

PROPAGATION OF SCALE-DEPENDENT EFFECTS FROM RECRUITS TO ADULTS IN BARNACLES AND SEAWEEDS

ELIZABETH T. METHRATTA^{1,3} AND PETER S. PETRAITIS^{1,2}

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

²Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Alameda 340, Casilla 114-D, Santiago, Chile

Abstract. The interplay between local and large spatial scale processes in open systems is often dependent upon ecological context and species specific factors such as longevity, dispersal capability, or vulnerability to predation. When disturbance clears patches in open systems, the successful reestablishment of adult colonizers and the trajectory of succession may depend upon both the scale of the disturbance event and scale of life history characteristics. Here we examine the links between the size of a disturbance event and long term patterns of variation in recruitment, density, and percent cover in a relatively short-lived but long-range disperser, the acorn barnacle *Semibalanus balanoides*, and a relatively long lived and short range disperser, the fucoid alga *Fucus vesiculosus*. Further, a model of linked scale-dependent processes is developed and we explore how long term patterns of scale-dependent recruitment are related to successful establishment of adults. Recruitment, densities, and cover were monitored for five years for both species in a single experiment using clearings of different sizes spread over two north-facing and two south-facing bays on Swan's Island, Maine, USA. Barnacle recruitment was particularly variable in small clearings and was lower overall at more interior sites within bays. While local-scale factors also strongly influenced patterns of variation in fucoid recruitment, fucoids dominate surface cover in large clearings and in south-facing bays. Recruitment was a poor predictor of density, whereas density itself was a good predictor of percent cover for both species. These results indicate that scale dependencies, location-specific factors, and life history traits contribute to patterns of community development on rocky shores and may ultimately determine whether an open patch converges to or diverges from its initial community state.

Key words: *Ascophyllum nodosum*; barnacles; *Fucus vesiculosus*; rocky intertidal; scale-dependence; seaweeds; *Semibalanus balanoides*; succession.

INTRODUCTION

Local processes such as predation and competition often dominate the dynamics of ecosystems, but their effects in open systems can be overshadowed by larger spatial and temporal scale processes. Yet the balance between the impacts of local and large-scale processes is ecosystem-specific because both scale and degree of openness are context-specific and depend on life history characteristics of the species involved. In terrestrial systems, large-scale perturbations, such as fires, hurricanes, tree falls, and volcanic eruptions, can have dramatic impacts on community dynamics (Zobel and Antos 1997, Cooper-Ellis et al. 1999, Niklasson and Granstrom 2000, Galhidy et al. 2006). Similarly, aquatic systems can be affected by a diversity of broadscale disturbances: for example, ENSO events, ice scour, oil spills, sediment deposition, and storm damage (Dayton et al. 1992, McCook and Chapman 1993, Dean and

Jewett 2001, Sousa 2001, Thrush et al. 2003, Halford et al. 2004).

Often the impacts of such events depend on the interplay between species-specific responses to disturbance and the spatial scale of the disturbance itself. These patch size-specific effects have been linked to variation in community composition in marine systems, tropical and temperate forests, and old-field communities (e.g., Connell and Keough 1984, Sousa 1984, Brokaw 1985, Galhidy et al. 2006). In forest gaps, for example, larger clearings are associated with greater light intensity, greater subsurface soil moisture and temperature, greater air temperature, greater soil nitrogen concentration, and lower humidity, all of which influence successional patterns (Galhidy et al. 2006, Shure et al. 2006). Such effects suggest that inherent characteristics of patch geometry such as area, the edge to area ratio or distances between the patch interior and the surrounding community are important for succession and community development. Not surprisingly, experiments have demonstrated that communities in small patches tend to converge with the surrounding community (e.g., Connell and Slayter 1977, Runkle 1981, Chapman and Underwood 1998). In contrast,

Manuscript received 23 May 2007; revised 21 December 2007; accepted 12 February 2008; final version received 17 March 2008. Corresponding Editor: J. J. Stachowicz.

³ E-mail: methratt@sas.upenn.edu

dynamics in large patches can become uncoupled from the processes occurring at the edge by virtue of distance from the surrounding community, and so may be more vulnerable to serendipitous events. Thus large experimental clearings have exhibited both convergence with (Connell et al. 1997, Shure et al. 2006) and divergence from (Petraitis and Dudgeon 2005) the surrounding community because the importance of patch size in succession also depends on the life history characteristics of the species involved. For example, patches that are successfully invaded by long-lived species can carry the signature of a single idiosyncratic colonization event for long periods of time.

The variation in community development with patch size is driven not only by the variation in the processes involved but also by the correlations among linked processes. For example, suppose the number of adults in a patch is a two-step process that depends on the arrival of propagules and their survivorship to adulthood (i.e., $N_t = N_0(1 - q)_t$, where N_t = number of adults at time t , N_0 = number of propagules arriving at time 0, and q_t = mortality rate). The combined effects of spatial (s) and temporal (t) scales of variation in arrival and survivorship can be seen by log-transforming the relationship so that $\log N_t = \log N_0 + \log(1 - q_t)$ and noting that the variance in the number of adults is now

$$\sigma_z^2(s, t) = \sigma_x^2(s, t) + \sigma_y^2(s, t) + 2r\sigma_x(s, t)\sigma_y(s, t)$$

where $z = \log N_t$, $x = \log N_0$, $y = \log(1 - q_t)$ and r is the correlation between arrival and survival. Spatial dependence implies that variance changes with s , and thus $\partial\sigma_z^2(s, t)/\partial s \neq 0$. For temporal dependence, $\partial\sigma_z^2(s, t)/\partial t \neq 0$, and canalization during succession occurs when the partial derivative is less than zero while divergent succession occurs when the partial derivative is greater than zero.

More importantly, spatial and temporal dependence can be dampened or enhanced via linked ecological processes, which has several interesting implications. First, if the linked processes are uncorrelated, then the variance in the final process or state (e.g., density of adults) should be larger than the variance of the other processes. Second, if the variance of the final process or state is less than the variance of the other processes, then the correlation between the linked processes must be negative. Third, the scale dependence of the final process or state depends not only on the scale dependence of the other processes but also on the correlation between the two. For example,

$$\frac{\partial\sigma_z^2}{\partial s} = \frac{1}{2}(1 + r\sigma_y)\frac{\partial\sigma_x}{\partial s} + \frac{1}{2}(1 + r\sigma_x)\frac{\partial\sigma_y}{\partial s}.$$

Thus we could imagine canalization of one process as spatial scale increased (e.g., $\partial\sigma_x/\partial s < 0$) and divergence in the other ($\partial\sigma_y/\partial s > 0$), but their relative contributions to the overall scale dependence depend on the correlation between the two. Finally, we have written the relationship between linked processes with the correla-

tion being scale independent, but there is no reason why this should be the case. It is easy to imagine that the correlation between recruitment and survivorship changes with spatial scale or during the course of succession. The end result is that the scale dependent variance of the final process cannot be predicted without an understanding of the scale dependence of the linked processes and the correlation between them.

Here, we examine these scale-dependent effects in a short-lived species, the barnacle *Semibalanus balanoides* and in a long-lived species, the furoid alga *Fucus vesiculosus* (see Plate 1). Barnacles live for several years and arrive on shore as larvae after spending several weeks in the water column. In contrast, *Fucus* may live 20 years or more and can regenerate from very small fragments of holdfasts (S. R. Dudgeon and A. R. O. Chapman, *personal communication*). *Fucus* recruits as zygotes that travel very short distances from parents; the median dispersal distance is on the order of 40 m in a closely related species, *Ascophyllum nodosum* (Dudgeon et al. 2001).

Long-term data on recruitment, density, and percent cover patterns of both species were used to explore the linkages between scale-dependent recruitment and adult success in patches of different sizes. For each species, we collected three sets of data using exactly the same experimental design, and this allowed us not only to address three sets of hypotheses about scale effects but also to make direct comparisons between species and among processes (Underwood and Petraitis 1993, Petraitis 1998). We hypothesized that the averages for and the variances in recruitment, density, and cover for barnacles and *Fucus* would vary on different scales because of life history differences. We also expected that the variances of recruitment, density, and cover would also show scale-dependence with patch size. Finally we expected that our ability to predict cover from densities and densities from recruitment would differ for *Fucus* and barnacles.

METHODS

Study sites and sampling methods

We provide only a short summary here because complete descriptions of the field sites, sampling methods, GPS locations of all experimental plots, and methods and rationale for making the plots can be found elsewhere (Dudgeon and Petraitis 2001, Petraitis and Vidargas 2006). Clearings were created in established beds of *A. nodosum* at 12 replicate sites in 1996 on Swan's Island, Maine, USA. At each site, four circular plots, which were 1, 2, 4, and 8 m in diameter, and an uncleared control plot were established. The clearings were within the size range of clearings made by infrequent ice scour (Petraitis and Vidargas 2006). Sites were spread over four sheltered bays with three sites per bay. Two bays, Mackerel Cove and Seal Cove, face north toward the mainland and two bays, Toothacker Cove and Burnt Coat Harbor, face south toward the

open ocean although the entrance of Burnt Coat Harbor is protected by a nearby island. Recruitment, density, and percent cover by barnacles and *Fucus* were monitored annually from 2000 to 2005. Barnacle recruits (cyprids and metamorphs) were counted on circular fiberglass resin plates (7.1 cm in diameter). *Fucus* recruitment (almost entirely zygotes) was monitored using 5 × 5 cm ceramic tiles with a 0.5 × 0.5 cm grid of grooves to provide settlement sites. Counts for five flats (0.5 × 0.5 cm) and five grooves (0.5 cm in length) on each tile were summed to give a single count per tile. Barnacle plates and *Fucus* tiles were deployed in early March and collected in late May. While this covers most of the period of barnacle recruitment and the early part of the season for *Fucus* recruitment, we purposely used the same sampling period so that recruits of both species were subject to the same conditions (e.g., wind patterns, currents, wave surge, etc). Barnacle recruitment onto plates is correlated with young-of-the-year on natural rock surfaces in June ($r = 0.69$; $P \leq 0.0001$; $n = 66$ pairs; unpublished data from 2004–2006). *Fucus* recruitment onto tiles is not correlated with juveniles in June ($r = -0.04$; $n = 60$ pairs; unpublished data from 1998), suggesting heavy post-settlement mortality.

Petraitis and Vidargas (2006) fully describe the methods used to sample densities and percent covers of *Fucus* and barnacles. Data are available (see Petraitis and Vidargas 2006 for 2000–2001 data; 2003–2005 data unpublished). *Fucus* densities are reported as number per 0.25 m², and barnacles densities as number per 4 cm². For barnacles, we excluded young-of-the-year. For percent cover, we estimated canopy cover by *Fucus* and understory cover by barnacles. For the analyses, we used the averages per plot per year (see Petraitis and Vidargas 2006 for rationale of using plot averages).

Analysis

We used mixed-model analysis of variance (ANOVA), variance components analysis and Levene's test to address differences in scale-dependent effects between *Fucus* and barnacles and among the three types of data: recruitment, density, and percent cover. The main effects were size, bay, site nested within bay, and year, and the model included all possible interactions. The effects of size, year, and size by year were treated as fixed factors, and all other main effects and all interactions were treated as random factors (see Appendix A for details). Years are fixed because we were interested in changes over time; repeated measures could not be used because of missing values. Differences between north-facing and south-facing bays were examined with post hoc tests because these differences were not seen until the data were analyzed. Variance components analyses were done using restricted maximum likelihood methods. Levene's tests were used to assess the variance differences among clearings of different sizes and among different years.

We then used stepwise regression and canonical correlation analysis to examine the linkages between

recruitment and density, and between density and cover. Analyses were done using data matrices of the 60 plots by the five years with plots as replicates and years as variables. Since canonical correlation analysis requires data sets with no missing values, we replaced missing values with the year averages.

Analyses were done using either procedures in SAS (i.e., GLM, VARCOMP, and CANCORR; SAS Institute, Cary North Carolina, USA) or JMP-IN software (SAS Institute). Data were $\log_{10}(100y + 1)$ -transformed, where y is the original variable. Original variables were multiplied by 100 to reduce rounding error and disproportionate effects of very small numbers. While percent cover data are usually arcsine-transformed, we also log-transformed these data so that all analyses would be based on the same underlying model (i.e., effects in all models were assumed to be log-linear).

RESULTS

One or more of the fixed effects of size, year, and size by year were significant in all six ANOVAs (Table 1, Appendix A). Barnacle recruitment, density, and cover mostly vary on the scale of sites within bays and in the interactions of sites within bays by years and by sizes (Table 1, Fig. 1). In contrast, *Fucus* recruitment, density, and cover vary across all scales, but in particular at the level of bays and the interactions of bays by years or by sizes. It was also clear from examining the data after the initial analysis that the large variance components for the bay effect for *Fucus* were due to north-south differences with greater recruitment rates, densities, and cover in south-facing bays (Fig. 2). Moreover, the effects of clearing size was quite evident in south-facing bays with larger clearings showing more recruitment, and greater densities and cover. The north-south difference was especially striking for the cover data.

Barnacle recruitment, density and cover tended to be greater in larger clearings and the pattern varied from year to year (Table 1, Fig. 1). Between 2000 and 2003, recruitment, densities, and cover were low in control plots, which had nearly 100% cover by *A. nodosum*, relative to the clearings, but there is no consistent relationship among the three responses and with clearing size. However, there was a striking pattern of good recruitment in 2001 followed by large densities in 2002 and 2003 and then large cover and low densities in 2004. Only barnacle cover had a consistent north-south pattern, and the variance component for the bay × year interaction was large and significant (Table 1, Appendix B).

We expected that there should be variation in the response of recruitment, density, and cover with clearing size (Petraitis and Latham 1999), and Levene's tests were significant in all cases except for *Fucus* recruitment (Appendix C). For barnacles, the response of recruitment, density and cover tended to be more variable in control plots and the smaller clearings. For *Fucus*

TABLE 1. Significance levels from analyses of variances of recruitment, density, and percent cover of *Fucus* and barnacles.

Source	<i>Fucus</i>			Barnacles		
	Recruit	Density	Cover	Recruit	Density	Cover
Size	0.1543	< 0.0001	0.0010	0.0046	0.0684	0.0014
Year	0.0090	0.0016	< 0.0001	0.0004	0.0008	0.0130
Size × year	0.0026	< 0.0001	0.8377	0.0919	0.0084	0.0016
Bay	0.0428	0.0066	0.0014	0.4377	0.1689	0.5193
N vs. S	0.0069	0.0021	0.0003	no test	no test	no test
Bay × size	0.0496	0.0523	0.0758	0.3346	0.6038	0.4792
N vs. S × size	0.0069	0.0640	no test	no test	no test	no test
Bay × year	0.0063	0.0640	0.8889	0.0992	0.0028	0.0143
N vs. S × year	0.0016	no test	no test	no test	0.2843	0.0040
Bay × size × year	0.6362	0.9984	0.4615	0.6351	0.6862	0.0609
Site(bay)	0.0286	0.1411	0.1895	0.0026	0.0707	0.0339
Size × site(bay)	0.2373	< 0.0001	< 0.0001	0.1908	< 0.0001	0.1005
Year × site(bay)	0.0169	0.2471	0.0501	0.8201	< 0.0001	0.1687

Notes: Tests in which $P < 0.05$ are shown in boldface type. Post hoc tests of north (N)–south (S) differences were done as linear contrasts and are shown below the related planned test. Details of ANOVAs are given in Appendix A.

density and cover, there was a decline in variability with increasing clearing size.

Stepwise regression and canonical correlation analyses were used to examine how well recruitment predicted density and how well density predicted cover. We used density and cover in 2005 as the dependent variables except for barnacle cover. Barnacle cover has a strong peak in 2004 (Fig. 2), and so we used cover in 2004 instead of 2005. Forward stepwise regression for barnacle density in 2005 entered recruitment in 2005, 2004, and 2001 as variables (Appendix D). Regression for barnacle cover in 2004 showed much the same pattern with densities in recent years (2003 and 2004) entering first and then followed by density in 2001. For *Fucus*, the best predictor of density in 2005 was recruitment prior to 2003 while the best predictors of cover in 2005 were a mixture of recent and older densities. For both barnacles and *Fucus*, there were both positive and inhibitory effects (i.e., positive and negative estimates for independent variables). Surprisingly, recruitment explained very little of the variation in density, but density explained most of the variation in cover.

Using the independent variables identified by stepwise regression, we carried out canonical correlation analyses, which allowed us to identify the combined effects of recruitment on density and of density on cover. As with the R^2 for stepwise regressions, the canonical correlations tend to be greater for density–cover analyses than the recruitment–density analyses (Fig. 3). Correlations of independent variables with the first canonical axes were large and generally mirrored the size and sign of the estimates from the regressions. ANOVAs of the scores on the first canonical axis revealed both north–south differences (*Fucus* density on cover and barnacle recruitment on density) and clearing size effects (density on cover for both *Fucus* and barnacles).

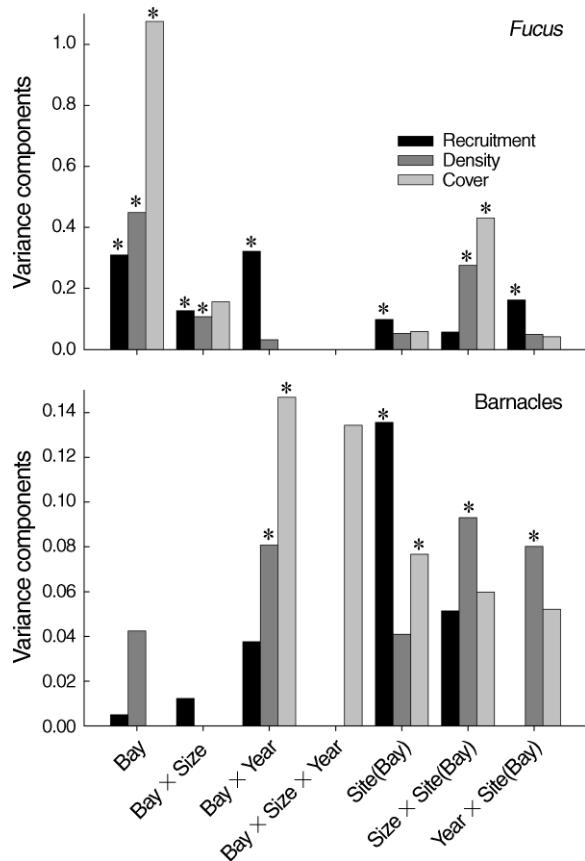


FIG. 1. Variance components for random effects from the mixed-model ANOVAs shown in Table 1. Asterisks above bars indicate significant effects (at $P < 0.05$). Variance components for residual errors are much larger and are not shown. The variance components for the residuals are: *Fucus* recruitment = 1.227; *Fucus* density = 0.738; *Fucus* cover = 0.712; barnacle recruitment = 0.914; barnacle density = 0.223; barnacle cover = 1.006.

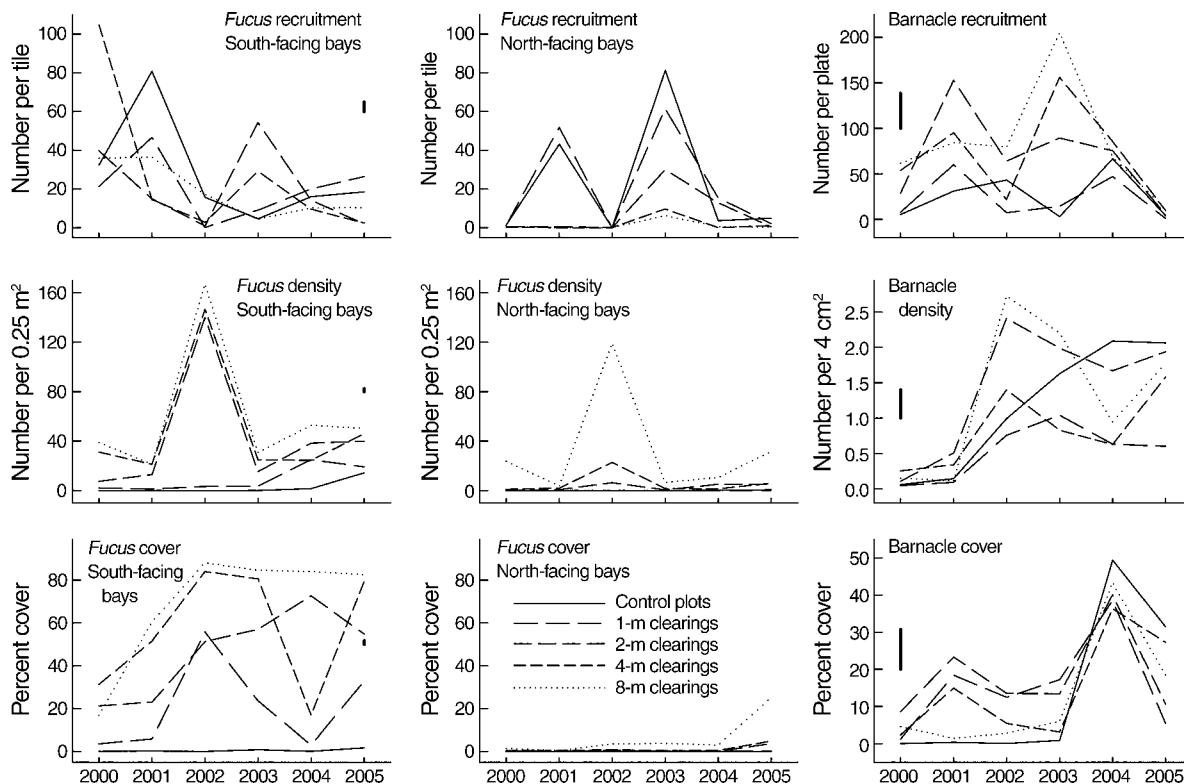


FIG. 2. Averages for recruitment, density, and percent cover by *Fucus* and barnacles. The thick vertical bars are the back-transformed range of two standard errors. Standard errors were taken from ANOVA outputs for the least-square averages. Since standard errors cannot be directly back-transformed and since the size of back-transformed ranges varies with the estimates of group averages, overall transformed averages plus or minus one standard error were used. These values were then back-transformed and the range was calculated.

DISCUSSION

We predicted that the variances of recruitment, density, and cover would show scale dependence with patch size because community responses tend to show convergence or return to initial conditions with small disturbances but either convergence or divergence after large perturbations (Sousa 1984, Knowlton 1992, Berlow 1997, Petraitis and Latham 1999). While our results indicate that patterns of and variation in recruitment, density and percent cover are influenced by both the scale of disturbance and location-specific factors, the patterns are not clear cut. Clearing size had a significant effect in some cases (e.g., percent cover and barnacle recruitment) but not in others (e.g., *Fucus* recruitment and barnacle density). More interestingly, there were no clear patterns in the changes of variance going from recruitment to density and then density to percent cover (Fig. 2), suggesting that these processes and the correlations among them are highly scale dependent and nonadditive (see model in *Introduction*).

As expected, barnacle recruitment in small clearings was more variable due to the edge effects inflicted by the surrounding algal fronds. Fronds can physically prevent initial barnacle settlement or sweep across the surface to remove already settled barnacles (Vadas et al. 1990,

Leonard 1999), and the *Ascophyllum* surrounding our small clearings often had fronds over 1 m in length, which could impact recruitment across the entirety of clearings ≤ 2 m in diameter.

Both local and broadscale processes influence recruitment of barnacles and fucoids, and we expected the impact of scale to differ with species because of the differences in life histories. We expected variation in barnacle recruitment to show both large- and small-scale effects. *S. balanoides* is a long distance disperser whose larvae may travel tens to hundreds of kilometers and spend up to several weeks in the water column before settling and attaching to the substrate. At the broad spatial scales of 10^2 km, oceanographic currents and gyres act to direct the overall direction of pelagic larval dispersal (Caley et al. 1996), and the long distance dispersal of barnacle larvae makes them particularly vulnerable to currents and oceanographic conditions and open to large-scale patterns of variation (e.g., Broitman et al. 2005). Yet barnacle recruitment is also known to show idiosyncratic site-specific differences (Caffey 1985, Raimondi 1990, Dudgeon and Petraitis 2001). Barnacles tended to recruit less at the sites that were far from the open ocean because of larvae settled prior to reaching these sites diluting the pool of available

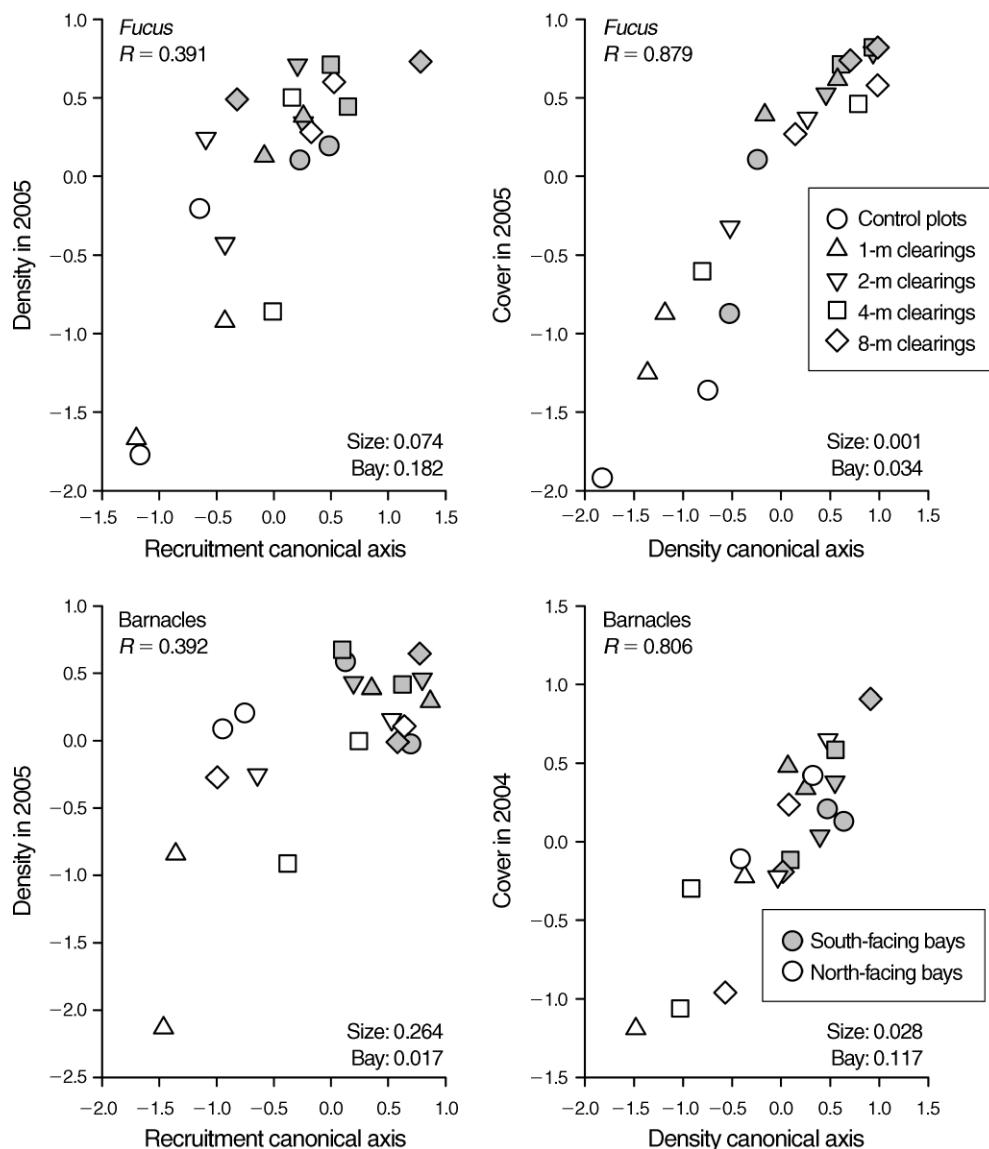


FIG. 3. Canonical correlation plots for the relationships of recruitment to density and density to cover. The x -axis is the first canonical axis, and the y -axis is the single dependent variable. Points are plotted as standardized values. R = adjusted canonical correlations. Numbers next to Size and Bay labels are probability levels from ANOVAs of standardized values on the first canonical axis. See Appendix D for details of analyses.

recruits. Differences in current direction, wind and wave energy varying at the scale of hundreds of meters may also influence site to site differences in barnacle recruitment (Bertness et al. 1996, Jonsson et al. 2004).

Surprisingly site-specific effects tended to dominate (Fig. 1). Barnacle recruitment, density, and percent cover were quite variable at the scale of sites within bays. We think differences in predation rates among bays are unlikely to be the cause of this pattern because a major predator of barnacles, the dogwhelk *N. lapillus*, does not vary on this scale (Petraitis et al. 2003; P. S. Petraitis, unpublished data). It is possible that oceanographic factors, which can affect the feeding and growth of

suspension feeding organisms via flow rate and food concentration (Frechette 1989, Grizzle and Morin 1989) may be potential contributors to site-specific variation in recruitment, density, and cover, but we have no evidence that would shed light on the importance of these processes.

We expected patterns of variation for *Fucus* to be more idiosyncratic and dependent on the presence of adults, which is very patchy on sheltered shores. Fucoïd zygotes settle close to parents, often traveling only a few 10s of m before attachment (Johnson and Brawley 1998, Dudgeon et al. 2001). Fucoïd zygotes are particularly sensitive to thermal stress, desiccation, wave motion,



PLATE 1. *Fucus vesiculosus* and *Semibalanus balanoides* in Toothacher Cove on Swan's Island, Maine (USA) in August 2008. The *F. vesiculosus* are young and relatively small individuals and likely between one and three years old. Two age classes of *S. balanoides* are visible. The smaller individuals are young-of-the-year and settled in spring 2008. The larger individuals are one or two years old. The snail on the *F. vesiculosus* frond is periwinkle, *Littorina littorea*, and is a common herbivore throughout the North Atlantic. For scale, young-of-the-year barnacles are approximately 5 mm across. Photo credit: P. S. Petraitis.

and herbivory (Vadas et al. 1990, Dudgeon et al. 2001), although canopy cover can provide some amount of protection from desiccation and wave motion but not herbivory.

Yet *Fucus* tended to show consistent broad-scale patterns among bays. Percent cover of *Fucus* in 2005 is consistent with observations made in 2002 and 2004 in the same plots (Petraitis and Dudgeon 2005, Petraitis and Methratta 2006). Dominance by *Fucus* in large clearings was unexpected because it is rare in undisturbed stands of *A. nodosum*, although there have been several reports of *F. vesiculosus* filling in large patches in New England (Bertness et al. 2002), the Canadian Maritimes (McCook and Chapman 1997), and in Northern Europe (Cervin et al. 2004, 2005, Jenkins et al. 2004). There was also significant variation between the north-facing and south-facing bays in cover, and we suspect north-south differences in early post-settlement mortality is the cause but have no direct evidence of this. We found recruitment was a poor predictor of density even though recruitment was more consistent in south-facing bays. Biomechanical stress imposed by wave action can limit the distribution of intertidal fucoid algae through frond breakage and holdfast dislodgement, but our experiments were conducted in sheltered bays where wave intensity rarely surpasses the >2 m/s rate required for dislodgement of many *Fucus* species (Jonsson et al. 2006).

While recruitment was a poor predictor of density for both *Fucus* and barnacles, our results are quite

consistent with the conclusions of Dudgeon and Petraitis (2001). They examined recruitment patterns in these same experimental plots immediately following the start of the experiment in 1997. Many of their conclusions regarding the effect of local and broad scale processes on recruitment variation in a single season apply to the long-term patterns that we observed between 2000 and 2005: nearly 10 years after the experiment was initiated.

Investigations into the link between recruitment and subsequent population level characteristics (e.g., density, abundance, percent cover) are not new in marine ecology (Gaines and Roughgarden 1985, Roughgarden et al. 1988, Caley et al. 1996). Evidence suggests that the relative role of recruitment compared to other demographic processes may depend upon species, environmental conditions, and geographic location (Fairweather 1988, Roughgarden et al. 1988, Raimondi 1990, Menge 1991). One generalization from these studies is that when recruitment is light, there should be a strong positive relationship between recruitment and subsequent population levels and that conversely, when recruitment is heavy, it will be a poor predictor of future population levels (Connell 1985, Menge 2000). Yet correlations between recruitment and subsequent population characteristics may be masked by agents of post-settlement mortality including predation, herbivory, and desiccation regardless of the amount of recruitment (Connell 1985, Petraitis 1987, Menge 2000, Deithier 2005).

The possibility that causes of post-settlement mortality are themselves scale-dependent can further complicate the linkage between recruitment and population effects. In our study, there is a distinct difference between uncleared control plots and experimental clearings. Links between recruitment and population effects may be most difficult to detect in uncleared plots where coverage by the canopy generates spatially heterogeneous environmental conditions (Eriksson et al. 2006). Pockets of moisture, hiding places for predators and prey, and vertical habitat complexity associated with the canopy could increase variability in future population levels and dampen the relationship between recruitment and percent cover. In open clearings, post-settlement stress factors operate in a more homogeneous environment; there are no hiding places and no protection from desiccation.

The longevity of individuals of a species may also influence our ability to detect a relationship between recruitment and future population properties. Barnacles generally have short life spans (one to two years [Wetthey 1985]), so it may be very difficult to link recruitment patterns to percent cover more than a year or two in the future. At best, cover in a given year would have a strong relationship with one or a few of the most recent recruitment events. At worst, there will be no relationship because most individuals may not live long enough to be censused even on an annual basis. For longer-lived organisms such as fucoid algae, average long-term recruitment and percent cover may be more tightly linked because individuals from each bout of recruitment have a greater probability of surviving for multiple seasons and contributing to the population at a subsequent point in time. In fact, we found that fucoid densities were correlated with multiple years of recruitment and that cover was linked to both recent and older densities. Barnacle cover, on the other hand, was explained best by only the most recent density patterns.

The problems affecting the linkages among dispersal, recruitment, and successful establishment are common across ecosystems (Howe and Smallwood 1982, Caley et al. 1996). In terrestrial—as in marine—communities, variability in these processes can influence community development following a disturbance (Shure et al. 2006, Martini and dos Santos 2007). In many plant species, propagules traverse spatial scales on the order of zero to tens of meters (Howe and Smallwood 1982), but dispersal distances in excess of 100 m, while less common, may occur through mechanisms involving wind, water, or vertebrate carriers and certainly play important roles in some cases of post-disturbance succession (Cain et al. 2000). Even so, both short and long distance dispersers must cope with locally varying environmental factors and the problems of locating suitable microsites (Clark et al. 2007). As with terrestrial systems, we found that recruitment patterns of both short- and long-distance dispersers were strongly driven by variation at a local scale.

In terrestrial systems as in our experiment, scale dependencies may underlie the variation in the rate of ecosystem recovery (Gehlhausen et al. 2000, Ritter 2005, Galthidy et al. 2006). For example, the rate of biomass accumulation in southern Appalachian forests following a logging event is much faster for larger (0.4, 2 ha) than smaller (0.016, 0.08 ha) disturbances (Shure et al. 2006). This pattern is attributable to greater resource release in larger clearings and the influence of light and successional changes in soil nutrient availability. Nitrogen is returned to the soil by short-lived, shade-intolerant, nitrogen-fixing trees and shrubs, which are favored in the larger gap interior regions where light is abundant. We do not have a clear understanding of the variation in the rate of recovery of our experimental clearings, but certainly local scale-dependent processes are important.

For example, edge effects in terrestrial plant communities, as in our study, can be pronounced and may uncouple growth rates and population dynamics between forest edges and the interior of gaps (Shure et al. 2006). Along the gradient from edge to interior, numerous factors may vary such as seed density, seed predation, species diversity, biomass accumulation, percent cover of individual species, relative cover of exotic species, number of pioneer species, and tree mortality (e.g., Whitney and Runkle 1981, Chen et al. 1992). At the forest edge where light is in greater supply, species that are intolerant to shade and unable to compete in the light-limited forest interior can find refuge (Gehlhausen et al. 2000). On the other hand, seed discovery and removal by seed predators, seedling germination, and seedling growth can be greater in the interior of forest gaps than in the surrounding understory (Restrepo and Vargas 1999, Devlaeminck et al. 2005). Plant species relying on animal seed dispersers may never reach patch interiors as some animals have a tendency to avoid forest gaps (Martini and dos Santos 2007).

Certainly, both scale dependencies and location-specific factors contribute to patterns of variation in community development following a disturbance, but the challenge is to move from simplistic generalizations to useful specifics. Such a shift requires data that are collected over broad enough spatial and temporal scales which match the scales of ecological phenomena and the life-history characteristics of species involved. We think our approach of using parallel studies of species with different life history characteristics provides a step in the right direction. In addition, similarities with terrestrial communities with regard to dispersal dynamics and recovery trajectories provide interesting cross-system insights, but we would stress the differences too. The potential for propagules to traverse hundreds of kilometers is more common in marine communities and thus local patterns of abundance and distribution may be driven by both regional dispersal dynamics and site-specific variation. For marine systems, the appro-

appropriate scale for experiments may be much longer and larger than is normally undertaken.

ACKNOWLEDGMENTS

We are grateful to the residents of Swan's Island who provided access to the shoreline. Numerous individuals helped with data collection, but we would especially like to thank Steve Dudgeon, Erika Carlson Rhile, and Nick Vidargas. Research was supported by grants from the National Science Foundation (OCE 95-29564 and DEB LTREB 03-14980) to P. S. Petraitis. P. S. Petraitis was supported by the Comisión Fulbright de Chile during the writing of the manuscript.

LITERATURE CITED

- Berlow, E. L. 1997. From canalization to contingency: historical effects in a successional rocky intertidal community. *Ecological Monographs* 67:435–460.
- Bertness, M. D., S. D. Gaines, and R. A. Wahle. 1996. Wind driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series* 137:103–110.
- Bertness, M. D., G. C. Trussell, P. J. Ewanchuk, and B. R. Silliman. 2002. Do alternative stable community states exist in the Gulf of Maine rocky intertidal zone? *Ecology* 83:3434–3448.
- Broitman, B. R., C. A. Blanchette, and S. D. Gaines. 2005. Recruitment of intertidal invertebrates and oceanographic variability at Santa Cruz Island, California. *Limnology and Oceanography* 50:1473–1479.
- Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66:682–687.
- Caffey, H. M. 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecological Monographs* 55:313–332.
- Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany* 87:1217–1227.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* 27:477–500.
- Cervin, G., P. Åberg, and S. R. Jenkins. 2005. Small-scale disturbance in a stable canopy dominated community: implications for macroalgal recruitment and growth. *Marine Ecology Progress Series* 305:31–40.
- Cervin, G., M. Lindgarth, R. M. Viejo, and P. Åberg. 2004. Effects of small-scale disturbances of canopy and grazing on intertidal assemblages on the Swedish west coast. *Journal of Experimental Marine Biology and Ecology* 302:35–49.
- Chapman, M. G., and A. J. Underwood. 1998. Inconsistency and variation in the development of rocky intertidal algal assemblages. *Journal of Experimental Marine Biology and Ecology* 224:265–289.
- Chen, J. Q., J. R. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecological Applications* 2:387–396.
- Clark, C. J., J. R. Poulsen, D. J. Levey, and C. W. Osenberg. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *American Naturalist* 170:128–142.
- Connell, J. H. 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* 93:11–43.
- 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.
- Connell, J. H., and M. J. Keough. 1984. Disturbance and patch dynamics and subtidal marine animals on hard substrata. Pages 125–151 in S. T. Pickett and P. S. White, editors. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, New York, USA.
- Connell, J. H., and R. O. Slayter. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119–1144.
- Cooper-Ellis, S., D. R. Foster, G. Carlton, and A. Lezberg. 1999. Forest response to catastrophic wind: results from an experimental hurricane. *Ecology* 80:2683–2696.
- Dayton, P. K., M. J. Tegner, P. E. Parnell, and P. B. Edwards. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecological Monographs* 62:421–445.
- Dean, T. A., and S. C. Jewett. 2001. Habitat-specific recovery of shallow subtidal communities following the Exxon Valdez oil spill. *Ecological Applications* 11:1456–1471.
- Deithier, M. N. 2005. Seaweeds under stress: manipulated stress and herbivory affect critical life-history functions. *Ecological Monographs* 75:403–418.
- Devlaeminck, R., B. Bossuyt, and M. Hermy. 2005. Inflow of seeds through the forest edge: evidence from seed bank and vegetation patterns. *Plant Ecology* 176:1–17.
- Dudgeon, S., J. E. Kübler, 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. R., and P. S. Petraitis. 2001. Scale-dependent recruitment and divergence of intertidal communities. *Ecology* 82:991–1006.
- Eriksson, B. K., A. Rubach, and H. Hillebrand. 2006. Biotic habitat complexity controls species diversity and nutrient effects on net biomass production. *Ecology*:246–254.
- Fairweather, P. G. 1988. Consequences of supply-side ecology: manipulating the recruitment of intertidal barnacles affects the intensity of predation upon them. *Biological Bulletin* 175:349–354.
- Frechette, M. 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis*. *Limnology and Oceanography* 34:19–36.
- Gaines, S. D., 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 Science (USA)* 82:3707–3711.
- Galhidy, L., B. Mihok, A. Hagyo, K. Rajkai, and T. Standovar. 2006. Effects of gap size and associated changes in light and soil moisture on the understory vegetation of a Hungarian beech forest. *Plant Ecology* 183:133–145.
- Gehlhausen, S. M., M. W. Schwartz, and C. K. Augspurger. 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. *Plant Ecology* 147:21–35.
- Grizzle, R. E., and P. J. Morin. 1989. Effect of tidal currents, seston, and bottom sediments on growth of *Mercenaria mercenaria*: results of a field experiment. *Marine Biology* 102:85–93.
- Halford, A., A. J. Cheal, D. Ryan, and D. M. Williams. 2004. Resilience to large-scale disturbances in coral and fish assemblages on the Great Barrier Reef. *Ecology* 85:1892–1905.
- Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201–228.
- Jenkins, S. R., T. A. Norton, and S. J. Hawkins. 2004. Long term effects of *Ascophyllum nodosum* canopy removal on mid shore community structure. *Journal of the Marine Biological Association of the United Kingdom* 84:327–329.
- Johnson, L. E., and S. H. Brawley. 1998. Dispersal and recruitment of a canopy-forming intertidal alga: the relative roles of propagule availability and post-settlement processes. *Oecologia* 117:517–526.
- Jonsson, P. R., K. M. Berntsson, and A. I. Larsson. 2004. Linking larval supply to recruitment: flow-mediated control of initial adhesion of barnacle larvae. *Ecology* 85:2850–2859.

- Jonsson, P. R., L. Granhag, P. S. Moschella, P. Åberg, S. J. Hawkins, and R. C. Thompson. 2006. Interactions between wave action and grazing control the distribution of intertidal macroalgae. *Ecology* 87:1169–1178.
- Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. *American Zoologist* 32:674–683.
- Leonard, G. H. 1999. Positive and negative effects of intertidal algal canopies on recruitment and survival of barnacles. *Marine Ecology Progress Series* 178:241–249.
- Martini, A. M. Z., and F. A. M. dos Santos. 2007. Effects of distinct types of disturbance on seed rain in the Atlantic forest of NE Brazil. *Plant Ecology* 190:81–95.
- McCook, L. J., and A. R. O. Chapman. 1993. Community succession following massive ice-scour on an exposed rocky shore: recruitment, competition and predation during early, primary succession. *Marine Biology* 115:565–575.
- McCook, L. J., and A. R. O. Chapman. 1997. Patterns and variations in natural succession following massive ice-scour of a rocky intertidal seashore. *Journal of Experimental Marine Biology and Ecology* 214:121–147.
- Menge, B. A. 1991. Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *Journal of Experimental Marine Biology and Ecology* 146:69–100.
- Menge, B. A. 2000. Recruitment vs. post-recruitment processes as determinants of barnacle population abundance. *Ecological Monographs* 70:265–288.
- Niklasson, M., and A. Granstrom. 2000. Long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology* 81:1484–1499.
- Petraitis, P. S. 1987. Factors organizing rocky intertidal communities of New England: herbivory and predation in sheltered bays. *Journal of Experimental Marine Biology and Ecology* 109:117–136.
- Petraitis, P. S. 1998. Timing of mussel mortality and predator activity in sheltered bays of the Gulf of Maine, USA. *Journal of Experimental Marine Biology and Ecology* 231:47–62.
- Petraitis, P. S., and S. R. Dudgeon. 2005. Divergent succession and implications for alternative states on rocky intertidal shores. *Journal of Experimental Biology and Ecology* 326:14–24.
- 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., and E. T. Methratta. 2006. Using patterns of variability to test for multiple community states on rocky intertidal shores. *Journal of Experimental Marine Biology and Ecology* 338:222–232.
- Petraitis, P. S., E. C. Rhile, and S. Dudgeon. 2003. Survivorship of juvenile barnacles and mussels: spatial dependence and the origin of alternative communities. *Journal of Experimental Marine Biology and Ecology* 293:217–236.
- Petraitis, P. S., and N. Vidargas. 2006. Marine intertidal organisms found in experimental clearings on sheltered shores in the Gulf of Maine, USA. *Ecology* 87:796.
- Raimondi, P. T. 1990. Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecological Monographs* 60:283–309.
- Restrepo, C., and A. Vargas. 1999. Seeds and seedlings of two neotropical montane understory shrubs respond differently to anthropogenic edges and treefall gaps. *Oecologia* 119:419–426.
- Ritter, E. 2005. Litter decomposition and nitrogen mineralization in newly formed gaps in a Danish beech (*Fagus sylvatica*) forest. *Soil Biology and Biochemistry* 37:1237–1247.
- Roughgarden, J. S., S. D. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* 241:1460–1466.
- Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the Eastern United States. *Ecology* 62:1041–1051.
- Shure, D. J., D. L. Phillips, and P. E. Bostick. 2006. Gap size and succession in cutover southern Appalachian forests: an 18 year study of vegetation dynamics. *Plant Ecology* 185:299–318.
- Sousa, W. P. 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. *Ecology* 65:1918–1935.
- Sousa, W. P. 2001. Natural disturbance and the dynamics of marine benthic communities. Pages 85–130 in M. D. Bertness and S. D. Gaines, editors. *Marine community ecology*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Thrush, S. F., J. E. Hewitt, A. Norkko, V. J. Cummings, and G. A. Funnell. 2003. Macrobenthic recovery processes following catastrophic sedimentation on estuarine sandflats. *Ecological Applications* 13:1433–1455.
- Underwood, A. J., and P. S. Petraitis. 1993. Structure of intertidal assemblages in different locations: how can local processes be compared? Pages 39–51 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Vadas, R. L., W. Wright, and S. L. Miller. 1990. Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality. *Marine Ecology Progress Series* 61:263–272.
- Wetley, D. S. 1985. Catastrophe, extinction, and species diversity: a rocky intertidal example. *Ecology* 66:445–456.
- Whitney, G. G., and J. R. Runkle. 1981. Edge versus age effects in the development of a beech–maple forest. *Oikos* 37:377–381.
- Zobel, D. B., and J. A. Antos. 1997. A decade of recovery of understory vegetation buried by volcanic tephra from Mount St. Helens. *Ecological Monographs* 67:317–344.

APPENDIX A

Details of the ANOVAs given in Table 1 and depicted in Fig. 1 (*Ecological Archives* E089-180-A1).

APPENDIX B

North–south differences in percent cover for barnacle cover (*Ecological Archives* E089-180-A2).

APPENDIX C

Levene's test of heterogeneity of variances and figure of variability in recruitment, density, and cover (*Ecological Archives* E089-180-A3).

APPENDIX D

Details of stepwise regressions and canonical correlation analyses (*Ecological Archives* E089-180-A4).