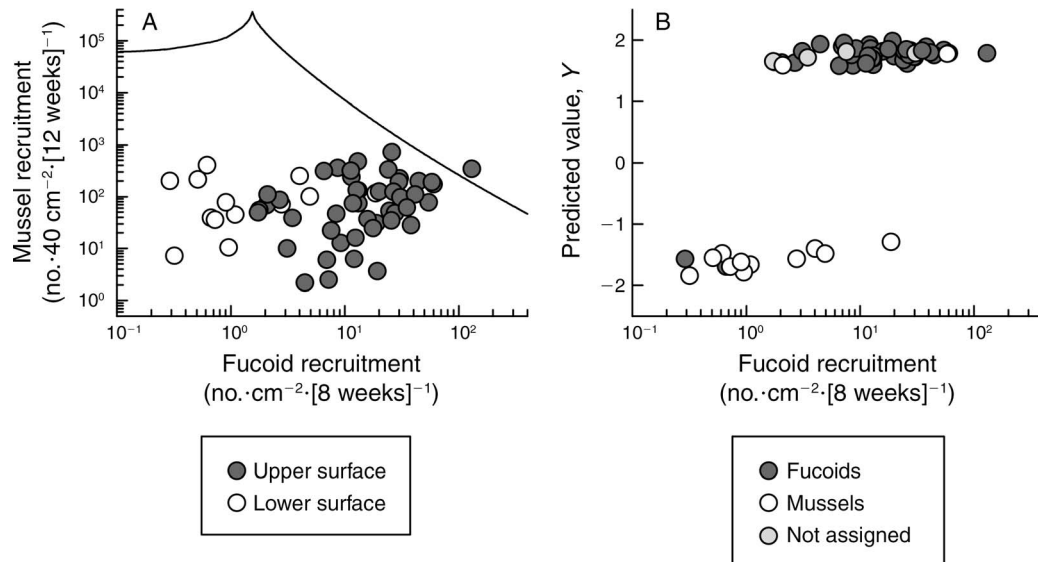


FIG. 4. Cover by barnacles, mussels, and rockweeds fitted onto a cusp catastrophe with mussel and furoid recruitment as parameters. Panel (A) shows the position of plots in parameter space defined by furoid recruitment (the alpha parameter) and mussel recruitment (the beta parameter); note the log–log axis scales. The solid line with the sharp point delimits the border of the region in which there are two stable states (compare with shaded surface in Fig. 1). The shading of the points denotes if a plot is on the upper surface (i.e., in a furoid state) or lower surface (in a mussel state). Note that only one plot is outside of the border. Positions of plots were back-calculated from estimates in Appendix A: Table A6. Panel (B) shows the predicted value of Y , which gives position of plot on either the upper or lower surface, vs. furoid recruitment (log scale), which is the splitting (alpha) parameter. Shading denotes classification of plots as rockweed stands or mussel beds (Petraitis et al. 2009b; see Supplement 2). Values for Y are a standardized linear combination of percent cover by barnacles, mussels, and rockweeds (see Appendix A: Table A6; Supplement 4).

well as the interactions between them, vary enormously from year to year.

The pattern differs for furoids when compared to barnacles and mussels. For both barnacles and mussels, >30% of the variation in their recruitment was due to the year-to-year effect alone and $\geq 10\%$ more due to interactions with year. Other studies of mussels and barnacles show similar patterns of spatial and temporal

variation. Mussel (*Mytilus edulis*) recruitment in New Jersey salt marshes shows greater variation among three years than among three sites (Bologna et al. 2005, see their Fig. 2). On the west coast of the USA, Broitman et al. (2008) report mussel and barnacle recruitment varied spatially over 4–5 orders of magnitude, while temporally over 2–3 orders of magnitude (*Mytilus* spp., *Balanus glandula*, *Chthamalus* spp.). This was an impressive

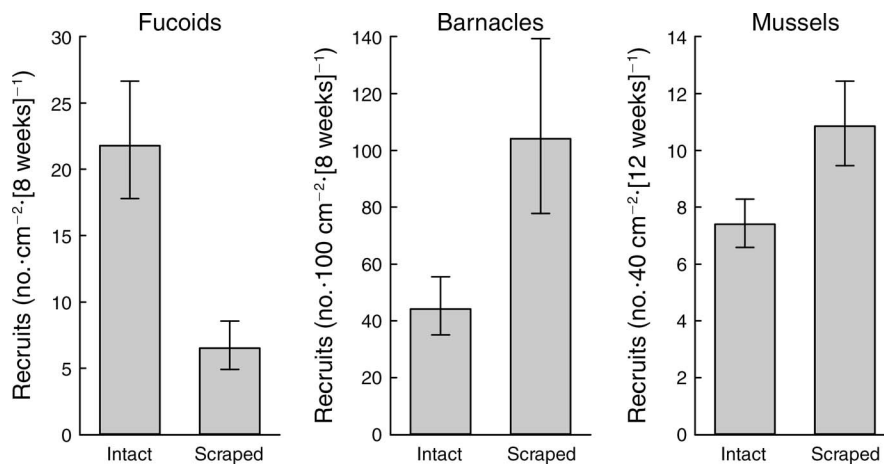


FIG. 5. Average recruitment by furoids barnacles and mussels in plots left intact vs. plots re-scraped. Error bars are 95% confidence limits. Averages were calculated across years, clearing sizes, and locations using log-transformed data; averages and confidence limits shown in figure were calculated by back-transforming log-averages and log-SEs.

study involving 26 sites spanning 1750 km of coastline and monthly sampling over eight years. For barnacles and mussels, which have relatively long-lived pelagic larvae, the large variation among years and areas likely reflects annual variation in oceanographic conditions and availability of phytoplankton in the water column (Kinlan and Gaines 2003, Siegel et al. 2008).

In contrast, furoid recruitment varied mostly from plot to plot with the residual term accounting for nearly 50% of the variance. This is not surprising given furoid zygotes disperse passively on the order of 1–30 meters (Chapman 1995, Dudgeon et al. 2001). Recruitment is thus idiosyncratic on a very small spatial scale, although this small-scale patchiness tends to average out over years and across bays. This averaging is due to the large numbers of zygotes in the water column at any one time during the entire reproductive season.

It is also likely that differences in the sources of post-settlement mortality contributed to the different recruitment patterns of furoids vs. those of barnacles and mussels. While we did not manipulate consumers, the substrates used for estimating recruitment are left out long enough to capture most if not the entire settlement window of each taxon, providing ample opportunity for settlers to die prior to data collection. For barnacles and mussels, small recruits are very susceptible to predation, and thus patterns of predation contribute to some degree to patterns of recruitment. For example, the large variance components for mussel recruitment with respect to year and site match the large variability in the effect size of predators (predation rates by crabs and dogwhelks; S. Dudgeon, E. Rhile, and P. Petraitis, unpublished data). On the other hand, mortality of furoids due to abiotic sources tends to exceed the weaker effects of variably abundant, but ubiquitous, consumers (Brawley and Johnson 1991, Cervin and Åberg 1997, Dudgeon and Petraitis 2005). Thus the large plot-to-plot variability in furoid recruitment reflects the combination of very small-scale variation in arrival of zygotes, abiotic conditions, and consumers.

Consistent patterns

The consistency in the patterns of recruitment for barnacles and mussels is remarkable. Despite enormous spatial and temporal variation, recruitment from a single year in 1997 is a good predictor of average recruitment in 2011–2012 and explains 26–49% of the variation (Appendix A: Fig. A2). In addition, the comparison of plots left intact with plots that were re-scraped in 2011 (Fig. 5) is almost identical with the pattern seen in control plots vs. cleared plots in 1997. Barnacles and mussels recruit more in cleared areas than in areas where the furoid canopy is intact. This is consistent with what is known about mussel and barnacle recruitment, which tends to be lower in areas with overlying canopy cover that also provides habitat for predators of recruits (Dudgeon and Petraitis 2001).

In contrast, patterns of furoid recruitment are not as consistent or predictable. Recruitment in 1997 explains only 19.3% of the variation in recruitment in 2011–2012 (Appendix A: Fig. A2), and for the data from 1997 to 2008, variance component for the residual variation is almost 50% (Fig. 2). Even though there appears to be an effect of re-scraping on furoid recruitment (Fig. 5), comparison of models including and lacking the effect of re-scraping shows nearly identical support for both models (see weights in Appendix A: Table A8). It is notable that furoid recruitment, for which the past is a poor predictor of the future, is the best predictor of the parameter that defines the two surfaces of the cusp catastrophe (Fig. 4).

The differences between barnacles and mussels on one hand and furoids on the other hand are rooted in differences in their biology. Furoid recruits, which are zygotes and disperse passively over very short distances (Dudgeon et al. 2001), show an exponential decline with distance from the edge of the clearing (Fig. 3). Barnacle and mussel recruits are larvae that are capable of positioning themselves in the water column and of dispersing long distances. Thus furoid recruitment is unpredictable at almost all spatial and temporal scales when compared to the more predictable recruitment of barnacles and mussels. This observation is consistent with earlier findings of the importance of life history characteristics in affecting recruitment success in marine, freshwater, and terrestrial ecosystems (McEuen and Curran 2004, Van De Meutter et al. 2007, Siegel et al. 2008, Sams and Keough 2012, Kappes et al. 2014).

Surprises

The long-term decline in mussel recruitment of 15% per year is one of the most surprising results of this study (Appendix A: Fig. A3). We can speculate about the causes but we have no data. It is possible that larval supply has been reduced by ocean acidification and warming (Gazeau et al. 2007, Kurihara 2008, Talmage and Gobler 2010). Another hypothesis is that the decline is due to the boom in green crab (*Carcinus maenas*) densities throughout the Gulf of Maine. The green crab is a nonnative species that arrived in the Gulf of Maine in the 1930s (Roman 2006), but within the last few years, there have been anecdotal reports of declines in clam and mussel beds due to green crab predation (B. Beal, J. Commito, W. Ambrose, personal communication; P. Petraitis and S. Dudgeon, personal observation). Our recruitment pads were not caged and thus open to post-settlement predation by small crabs.

The decline in mussel recruitment has two potential impacts on community dynamics. First, the intertidal system in the Gulf of Maine may become more propagule limited and thus more similar to terrestrial plant communities, which are often seed limited. Second, it is possible that mussel beds may disappear as an alternative state because beds cannot form without the input of recruits. It is an open question if barnacle

barrens will replace mussel beds as an alternative state or if the loss of mussels will lead to a slow but steady reversion of all clearings to rockweed stands.

Implications for the establishment of alternative community states

Most theoretical and experimental studies of the underlying drivers of alternative stable states have focused on biotic interactions and resource availability rather than variation in donor processes such as recruitment (Petraitis 2013). The roles of grazing, competition, and nutrients in the development of alternative stable states have been closely examined (e.g., May 1977, Scheffer et al. 1993, 2001, Chase 2003b, Schröder et al. 2005). While there are a number of models of how variation in recruitment can affect alternative stable states (e.g., Drake 1991, Fukami 2001, Chase 2003a, Shurin et al. 2004, Fukami and Nakajima 2011), there have been few experimental tests on the role of recruitment in alternative stable states. Two notable exceptions are Sutherland's (1974) early work on fouling communities and recent work on rock pools in South Africa (Vanschoenwinkel et al. 2007, 2008, Buschke et al. 2013).

Our results show how variation in recruitment can drive the establishment of alternative states. The cusp analysis suggests the two alternative states, fucoid stands vs. mussel beds, are largely driven by variation in fucoid recruitment (Fig. 4). The more consistent and predictable recruitment by barnacles and mussels does not contribute to the splitting parameter that defines the alternative states. It is also interesting to note that the assignment to mussel or fucoid community states in the cusp analysis matches our prior assignment using discriminant analysis (Petraitis et al. 2009b). Using data collected from naturally occurring mussel beds and rockweed stands in Maine and independent from our study sites to develop a discriminant criterion, Petraitis et al. (2009b) showed that large experimental plots could be classified as mussel beds or rockweed stands. The cusp analysis, which is quite different in approach, produces nearly the same classification.

Other investigators have suggested mussel beds and rockweed stands are not alternative states (Bertness et al. 2002, 2004a, 2004b, Silliman et al. 2013). Implicit in this contention is the idea that mussel beds and rockweed stands are two ends of a spectrum and are different states not alternative states. Yet both scenarios can be accommodated in a single model, such as a cusp catastrophe. If either mussel or rockweed recruitment is extremely dense, then a single stable point for either mussel beds or rockweed stands is expected to prevail. These alternative outcomes would be expected either in areas receiving consistently high input of larval mussels or in areas with consistent rockweed recruitment due to zygote retention, such as in habitats with very little flow, giving rise to rockweed stands (e.g., see descriptions of sites used in Bertness et al. [2002, 2004b]).

Fucoid recruitment is very patchy and highly variable on a very small scale (Fig. 2), and this has three implications for its role in the establishment of alternative states. First, the small-scale spatial variation in fucoid recruitment suggests the development of alternative states is likely to be unpredictable. This unpredictability is due to small differences in starting conditions that cannot be anticipated (i.e., the level of recruitment when a new patch opens for colonization). This variation in starting conditions and its effect on the development of alternative states is known as "the flag of divergence" in catastrophe theory (Zeeman 1976, Gilmore 1981, Petraitis 2013) and is slightly different than Schröder et al.'s (2005) usage of divergence in their discussion of alternative stable states.

Second, fucoid recruitment has some of the characteristics found in seed dispersal of terrestrial plants, and so it is possible that the development of alternative states in our system may be more similar to what is found in terrestrial systems rather than other marine systems. Seed limitation and dispersal distance are critical determinants of plant success or failure (e.g., McEuen and Curran 2004, Freestone and Inouye 2006), and these features are implicit in many models of alternative stable states in plant ecology (Shurin et al. 2004, Fukami and Nakajima 2011). Like the dispersal and establishment patterns of many terrestrial plant species, the small scale patchiness of fucoid recruitment is a consequence of the fact that zygotes disperse very short distances and thus the development of mussel beds vs. fucoid stands may hinge on which species gets to a new open patch first. This gives rise to a priority effect that is scale-dependent, for which McEuen and Curran (2004) coined the phrase, "winning by forfeit."

Third, spatial or temporal variation may cause effects of recruitment to cascade as a consequence of Jensen's inequality, and as a first approximation, size of the bias is proportional to variance (Ruel and Ayres 1999, Martin and Huey 2008). Given that we have shown recruitment rates for mussels, barnacles, and fucoids vary over 3–4 orders of magnitude, it is likely variation in recruitment has a profound effect on the development of mussel beds and fucoid stands as alternative states.

Closing remarks

Variation in ecological processes in space and time colors the intuition of ecologists about how natural ecosystems function. The results of this long-term study demonstrate that temporal and spatial variation in ecological processes following disturbance are extremely important in influencing the trajectory of community development and its outcome. The enormous variation in recruitment underscores the importance of sampling across many sites and over many years if we hope to find robust general patterns in nature. Large variation from place to place or year to year means that conclusions drawn from experiments done over a short timescale or on a small spatial scale are unlikely to provide good

generalizations about ecological phenomena (see comments in Bourget and Fortin [1995] on “hit and run” ecology). Therefore, long-term studies at many sites are necessary to capture the full range of ecological dynamics that shape natural ecosystems.

ACKNOWLEDGMENTS

We are indebted to Erika Rhile and to her students from the Cheverus School in Portland, Maine who helped collect and enter the data. The research was supported by NSF’s program for Long-Term Research in Environmental Biology (DEB 1020480).

LITERATURE CITED

- Åberg, P. 1992. A demographic study of 2 populations of the seaweed *Ascophyllum nodosum*. *Ecology* 73:1473–1487.
- Becker, B. J., and M. J. Wu. 2007. The synthesis of regression slopes in meta-analysis. *Statistical Science* 22:414–429.
- 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.
- Bertness, M. D., G. C. Trussell, P. J. Ewanchuk, and B. R. Silliman. 2004a. Do alternate stable community states exist in the Gulf of Maine rocky intertidal zone? Reply. *Ecology* 85:1165–1167.
- Bertness, M. D., G. C. Trussell, P. J. Ewanchuk, B. R. Silliman, and C. M. Crain. 2004b. Consumer-controlled community states on Gulf of Maine rocky shores. *Ecology* 85:1321–1331.
- Bologna, P. A. X., M. L. Fetzer, S. McDonnell, and E. M. Moody. 2005. Assessing the potential benthic–pelagic coupling in episodic blue mussel (*Mytilus edulis*) settlement events within eelgrass (*Zostera marina*) communities. *Journal of Experimental Marine Biology and Ecology* 316:117–131.
- Bourget, E., and M. J. Fortin. 1995. A commentary on current approaches in the aquatic sciences. *Hydrobiologia* 300:1–16.
- Brawley, S. H., and L. E. Johnson. 1991. Survival of furoid embryos in the intertidal zone depends upon developmental stage and microhabitat. *Journal of Phycology* 27:179–186.
- Broitman, B. R., C. A. Blanchette, B. A. Menge, J. Lubchenco, C. Krenz, M. Foley, P. T. Raimondi, D. Lohse, and S. D. Gaines. 2008. Spatial and temporal patterns of invertebrate recruitment along the west coast of the United States. *Ecological Monographs* 78:403–421.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.
- Buschke, F. T., S. Esterhuysen, M. E. Kemp, M. T. Seaman, L. Brendonck, and B. Vanschoenwinkel. 2013. The dynamics of mountain rock pools: Are aquatic and terrestrial habitats alternative stable states? *Acta Oecologica International Journal of Ecology* 47:24–29.
- Cervin, G., and P. Åberg. 1997. Do littorinids affect the survival of *Ascophyllum nodosum* germlings? *Journal of Experimental Marine Biology and Ecology* 218:35–47.
- Chapman, A. R. O. 1995. Functional ecology of furoid algae: 23 years of progress. *Phycologia* 34:1–32.
- Chase, J. M. 2003a. Community assembly: When should history matter? *Oecologia* 136:489–498.
- Chase, J. M. 2003b. Experimental evidence for alternative stable equilibria in a benthic pond food web. *Ecology Letters* 6:733–741.
- Cornell, H. V., and S. P. Harrison. 2013. Regional effects as important determinants of local diversity in both marine and terrestrial systems. *Oikos* 122:288–297.
- Doherty, P., and A. Fowler. 1994. Demographic consequences of variable recruitment to coral-reef fish populations: a congeneric comparison of 2 damselfishes. *Bulletin of Marine Science* 54:297–313.
- Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. *American Naturalist* 137:1–26.
- Dudgeon, S., J. E. Kubler, W. A. Wright, R. L. Vadas, and P. S. Petraitis. 2001. Natural variability in zygote dispersal of *Ascophyllum nodosum* at small spatial scales. *Functional Ecology* 15:595–604.
- Dudgeon, S., and P. S. Petraitis. 2001. Scale-dependent recruitment and divergence of intertidal communities. *Ecology* 82:991–1006.
- Dudgeon, S., and P. S. Petraitis. 2005. Early life demography of a foundation species and the community-level implications. *Oikos* 109:405–415.
- Fogarty, M. J., M. P. Sissenwine, and E. B. Cohen. 1991. Recruitment variability and the dynamics of exploited marine populations. *Trends in Ecology and Evolution* 6:241–246.
- Freestone, A. L., and B. D. Inouye. 2006. Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. *Ecology* 87:2425–2432.
- Fukami, T. 2001. Sequence effects of disturbance on community structure. *Oikos* 92:215–224.
- Fukami, T., and M. Nakajima. 2011. Community assembly: alternative stable states or alternative transient states? *Ecology Letters* 14:973–984.
- Gaillard, J. M., A. Loison, C. Toigo, D. Delorme, and G. Van Laere. 2003. Cohort effects and deer population dynamics. *Ecoscience* 10:412–420.
- Gazeau, F., C. Quiblier, J. M. Jansen, J.-P. Gattuso, J. J. Middleburg, and C. H. R. Heip. 2007. Impact of elevated CO₂ on shellfish calcification. *Geophysical Research Letters* 34:L07603.
- Gilmore, R. 1981. Catastrophe theory for scientists and engineers. John Wiley and Sons, New York, New York, USA.
- Grasman, R. P. P., H. L. J. van der Maas, and E. J. Wagenmakers. 2009. Fitting the cusp catastrophe in R: a cusp package primer. *Journal of Statistical Software* 32:1–27.
- Hairston, N. G. 1996. Zooplankton egg banks as biotic reservoirs in changing environments. *Limnology and Oceanography* 41:1087–1092.
- Herrera, C. M., P. Jordano, J. Guitian, and A. Traveset. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *American Naturalist* 152:576–594.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–528.
- Kappes, H., O. Tackenberg, and P. Haase. 2014. Differences in dispersal- and colonization-related traits between taxa from the freshwater and the terrestrial realm. *Aquatic Ecology* 48:73–83.
- Kinlan, B. P., and S. D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84:2007–2020.
- Koenig, W. D., R. L. Mumme, W. J. Carmen, and M. T. Stanback. 1994. Acorn production by oaks in central coastal California: variation within and among years. *Ecology* 75:99–109.
- Kurihara, H. 2008. Effects of CO₂-driven ocean acidification on the early developmental stages of invertebrates. *Marine Ecology Progress Series* 373:275–284.
- Martin, T. L., and R. B. Huey. 2008. Why “suboptimal” is optimal: Jensen’s inequality and ectotherm thermal preferences. *American Naturalist* 171:E102–118.
- Martiny, J. B. H., et al. 2006. Microbial biogeography: putting microorganisms on the map. *Nature Reviews Microbiology* 4:102–112.

- May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269:471–477.
- McEuen, A. B., and L. M. Curran. 2004. Seed dispersal and recruitment limitation across spatial scales in temperate forest fragments. *Ecology* 85:507–518.
- Navarrete, S. A., E. A. Wieters, B. R. Broitman, and J. C. Castilla. 2005. Scales of benthic-pelagic and the intensity of species interactions: from recruitment limitation to top-down control. *Proceedings of the National Academy of Sciences USA* 102:18046–18051.
- Petraitis, P. S. 2013. Multiple stable states in natural ecosystems. Oxford University Press, Oxford, UK.
- Petraitis, P. S., and S. R. Dudgeon. 1999. Experimental evidence for the origin of alternative communities on rocky intertidal shores. *Oikos* 84:239–245.
- Petraitis, P. S., and S. R. Dudgeon. 2004. Do alternate stable community states exist in the Gulf of Maine rocky intertidal zone? *Comment. Ecology* 85:1160–1165.
- Petraitis, P. S., and S. R. Dudgeon. 2005. Divergent succession and implications for alternative states on rocky intertidal shores. *Journal of Experimental Marine Biology and Ecology* 326:14–26.
- Petraitis, P. S., and R. E. Latham. 1999. The importance of scale in testing the origins of alternative community states. *Ecology* 80:429–442.
- Petraitis, P. S., H. Liu, and E. C. Rhile. 2008. Densities and cover data for intertidal organisms in the Gulf of Maine, USA, from 2003 to 2007. *Ecology* 89:588.
- Petraitis, P. S., H. Liu, and E. C. Rhile. 2009a. Barnacle, fucoid, and mussel recruitment in the Gulf of Maine, USA, from 1997 to 2007. *Ecology* 90:571.
- Petraitis, P. S., E. T. Methratta, E. C. Rhile, N. A. Vidargas, and S. R. Dudgeon. 2009b. Experimental confirmation of multiple community states in a marine ecosystem. *Oecologia* 161:139–148.
- Petraitis, P. S., and N. A. Vidargas. 2006. Marine intertidal organisms found in experimental clearings on sheltered shores in the Gulf of Maine, USA. *Ecology* 87:796.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Roman, J. 2006. Diluting the founder effect: cryptic invasions expand a marine invader's range. *Proceedings of the Royal Society B* 273:2453–2459.
- Ruel, J. J., and M. P. Ayres. 1999. Jensen's inequality predicts effects of environmental variation. *Trends in Ecology and Evolution* 14:361–366.
- Sams, M. A., and M. J. Keough. 2012. Effects of pulse versus steady recruitment on sessile marine communities. *Oecologia* 170:209–219.
- Santelices, B. 1990. Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanography and Marine Biology* 28:177–276.
- Santos, R., and P. Duarte. 1996. Fecundity, spore recruitment and size in *Gelidium sesquipedale* (Gelidiales, Rhodophyta). *Hydrobiologia* 327:223–228.
- Savage, M., B. Sawhill, and M. Askenazi. 2000. Community dynamics: What happens when we rerun the tape? *Journal of Theoretical Biology* 205:515–526.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–596.
- Scheffer, M., S. H. Hosper, M. L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution* 8:275–279.
- Schröder, A., L. Persson, and A. M. De Roos. 2005. Direct experimental evidence for alternative stable states: a review. *Oikos* 110:3–19.
- Schwartz, M. W., J. D. Hoeksema, C. A. Gehring, N. C. Johnson, J. N. Klironomos, L. K. Abbott, and A. Pringle. 2006. The promise and the potential consequences of the global transport of mycorrhizal fungal inoculum. *Ecology Letters* 9:501–515.
- Secor, D. H. 2007. The year-class phenomenon and the storage effect in marine fishes. *Journal of Sea Research* 57:91–103.
- Shurin, J. B., P. Amarasekare, J. M. Chase, R. D. Holt, M. F. Hoopes, and M. A. Leibold. 2004. Alternative stable states and regional community structure. *Journal of Theoretical Biology* 227:359–368.
- Siegel, D. A., S. Mitarai, C. J. Costello, S. D. Gaines, B. E. Kendall, R. R. Warner, and K. B. Winters. 2008. The stochastic nature of larval connectivity among nearshore marine populations. *Proceedings of the National Academy of Sciences USA* 105:8974–8979.
- Silliman, B. R., M. W. McCoy, G. C. Trussell, C. M. Crain, P. J. Ewanchuk, and M. D. Bertness. 2013. Non-linear interactions between consumers and flow determine the probability of plant community dominance on Maine rocky shores. *PLoS ONE* 8(8):e67625.
- Sutherland, J. P. 1974. Multiple stable points in natural communities. *American Naturalist* 108:859–873.
- Talmage, S. C., and C. J. Gobler. 2010. Effects of past, present and future ocean carbon dioxide concentrations on the growth and survival of larval shellfish. *Proceedings of the National Academy of Sciences USA* 107:17246–17251.
- Taylor, J. W., E. Turner, J. P. Townsend, J. R. Dettman, and D. Jacobson. 2006. Eukaryotic microbes, species recognition and the geographic limits of species: examples from the kingdom Fungi. *Philosophical Transactions of the Royal Society B* 361:1947–1963.
- Van De Meutter, F., L. De Meester, and R. Stoks. 2007. Metacommunity structure of pond macro invertebrates: effects of dispersal mode and generation time. *Ecology* 88:1687–1695.
- Vanschoenwinkel, B., C. De Vries, M. Seaman, and L. Brendonck. 2007. The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. *Oikos* 116:1255–1266.
- Vanschoenwinkel, B., S. Gielen, M. Seaman, and L. Brendonck. 2008. Any way the wind blows: frequent wind dispersal drives species sorting in ephemeral aquatic communities. *Oikos* 117:125–134.
- Witman, J. D., S. J. Genovesi, J. F. Bruno, J. W. McLaughlin, and B. I. Pavlin. 2003. Massive prey recruitment and the control of rocky subtidal communities on large spatial scales. *Ecological Monographs* 73:441–462.
- Zeeman, E. C. 1976. Catastrophe theory. *Scientific American* 234:65–83.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B and Supplements 1–6 are available online: <http://dx.doi.org/10.1890/14-2107.1.sm>