



ELSEVIER

Journal of Experimental Marine Biology and Ecology 314 (2005) 3–39

**Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY**

www.elsevier.com/locate/jembe

Stasis or kinesis? Hidden dynamics of a rocky intertidal macrophyte mosaic revealed by a spatially explicit approach

Bruce A. Menge^{a,*}, Gary W. Allison^b, Carol A. Blanchette^c, Terry M. Farrell^d,
Annette M. Olson^a, Teresa A. Turner^e, Peter van Tamelen^f

^aDepartment of Zoology, Oregon State University, Corvallis, Oregon 97331-2914, USA

^bDepartment of Evolution, Ecology and Organismal Biology, The Ohio State University, Columbus, OH 43212-1156, United States

^cDepartment of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, United States

^dBiology Department, Box 8270, Stetson University, 421 North Woodland Blvd, DeLand, FL 32720, United States

^eDivision of Science and Mathematics, University of the Virgin Islands, St. Thomas, USVI, 00802, United States

^f14320 Otter Way, Juneau, AK 99801, United States

Received 8 August 2004; received in revised form 28 August 2004; accepted 5 September 2004

Abstract

Macrophyte mosaics, or tile-like assemblages of turf marine macroalgae and surfgrass (*Phyllospadix scouleri*), are persistent and highly diverse along the central Oregon coast. To test the hypothesis that spatial pattern and species abundances are relatively invariant in this system, we studied community structure, disturbance, and species interactions from 1985 to 1990. Abundances and disturbance in permanently marked plots at each of five sites spanning wave-exposed to wave-protected areas were monitored photographically each year. The analysis was spatially explicit, incorporated position effects, and allowed determination of species displacements. To interpret the potential influence of substratum on disturbance, we quantified rock hardness and sediment depth at each site. Field experiments tested the role of grazers and spatial interactions on maintenance of between-patch boundaries.

Mosaic dynamics varied with wave exposure. At wave-exposed and wave-protected sites, average patterns of abundance and assemblage structure were relatively constant through time, but analysis of transition probabilities showed high rates of change among mosaic elements at wave-exposed sites and low rates of change at wave-protected sites. At wave-exposed sites, most changes involved *Phyllospadix* displacing neighboring macroalgal turfs but rarely the reverse. At all wave-exposures, surfgrass was the most frequently disturbed mosaic element. Disturbed areas were quickly colonized by macroalgae. At wave-exposed sites, disturbances were closed by regrowth of surfgrass. Disturbance rates were similar across wave-exposures, with wave forces causing most loss at wave-exposed sites and a combination of substratum failure and sediment burial causing most loss at wave-protected sites. At wave-exposed sites, disturbances tended to be larger (436.7 vs. 278.6 cm²) but less numerous (228 vs. 484 total disturbances) than at wave-protected sites.

At wave-exposed sites, surfgrass overgrew all other species except the kelp *Lessoniopsis littoralis*, which was competitively equivalent to surfgrass. Grazing had no effect on spatial interactions. Disturbance prevented surfgrass monocultures, and with

* Corresponding author. Tel.: +1 541 737 5358; fax: +1 541 737 3360.

E-mail address: MengeB@oregonstate.edu (B.A. Menge).

variable dispersal and patchy recruitment, maintained mosaic structure. At wave-protected sites, standoffs were the usual outcome of interactions, and patchiness resulted primarily from colonization of disturbances and subsequent succession. Like mussels, *Phyllospadix* are simultaneously dominant competitors, the most disturbance-susceptible species, and poor colonizers. These features are shared by theoretical models exploring the processes underlying spatially structured assemblages, and may characterize spatially structured systems in general.

© 2004 Elsevier B.V. All rights reserved.

Keywords: Competition; Disturbance; Grazing; Macrophyte mosaics; Oregon; *Phyllospadix scouleri*

1. Introduction

In his final contribution to science, MacArthur (1972) commented that “to do science is to search for repeated patterns, not simply to accumulate facts, and to do the science of geographical ecology is to search for patterns of plant and animal life that can be put on a map.” Plants in particular but also sessile marine animals often show repeated patterns “that can be put on a map” such as zonation and patchiness, and ecologists have dealt with such patterns using two general approaches. One uses a “mean field approach,” meaning that averaged abundances are used to represent the pattern, while the other uses a “spatially explicit approach,” meaning that the actual pattern of space occupancy across two-dimensional space represents the pattern (e.g., Tilman and Kareiva, 1997). This latter intellectual descendant of MacArthur’s (1972) vision, i.e., a focus on the generation of spatial pattern, or structure (defined as the arrangement of organisms in space) and the community consequences of position in a system has become known as “spatial ecology” (Tilman and Kareiva, 1997).

Why is a spatially explicit approach a useful method of addressing spatial pattern? Perhaps most importantly, one of the most universal modes of species interactions involves space. For example, neighbors are more likely to influence each other directly than are individuals separated in space, and thus the clearest understanding of local-scale change in abundance is likely to involve how interactions are mediated by their spatial position relative to one another. Mean-field approaches, in contrast, “blur” out these local-scale dynamics by representing change as an average across some unit of space. A second important reason for using spatially explicit approaches is that averages can actually produce a very

misleading view of the dynamics that underlie pattern. For example, in a system where the overall abundances and diversity of organisms change little through time, but within which neighbors are overgrowing one another, invading each other’s space, and recruiting or dying, a spatially explicit approach would reveal a highly dynamic scenario while the mean-field approach would suggest that the system changes little through time.

This is the exact scenario addressed in this paper. We present a study of a macrophyte-dominated community in the low rocky intertidal region on the Oregon coast. Our focus is on macrophyte mosaics, or tile-like patchy assemblages of marine seaweeds. Such patterns are arguably the most complex spatial pattern in natural communities.

1.1. Spatial ecology and mosaic pattern

What factors generate and maintain mosaics? Answering this question will contribute to understanding spatial pattern in ecology, and has been the focus of both theorists and empiricists (Turkington and Harper, 1979; Dethier, 1984; Sousa, 1984a; Menge et al., 1993; Lavorel et al., 1994; Levin and Pacala, 1997; Pacala and Levin, 1997; Burrows and Hawkins, 1998; Johnson et al., 1998; Wootton, 2001; Guichard et al., 2003). The history of ecology demonstrates that spatial considerations are critical to the understanding of, among other things, population and community stability, species diversity, species coexistence, and invasions (Armstrong, 1976; Horn and MacArthur, 1972; Huffaker, 1958). Considering the spatially explicit aspects of species in assemblages has led to surprising results. For example, in spatial models, patchiness or clumping arise unavoidably even in homogeneous environments

(Durrett and Levin, 1994a,b; Steinberg and Kareiva, 1997; Tilman et al., 1997). All environments are heterogeneous, however, further complicating efforts to understand the basis of pattern genesis, maintenance and diversity. Spatial structure can thus vary as a function of factors both intrinsic and extrinsic to a system, including species interactions, dispersal, physical disturbance, and environmental stress (Durrett and Levin, 1994a,b; Burrows and Hawkins, 1998; Wootton, 2001; Robles and Desharnais, 2002; Guichard et al., 2003). Spatial pattern is also strongly dependent on scaling (Levin, 1992; Levin and Pacala, 1997). Taken together, these details expose the downside of spatial ecology: combining even a few factors, scales and structural elements in a study of community structure can yield an investigation of great complexity and difficulty, and constraints on replication can undermine efforts to empirically test model predictions (Steinberg and Kareiva, 1997). Despite such impediments, considerable progress has been made (see above references).

The work presented here addresses the mean-field vs. spatially explicit paradox that lies at the heart of studies of spatial structure and dynamics. When viewed using a “mean-field” approach, the macrophyte mosaic appears to be relatively static through time. For example, the sites investigated in the present study have looked qualitatively and quantitatively the same since ~1980 when we first began work at these sites (Menge, personal observations, unpublished data). However, when viewed using a spatially explicit approach, spatial patterns that seemingly have changed little at larger scales are revealed as highly kinetic, and actually undergo striking change at smaller scales (e.g., between neighboring individuals or clones). In addition to revealing insight into how such systems are structured, such dynamism is likely to be an important determinant of the resilience of a system, or its ability to absorb perturbations without a major shift in system state (e.g., Beisner et al., 2003).

1.2. Rocky intertidal mosaics

Rocky intertidal communities are especially useful in spatially explicit approaches to the study of community pattern and dynamics (Burrows and Hawkins, 1998; Wootton, 2001; Robles and Desharnais, 2002; Guichard et al., 2003). The combination of

sessile or sedentary and relatively small organisms laid out on a mostly two-dimensional surface, rapid temporal responses to perturbations and compact habitat space enhances the ease and feasibility of the mechanistic study of the determinants of spatio-temporal pattern. In a spatially explicit study of the determinants of a fucoid alga–limpet herbivore–barnacle-bare space mosaic on the Isle of Man, for example, the system has gone through at least two cycles of five different states since the beginning of the study in the late 1970s (Hawkins and Hartnoll, 1983; Hartnoll and Hawkins, 1985; Hawkins et al., 1992; Johnson et al., 1997; Burrows and Hawkins, 1998). Key mechanisms underlying these cycles appear to be physical disturbance, dispersal and larval supply (of barnacles), and species interactions (between limpets, barnacles and the fucoid canopy).

On rocky shores of the northeastern Pacific, low intertidal shorescapes are often nearly completely covered by a multispecific assemblage of macrophytes. Macrophyte assemblages are patchy at two spatial scales, the among shorescape-element scale whose elements include kelps, surfgrass and turfs, and the within shorescape-element scale. Patches within the turf and surfgrass elements commonly occur in the mosaic pattern, defined explicitly as an arrangement of contiguous, irregularly shaped, intermingled polygons (Dethier, 1984; Menge et al., 1993; Allison, 2004). Patches in such mosaics are often monospecific and mosaics can include up to 20 species, so pattern diversity is high. Macrophyte mosaics occur on shores ranging from high to low wave-exposure. In wave-exposed areas, elements can include intertidal kelps (Laminariales; *Hedophyllum sessile*, *Lessoniopsis littoralis*), surfgrasses (Angiospermae: *Phyllospadix* spp.), and a variety of turf-forming red algae (Rhodophyta). In wave-protected areas, kelps are sparse to absent, leaving surfgrass and red algal turfs as dominant space occupiers.

1.2.1. Succession in surfgrass-dominated mosaics

In wave-protected areas along the Oregon coast, succession following removal of surfgrass (*Phyllospadix scouleri*) can follow different trajectories (Turner, 1983a). In Turner's (1983a) study, disturbed areas were colonized by either the green alga *Ulva* sp. (winter/spring) or by the brown alga *Phaeostrophion irregulare* (late summer/fall). Early colonists persisted

in some plots, but in others were replaced by mid-successional species such as the red algae *Cryptosiphonia woodii*, *Odonthalia floccosa*, and *Neorhodomela larix*. Recovery by surfgrass was slow and mostly vegetative (as opposed to recovery derived from new recruits), reaching ~15% cover after three years, with an annual rate of reinvasion into 0.25 m² plots of about 6 cm/year (Turner, 1985). Recruitment of surfgrass seedlings was infrequent and depended on facilitation by certain mid-successional species (Turner, 1983b). Such recruitment facilitation by existing host plants appears general in surfgrasses; similar results were obtained in studies of *Phyllospadix torreyi* recruitment in southern California (Blanchette et al., 1999) as well as with *P. torreyi* and *P. serrulatus* in Oregon (Turner and Lucas, 1985). Transitions between successional stages depended on several mechanisms, including inhibition, grazing, facilitation and overgrowth. Surfgrass dominance was maintained by its ability to preempt space and prevent invasion. Disturbance rates were low (0.13% and 0.04% of the area per year at two sites), but in combination with slow recovery rates were deemed sufficient to maintain a diverse mosaic (Turner, 1985).

Tidepool communities in Washington state also demonstrated relatively slow recovery by surfgrass from disturbance (Dethier, 1984). At a wave-protected site in the San Juan Islands (Cattle Point), 0% recovery occurred after 4 years. At a somewhat more wave-exposed site (Pile Point), recovery ranged from 10% to 18% after 2 years, while at a wave-exposed outer coast site (Shi-Shi), recovery ranged from 0% to 50% after 3 years. The wide variation in recovery rates was attributed to a lack of appropriate facilitators for seed recruitment, limpet grazing, and invasion by a preemptive alternative dominant, anemones (Dethier, 1984). Dethier (1984) estimated that for many tidepools, recovery after disturbance would take at least a decade. The variable rates of recovery, possible effects of grazers and variable mechanisms of spatial interactions in these studies suggested that wave-exposure, position in the mosaic and the identity of the occupant of the neighboring patch were important aspects of the dynamics of these mosaics.

Here we combine quantitative observation of spatial patterns occurring at sites along a wave-exposure gradient with field experiments to evaluate the roles of both physical and biotic factors. The spatial

scope of the study thus ranged from tens of centimeters (within-quadrat scales) to hundreds of meters (among-locations within a site). We focused on three stages of space occupation (clearance, colonization, and succession), and on the ecological processes affecting each one (Connell and Slatyer, 1977; Sousa, 1979a,b, 1984b). We addressed the following questions:

1. How dynamic is mosaic structure? Is patch position static, or constantly shifting?
2. What are the patterns and rates of disturbance, and how do they vary with wave-exposure and substratum?
3. What are the rates of recovery from disturbance, and how do they vary with wave-exposure?
4. What are the patterns, rates and outcomes of interactions among the most common mosaic elements, and how do these vary with wave-exposure?
5. What are the effects of grazers on interactions among mosaic elements at wave-exposed sites?
6. How comparable are the dynamics of this algal mosaic to those of similar systems?

2. Methods

2.1. Study sites

Our study was done from 1985 to 1991 in the low zone of rocky intertidal shores at two well-studied closely adjacent areas, Boiler Bay and Fogarty Creek (44°50' N, 124°03' W) (see descriptions in Turner, 1983a,b, 1985; Farrell, 1991; Menge et al., 1993; Blanchette, 1996; Allison, 2004) (see Fig. 1). We selected five sites within these areas spread across a wave-exposed (two sites) to wave-intermediate (one site) to wave-protected (two sites) gradient of wave force. The site at Fogarty Creek (E-FC for Exposed-Fogarty Creek) was an exposed, basaltic headland ≈ 0.8 km to the north of Boiler Bay (Fig. 1, Appendix 1). Each of three Boiler Bay sites (E-BB, I-BB, and P-BBC, or Exposed-Boiler Bay, Intermediate-Boiler Bay, and Protected-Boiler Bay Cove, respectively) was on a separate, gently inclined bench of similar substratum (basalt overlying mudstone) but differing wave exposure. A fourth site at Boiler Bay (P-BBM or Protected-Boiler Bay Mudstone; Fig. 1, Appendix 1)

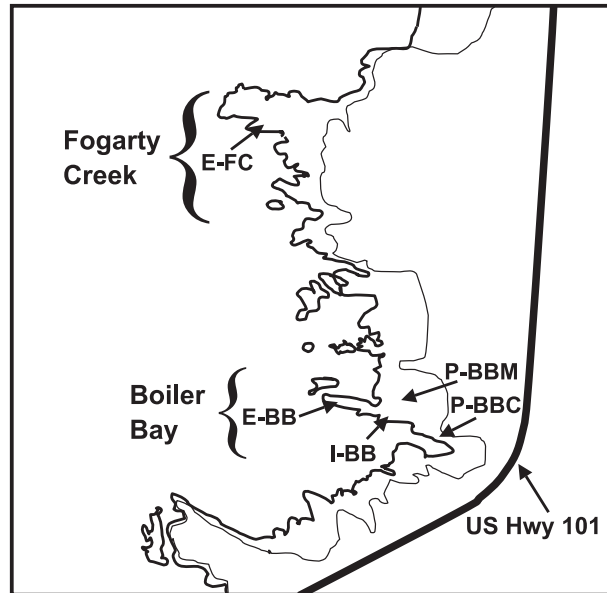


Fig. 1. Map of the Boiler Bay–Fogarty Creek intertidal reef complex ($44^{\circ}50' N$, $124^{\circ}03' W$) showing the location of the five study sites: E-FC or Exposed Fogarty Creek; E-BB, or Exposed Boiler Bay; I-BB or Intermediate Boiler Bay; P-BBM or Protected Boiler Bay Mudstone; and P-BBC or Protected Boiler Bay Cove. Thick wiggly line is low tide mark and thin wiggly line is high tide mark. Highway 101 is shown for reference. Drawn from an aerial photograph of the area. Scale: 1.5 km from top to bottom of frame.

was located on a mudstone bench sheltered from waves by the intermediate and exposed benches.

2.2. Sources of natural disturbance

2.2.1. Wave exposure

The gradient of wave-exposure was confirmed by estimates of wave exposure that employed maximum wave-force dynamometers (Menge et al., 1996). Under most circumstances, physical disturbance caused by dislodgement by large waves increases with increasing wave exposure (Dayton, 1971; Menge, 1976; Denny, 1995; Sousa, 2001).

2.2.2. Rock hardness

The hardness of the substratum can influence disturbance rates because softer rock might be more prone to failure under wave-generated and other forces (Sousa, 2001). Quantitative estimates of rock hardness at each site (Appendix 1) demonstrated that the substratum was substantially harder at E-BB, E-FC, and I-BB than at P-BBC and P-BBM (Appendix 1; one-way ANOVA on \log_{10} -transformed seconds to reach a fixed depth in the rock, $F=384$; $p<0.0001$; 4, 95 *df*).

2.2.3. Sediment depth

Physical disturbance (i.e. loss of macrophytes) could also result from sediment burial, which is inversely correlated with wave exposure (Sousa, 2001). Although none of our sites was subject to seasonal sand burial, we observed accumulations of finer sediments in the macrophyte mosaics at our more wave-protected (P-BBM, P-BBC) and intermediate (I-BB) sites, but not at our exposed sites (E-BB, FC; Appendix 1, Table 1). Sediments were consistently deeper at P-BBM than at P-BBC (Appendix 1), and tended to be deeper in summer (August 1987, September 1988) than in other months. August 1987 was the only month in which measurable sedimentation occurred at I-BB; no measurable sediments occurred at the wave-exposed sites throughout the study (1985–1990).

2.3. Elements of the macrophyte mosaic

Dominant elements of the mosaic at each of the five study sites are listed in Appendix 1; a comprehensive list of the component macrophytes with taxonomic authorities is available elsewhere (Table 1 in Menge et

Table 1
Variation in average sediment depth by site (P-BBC vs. P-BBM) and plot (1–4), analyzed with nested repeated measures analysis of variance (nested RM-ANOVA)

Univariate statistics				
Source	df	MS	F	p
<i>Between subjects</i>				
Site	1	37.490	5.92	0.0516
Plot(Site)	6	6.338	6.04	0.00006
Error	56	1.050		
<i>Within subjects</i>				
Time	6	16.746	41.44	<0.0001
Time×Site	6	1.160	2.87	0.049
Time×Plot(Site)	36	0.404	1.93	0.005
Error	336	0.209		
Multivariate statistics				
Source	df	Wilk's Lambda	F	p
Time	6, 51	0.1053	72.2	≪0.000005
Time×Site	6, 51	0.4711	9.54	≪0.000005
Time×Plot(Site)	36, 226	0.2656	2.22	0.0002

Data were mean sediment depth in each of eight 0.5×0.5-m² subplots (average of 16 measurements per each subplot). Error terms for site (between subjects), time and time×site (within subjects) were plot(site) and time×plot(site), respectively. The assumption of compound symmetry failed (Mauchly criterion; $p < 0.0001$) so we present Huynh–Feldt-adjusted p 's (new df : time×site=4.4, time×plot(site)=26.3). Statistically significant values are shown in boldface.

al., 1993). Surfgrass (*Phyllospadix* spp.) is ubiquitous at the five sites. Although three surfgrass species occur along the Oregon coast, we focused on *P. scouleri*, which occupies the upper portions of the low intertidal macrophyte zone (Turner and Lucas, 1985). Two other surfgrass species occur in mostly monospecific stands. The mid-zone species *P. serrulatus* is relatively uncommon and the low-zone species *P. torreyi* is accessible only on the lowest and calmest low tides. Throughout this paper, “surfgrass” will refer to *P. scouleri*, unless otherwise specified.

At the wave-exposed sites (E-BB, E-FC), the primary mosaic elements studied were the surfgrass, *P. scouleri*, and several species of red algae, including *Constantinea simplex*, and two functional groups, “*Hymenena* complex,” and “*Dilsea* complex.” The functional groups each included several species of foliaceous red algae (Appendix 1) that were difficult to distinguish in photographs. Hereafter, we will refer to these complexes as “*Hymenena*” and “*Dilsea*.”

Although the potentially variable composition of the complexes leaves us subject to the criticism that the outcome of experiments involving these groups might vary depending on the actual species present, our observations and the results of experiments presented below suggested that ecologically, each of these mosaic components behaved uniformly. Other common mosaic species included articulated corallines (e.g., *Corallina vancouveriensis*, *Bossiella plumosa*), which usually occurred in multispecific patches. At the wave-intermediate (I-BB) and wave-sheltered sites (P-BBC and P-BBM), dominant mosaic elements were *P. scouleri*; the canopy-forming kelp, *H. sessile* (I-BB only); and the perennial red algae *N. larix*, *O. floccosa*, and *Mazzaella* spp. Additionally, *C. woodii*, *Ptilota filicina* and *Polysiphonia* spp. were patchily abundant.

2.4. Photographic sampling of mosaics and disturbance

2.4.1. Mosaic quantification

To quantify spatial patterns of macrophyte abundance and annual disturbances, in May 1985 we established four 2×2-m marked grids in the low zone at each site (Fig. 2). Grids were separated by at least 1 m, but placement was dependent on topographic constraints and was therefore not randomly positioned. Where possible, grids were positioned on rock surfaces with sufficient space for each 2×2-m grid between the mid-zone mussel bed and the very low zone *P. torreyi* bed. To facilitate photography, we sought surfaces with relatively homogeneous topography. Each grid was divided into four contiguous 1×1-m plots (Fig. 2A). In each grid, we selected two diagonally opposed plots for the spatially explicit analysis (Fig. 2A, plots A and B). The configuration of these plots, whether upper left/lower right or lower left/upper right, was determined by flipping a coin. Each selected plot was further subdivided into 0.5×0.5-m quadrats (Fig. 2B).

In July of each year, we photographed each of the 0.5×0.5-m quadrats (Fig. 2B; 32 quadrats/site) using a photographic framer (Lundalv, 1971, 1986; Torlegard and Lundalv, 1974). The device consisted of a 0.5×0.5-m aluminum-sampling frame, to which a camera was mounted by four upright 1-m-long aluminum angle-irons. Notches in the two upper corners of the frame allowed us to fit the device over each quadrat in the

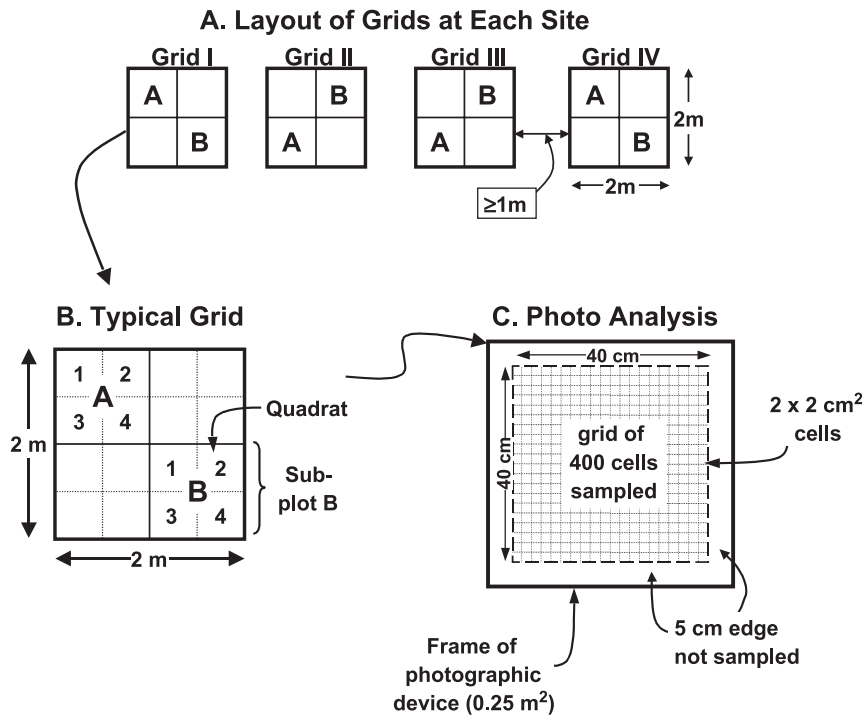


Fig. 2. Design of the mosaic grid monitoring study. At both E-BB and P-BBM space limitation for Grid IV forced a 1×4 -m rectangular shape, rather than a 2×2 -m square. (A) Grid layout. (B) Configuration of a 1×1 -m subplot (plot A or B). (C) Detail of each 0.5×0.5 -m subplot, showing the 5-cm buffer zone for each plot that was not included in the spatially explicit analysis.

same orientation and position each time by holding the notches against the two screws that marked the upper corners of each quadrat. To facilitate laboratory analysis, we identified and recorded species lists for each quadrat during photographic sampling.

In the laboratory, slides were projected onto a 20×20 grid of cells (Fig. 2C), and the occupant of each cell was identified, producing a spatially explicit 400-cell matrix of macrophyte occupancy for each quadrat on each sample date. We calculated transition probabilities for each cell in the subplots at each site—as the probability that a given cell occupant would either remain the same or change to another species—for year-to-year and initial-to-final transitions.

In the analyses, our primary focus was on macroalgal turfs. At wave-exposed sites, fronds of kelp canopy species (*L. littoralis*, *H. sessile*) were moved aside during photography so that the turfs could be seen in the photos. Similarly, at all sites, surfgrass blades were repositioned so that patch edges could be readily seen during analysis. Macroalgal turfs included early successional (coralline crusts, articu-

lated corallines, *Plocamium cartilagineum*, *Acrosiphonia coalita*, and ulvoids) and later successional species or species groups (*Hymenena*, *Mazzaella* spp., *N. larix*, *O. floccosa*, *Dilsea*, *C. simplex*, *Osmundea spectabilis*, and *Erythrophyllum delesserioides*). All other space occupiers were relatively scarce and were lumped into a broad “other” category.

2.4.2. Disturbance regime

To determine annual patterns of disturbance, each summer we photographed new disturbances generated during the previous winter (Fig. 2A). Each 2×2 -m grid was examined for recently disturbed patches, distinguishable by their lack of macrophyte cover, bare rock surface, and, commonly, by the presence of recently broken surfgrass rhizomes. In years 2–4 (1986–1988), we re-photographed older disturbances to quantify rates of recovery or further expansion of disturbances. In the laboratory, slides were either projected onto a digitizer, or scanned with a slide scanner. The area (cm^2) and perimeter (cm) of each disturbance, and of all changes in macrophyte cover in experiments described

below, was estimated using computer software (either SigmaScan®, or NIH Image®). Disturbances were classified relative to their original size as expanding (larger area) or recovering (smaller area).

2.5. Effect of biotic interactions on between-patch boundaries

Experiments were run to understand how the mosaic pattern was maintained, with a focus on factors affecting changes at the edges of mosaic patches (Fig. 3). For example, competition for space or facilitation or selective grazing by macro-herbivores (limpets, chitons, sea urchins) could control changes in between-patch boundaries. Unfortunately, limited numbers of appropriate boundaries prevented simultaneous tests of the effects of neighbors and grazers.

2.5.1. Grazing effect

Macro-herbivore fence-exclosure experiments at E-BB tested the hypothesis that grazing influences

between-patch boundaries at wave-exposed sites (similar tests at wave-protected sites were precluded by the near-absence of herbivores within the mosaic at these sites; Fig. 3). Two species pairs were investigated: *P. scouleri* vs. *C. simplex* and *P. scouleri* vs. *Dilsea*. Plots (15×30 cm) were centered on between-patch boundaries and subjected to three treatments: the “normal” situation (+Grazers –Fence), a partial fence control for inadvertent effects of exclosures (+Grazers +Fence), and an exclusion fence (–Grazers +Fence). Screws marked a 15-cm border along the boundary, and the four corners of the plot, forming adjacent contiguous marked squares extending 15 cm into each patch. Stainless steel fences were seven cm high and fastened to the rock using stainless steel screws. During biweekly to monthly monitoring visits, the few herbivores invading the exclosures were removed. The experiments were monitored photographically in July, November, and December 1985, March and July 1986, June 1987 and July 1988. The response variable was the change in the

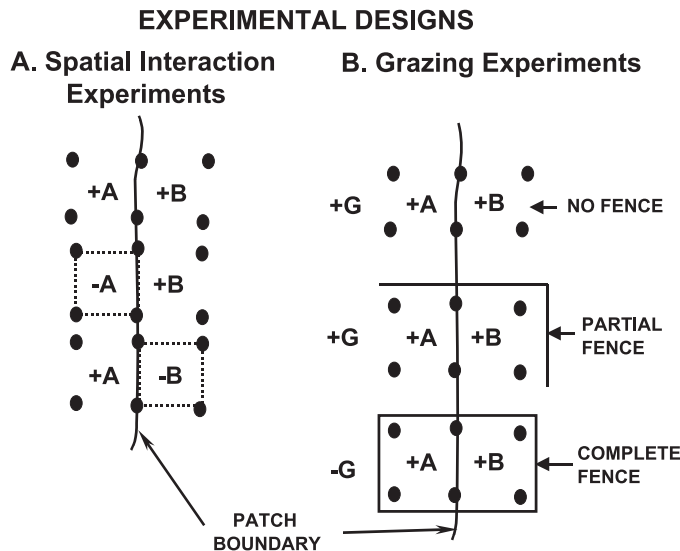


Fig. 3. Design of the competition and grazing experiments. In the competition experiment, each replicate included three plots: a reference (both competitors present; +A +B) and two manual removals of either competitor (–A +B and +A –B). Dots indicate position of marking screws on, and on either side of the patch boundary. At E-BB, spatial interactions between the following five pairs, all with four replicates each, were established: *Phyllospadix* vs. *Constantinea*, *Phyllospadix* vs. “*Dilsea*,” *Constantinea* vs. “*Dilsea*,” *Constantinea* vs. “*Hymenena*,” and “*Dilsea*” vs. “*Hymenena*.” At P-BBM, spatial interactions between three pairs were tested: *Phyllospadix* vs. *Neorhodomela* (eight replicates), *Phyllospadix* vs. *Odonthalia* (five replicates), and *Neorhodomela* vs. *Odonthalia* (five replicates). In the grazing experiment, each of four replicates included three plots: a reference (both competitors present and grazers present with no fence; +A +B/+G–fence), a fence control (both competitors present and grazers present with a partial fence; +A +B/+G+fence), and a grazer exclusion (both competitors present and grazers absent with a complete fence; +A +B/–G+fence). Two pairs were tested: *Phyllospadix* vs. “*Dilsea*” and *Phyllospadix* vs. *Constantinea*. Because grazers were essentially absent from the wave-sheltered surfgrass beds and working time was limited at wave-exposed sites, the grazing experiment was done only at E-BB.

distance moved towards the neighbor in centimeter (average of three evenly spaced measurements) along the boundary between patches.

2.5.2. Spatial interactions among established patches

We established spatial interaction experiments at E-BB and P-BBM to test the effects of interactions between neighbors (Fig. 3). At E-BB, we investigated five sets of pairwise spatial interactions, each replicated four times; *P. scouleri* vs. *C. simplex*, *P. scouleri* vs. *Dilsea*, *C. simplex* vs. *Dilsea*, *C. simplex* vs. *Hymenena*, and *Dilsea* vs. *Hymenena*. Three sets of pairwise interactions were studied at P-BBM; *P. scouleri* vs. *N. larix* (eight replicates), *P. scouleri* vs. *O. floccosa* (five replicates), and *N. larix* vs. *O. floccosa* (five replicates). Insufficient numbers of other species pairings were available for experimentation.

As in the macrograzer experiments, replicates were three rectangular plots (15×30 cm) centered over the boundary between two adjacent patches (Fig. 3). For patch species “A” and “B,” the three treatments were both species present (+A +B), species A present/species B absent (removed with scrapers; +A –B), and species A absent/species B present (–A +B). Cleared space not covered by the advancing neighbor was periodically re-scraped, approximately seasonally in fall and winter, and somewhat more often in spring and summer. The E-BB experiment was monitored on the same dates as the herbivore-effect experiments. P-BBM experiments were photographed in July and December 1985, March and July 1986, May 1987 and May 1988.

2.5.3. Recruit–adult interactions: *Phyllospadix* vs. *Neorhodomela*

Space at all wave-intermediate and wave-protected locations was dominated by surfgrass and the red alga *N. larix*. Since the spatial interaction experiments suggested that both competition and facilitation could be important in mediating interactions among established mosaic elements, we tested the impact of these factors on the establishment of these two dominants.

Prior studies (Turner, 1983b) had shown that recruitment of *P. scouleri* is facilitated by certain macroalgae (such as *N. larix*) having a central axis ~1 mm in diameter to which the hooked surfgrass seeds can attach. *N. larix* should thus positively influence

surfgrass recruits. The reciprocal effect, of resident surfgrass on colonization of *N. larix* was unstudied, although a prior investigation showed that *N. larix* recruitment rates were very low (Menge et al., 1993). Hence, the high abundance of *N. larix* seemed most likely maintained by lateral vegetative spread of the basal holdfast system of this alga.

We established reciprocal recruit–adult experiments to determine either if *N. larix* recruits could increase in abundance in the presence of resident surfgrass, or if surfgrass recruits could increase in the presence of resident *N. larix*. We defined *N. larix* recruits as clumps of 1–5 thalli (~2–10 cm² in area) surrounded by (“resident”) *P. scouleri*, and defined *P. scouleri* recruits as plants of one or few blades growing out of seeds attached to the surrounding (“resident”) *N. larix*. Nine replicate pairs of *N. larix* recruits and ten replicate pairs of *P. scouleri* recruits (five each at the upper and lower edges of the low zone) were marked with three stainless steel screws arranged in a triangle around each recruit. Treatment pairs were +recruit +resident, and +recruit –resident, assigned using a coin flip. Encroaching residents were removed periodically to maintain the –resident treatment. Experiments were established at I-BB in August 1987, and were monitored photographically in August, September and November 1987 and January, May and August 1988.

2.6. Data analysis

Data were analyzed using SYSTAT statistical software (version 10; SPSS) and JMP (SAS) on an IBM-compatible PC. Linear regression was used to determine the relationship between abundance of species in the marked plots in successive years. Calculation of transition probabilities was determined using a program written in Pascal. The effects of wave exposure and year on the disturbance regime, including disturbance density, mean disturbance area, total proportion of each plot disturbed, perimeter/area ratio, and departure from circularity, was analyzed using two-way analysis of variance (ANOVA) for each component. We used linear contrasts to make pairwise comparisons, and for calculation of estimates for use in determining effect sizes. In this and all other analyses, we examined probability plots of studentized residuals and plots of studentized resid-

uals against estimated values, respectively, to determine if residuals were normally distributed and if errors were independent (Wilkinson, 1998). These assumptions were met in most cases after transformation (\log_{10} or $\ln(x+1)$ for areas, densities or ratios and $\arcsin[\text{square root}]$ for percent cover and proportional data). Where assumptions were not met even after transformation, probabilities were highly significant indicating that the analysis was probably reliable (Underwood, 1981). Cochran's *C* test was used to test the assumption of equality of variances (Winer et al., 1991).

Because the residuals in regression analysis between initial disturbance area and percent recovery in the first year were not normal or independent, even with transformation, we analyzed recovery rates of disturbed patches using log-linear model analysis (Ramsey and Schafer, 1997; Quinn and Keough, 2002). The analysis was performed on counts of disturbances categorized by their rates of recovery (<50%, 51–90% and >90% recovery in the year following disturbance), initial area (<500 and >500 cm²) and wave exposure (exposed, intermediate, protected). In contrast, analysis of rates of expansion of disturbed patches satisfied assumptions of normality and independence, so we employed analysis of covariance, with initial area as the covariate. Linear regression was used to establish the relationship between initial disturbance area and percent recovery or percent expansion after 1 year.

Variation in sediment depth by plot nested within the wave-protected sites was analyzed using nested repeated measures analysis of variance (nested RM-ANOVA), because measurements were taken repeatedly on the same grid of points in each plot. The effects of height on the shore and presence of competition on recruit growth for surfgrass, and the effect of competition on recruit growth for *N. larix* were tested using two-way or one-way RM-ANOVA, respectively. We used the Mauchly Criterion to evaluate the multivariate assumption of compound symmetry in RM-ANOVA (Crowder and Hand, 1990), and adjusted the critical value by reducing the degrees of freedom by multiplying by the Huynh-Feldt ϵ (<1.0). Finally, the effects of macrograzers on between-patch boundaries and of competitors on growth of surfgrass and its competitors were all tested using one-way ANOVA.

3. Results

3.1. Mosaic structure: diversity and abundance

The taxon richness and abundance of mosaic elements (defined as *P. scouleri*, bare rock, and the different “early” and “late” successional algal groups) remained remarkably constant through time, but varied among sites. *P. scouleri* dominated at all sites (Fig. 4A–C), but diversity (richness) of other mosaic elements declined across the wave-exposure gradient from 13 to 10 elements/site (an average of 6.3 to 4.3 elements/plot, Appendix 1), reflecting an almost complete turnover of algal groups. Within sites, however, total macrophyte abundance and composition were comparatively constant through time and similar at a given wave-exposure.

Surfgrass was the dominant space occupant at all five sites over the entire study period (Fig. 4A–C). Mean surface area covered by *P. scouleri* ranged from ~34% (E-BB, 1989) to ~62% (P-BBM, 1989). Surfgrass cover varied little through time, with annual means differing by only 10% to 20% (39–49% at P-BBC; ~37–57% at I-BB, respectively). These inter-annual fluctuations exhibited no obvious synchrony among sites. Years of minimum and maximum mean cover by site were 1989 and 1986 (E-BB), 1987 and 1990 (E-FC), 1985 and 1990 (I-BB), 1985 and 1989 (P-BBC), and 1990 and 1989 (P-BBM).

Among the other elements of the mosaic, early successional elements were relatively minor components of the mosaic, with average total abundances varying from 0% to 8.1%. Early elements are those that typically regrow rapidly upon release from shading (crustose and articulated coralline algae) or rapidly re-colonize (*P. cartilagineum*, *P. filicina*, *A. coalita*, ulvoids) following disturbance. Their cover and that of bare rock was low, but relatively constant through time, suggesting a low rate of disturbance (also see direct measures of disturbance in Section 3.3). Coralline algae were abundant only at wave-exposed sites, while cover of *P. cartilagineum* was intermediate at wave-exposed sites (E-BB, E-FC) and highest at the most wave-protected site (P-BBM).

Later successional elements were frequently co-dominant with *P. scouleri*, maintaining relatively constant cover within a given site over time. Their composition, however, varied markedly among sites.

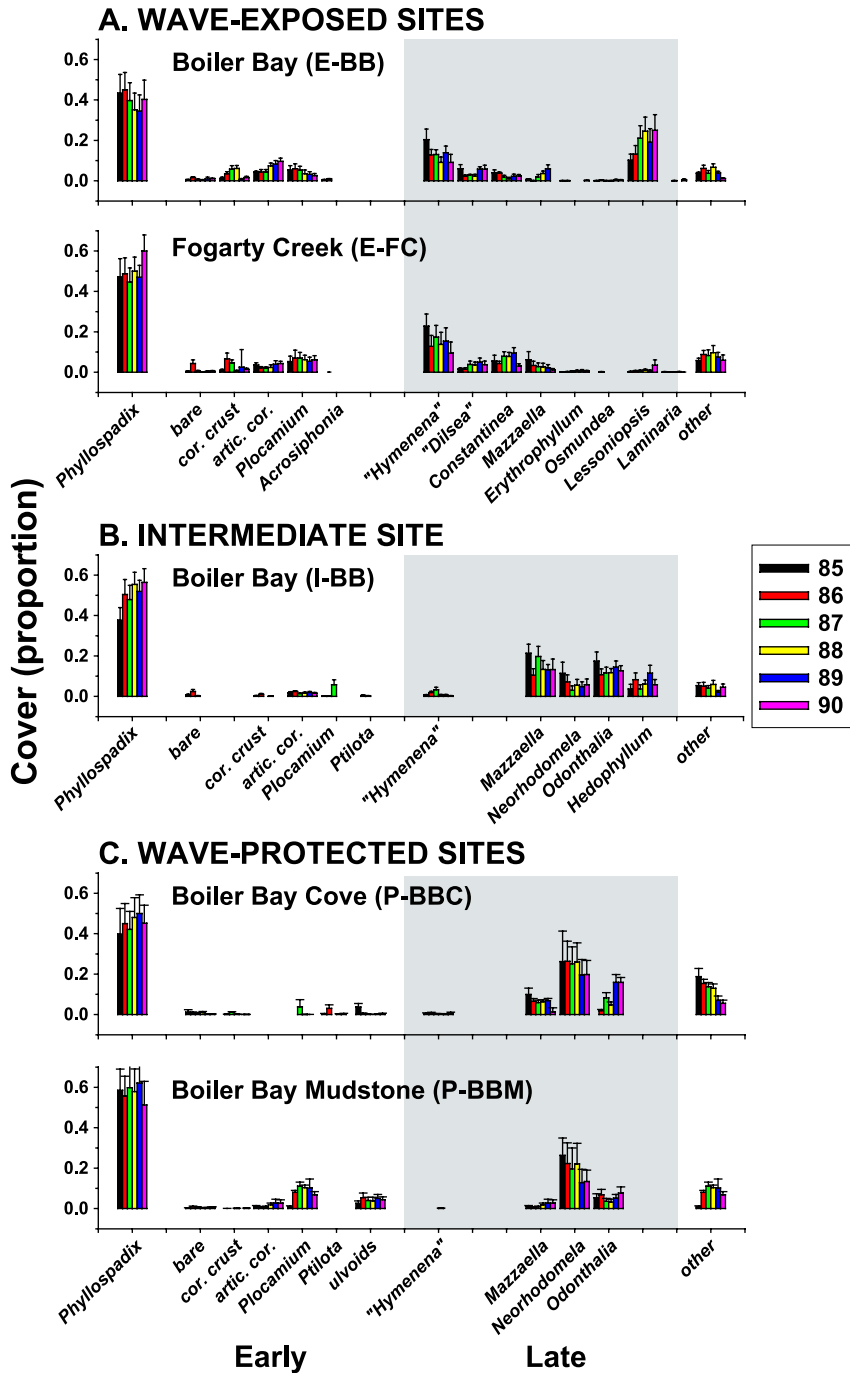


Fig. 4. Abundance (percent cover) of the most common macrophyte mosaic elements at (A) two wave exposed sites, Exposed Boiler Bay (E-BB, A) and Exposed Fogarty Creek (E-FC, B), (B) the site of intermediate wave exposure, Intermediate Boiler Bay (I-BB), and (C) two wave-protected sites, Protected Boiler Bay Cove (P-BBC and Protected Boiler Bay Mudstone (P-BBM), from 1985 to 1990. Data are mean cover per $m^2 + 1$ S.E. Because each 1×1 -m plot is separated from the others by a 10-cm buffer that was not included in the analysis (see Fig. 1C), we consider each subplot an independent replicate with $n=8$. Late successional species are grouped on the right in the shaded portion.

For example, the turf-forming elements (*Hymenena*, *Dilsea*, *C. simplex*, *O. spectabilis*) were important only at the more wave-exposed sites. In contrast, the branched red algae *N. larix* and *O. floccosa* were absent from wave-exposed sites, but were strong co-dominants at intermediate and protected sites. The red blade macroalga *Mazzaella* spp., occurred at all sites, but reached its highest abundance at the intermediate (I-BB) and one protected (P-BBC) site. The canopy-forming kelps, *L. littoralis* and *H. sessile*, were common subdominants at only one site each (E-BB and I-BB, respectively).

These data confirmed our impression, gained over the previous 5 years that patterns of relative abundance of the different components of the macrophyte mosaic are relatively static through time, but vary with wave-exposure. At each site, comparison of the abundances (proportional cover) of each component in year t to that in year $t+1$

suggests only modest inter-annual shifts in abundance in successive years (Fig. 5; 21 of 25 coefficients of determination, r^2 's, were >0.85). Longer-term (1985–1990) comparisons reveal larger proportionate changes than do year-to-year comparisons (all five r^2 's were <0.78), although final abundances were still quite similar to initial abundances.

Examination of time-series photos dispels the notion of a relatively static or unchanging community. For example, at E-BB and P-BBM, both annual and longer-term (6 years) changes were generally substantial (Figs. 6 and 7). Surfgrass patches in particular tended to shift positions in the plots, both advancing over neighboring turfs, and retreating from or abandoning space previously occupied. Species also came and went over time. Thus, spatially explicit observations suggested a level of dynamism that would have been missed had we

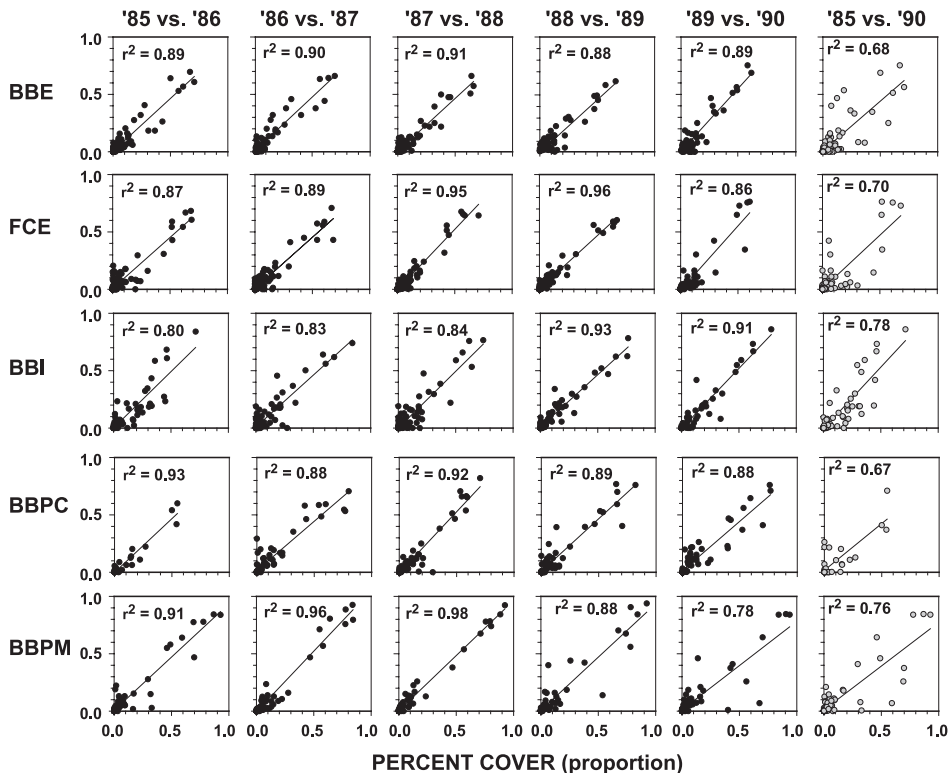


Fig. 5. Scatterplots of the proportion of cover of each mosaic element in year x (abscissa) vs. its cover in year $x+1$ (ordinate). Year-by-year comparisons are shown in the left five columns (e.g., 1985 vs. 1986, 1986 vs. 1987, etc.); the right column shows the comparison between initial and final cover. Site code is as indicated in Fig. 3 captions. Coefficients of determination (r^2) are shown for each comparison.

analyzed temporal changes in mosaic structure using average percent cover.

3.2. Mosaic structure: spatially explicit analysis

Analysis of transition probabilities was consistent with the high degree of constancy in composition over time at all five sites (Fig. 8A–C). *P. scouleri* was the most abundant single species, and total abundance of late-successional macroalgae also approached that of *P. scouleri* at some sites. Surfgrass and other late-successional elements retained most of the space from 1 year to the next, and *P. scouleri* was as likely to be replaced by one of the late elements

(primarily *Lessoniopsis*; see following paragraph), as it was to replace them. Spatial extent of disturbance as coarsely indicated by change from any mosaic category to early-successional elements (second column in all panels) appeared to be low but nearly constant at all sites. By this measure, late successional algae were as likely as surfgrass to be replaced by early elements. Recovery from disturbance, coarsely indicated by change from early successional elements to surfgrass or later successional elements (second row in all panels), was higher at exposed than at intermediate or protected sites (but see Section 3.3 for a more detailed analysis). In sum, at the scale of functional groups, the successional

Wave-Exposed Time Series (BBE)

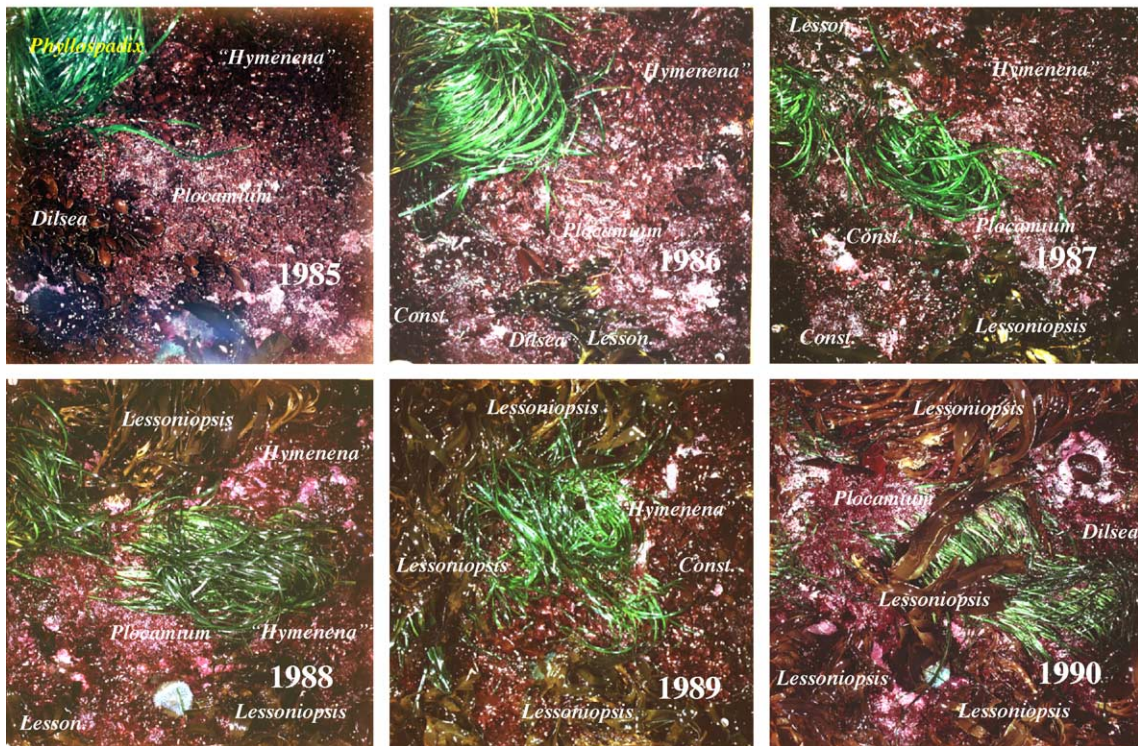


Fig. 6. Time series of annual photos (taken in July) of the same plot at a wave-exposed site (E-BB) from 1985 to 1990. The clump of surfgrass (green) in the upper left in 1985 moves toward the lower right corner in 1986, moves further toward the lower right corner and splits into two in 1987, moves rightward (right half of clump) or remains stationary (left half) in 1988, moves largely out of the frame (left half) or back toward the upper left (right half) in 1989 and moves toward the lower right corner again in 1990. Other species showing shifts in position are *Hymenena* (upper right), *Constantinea*, *Dilsea*, and *Plocamium*. The kelp *Lessoniopsis* invades from the top in 1987 and expands downward and rightward to 1990. Another *Lessoniopsis* expands into the plot from below starting in 1985. A chiton, *Katharina tunicata* appears in a small gap, which it presumably has grazed down to the underlying coralline crust in the upper right corner in 1990. An anemone *Anthopleura xanthogrammica* is visible in the lower center in 1988.

Wave-Protected Time Series (BBPM)

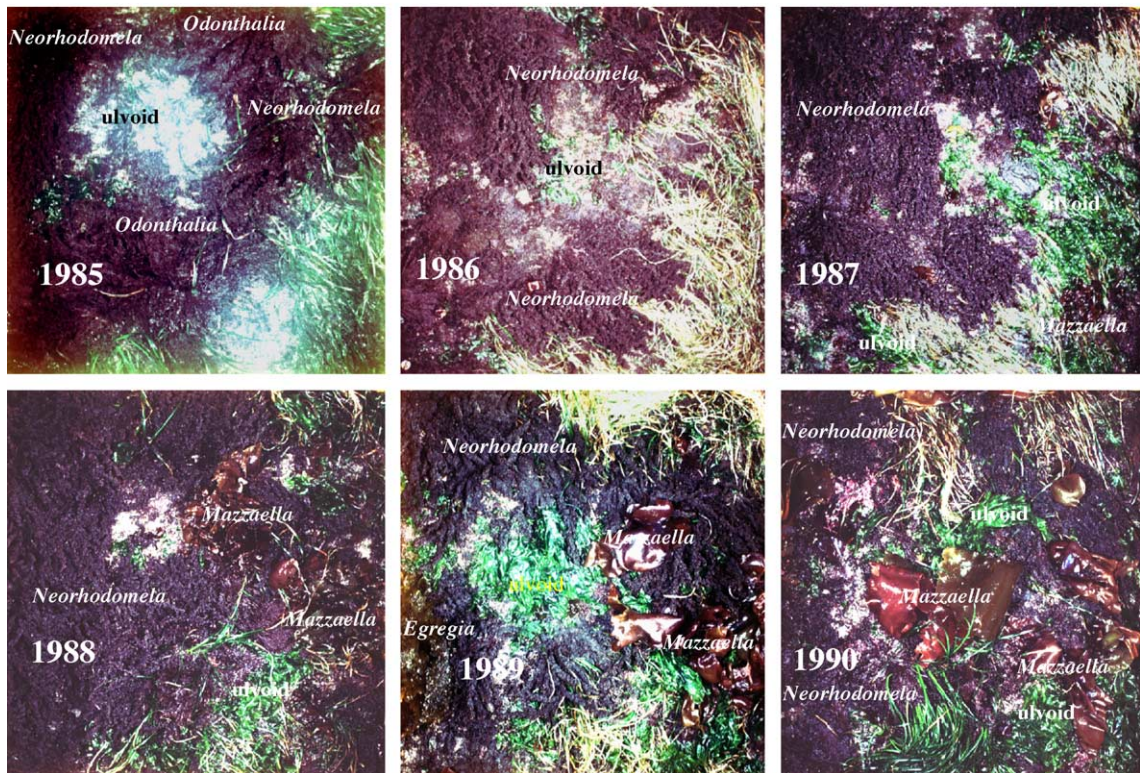


Fig. 7. Time series of annual photos (taken in July) of the same plot at a wave-protected site (P-BBM) from 1985 to 1990. The surfgrass patch on the right experienced a disturbance between 1986 and 1987 (seen as the ulvoid patch at right center in 1987). Another disturbance removed some *Neorhodomela* between 1988 and 1989 (ulvoid in center of plot, 1989). Surfgrass moved into the plot from the top between 1988 and 1990. Other changes are evident also, including replacement of ulvoid and *Odonthalia* patches by *Neorhodomela* (1985–1987), and invasion of *Mazzaella* (right center; replaced ulvoid from 1987 to 1988 and center, replaced ulvoid from 1989 to 1990).

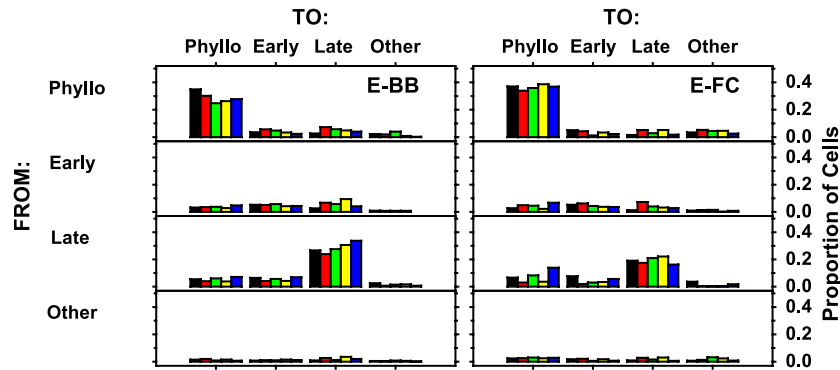
dynamics of the mosaic appeared similar among sites (Fig. 8), despite dramatic differences in the composition of the macrophyte mosaic.

Because *Phyllospadix* was the most abundant element of the mosaic, we focused a more detailed analysis on interactions of surfgrass with its neighbors (i.e. the top row and first column of Fig. 8). At all sites, surfgrass tended to displace neighbors at higher rates than it was itself displaced (Fig. 9). Averaged across years, the probability that surfgrass would replace an algal neighbor was often many times greater than the probability that the alga would replace surfgrass. These trends were similar between each of the two sites at wave-exposed (Fig. 9A) and wave-protected (Fig. 9C) areas, and among exposures (similar patterns were seen among all five sites).

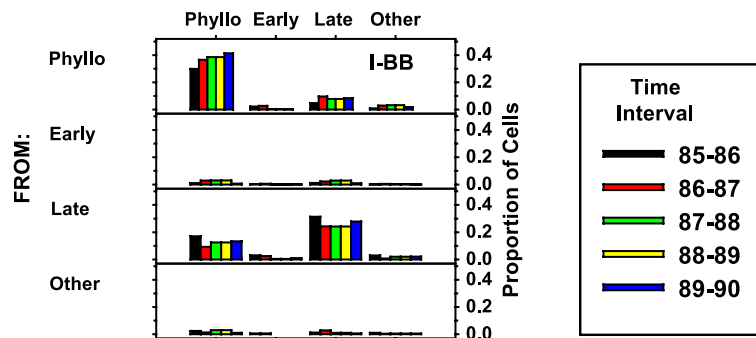
These patterns suggest that *Phyllospadix* may be a dominant competitor for space in the mosaic. The only interactor that exhibited equivalent displacement capabilities was *Lessoniopsis*, which overgrew surfgrass about as frequently as it was overgrown by surfgrass (mean transition percentages of $8.3 \pm 1.1\%$ vs. $8.8 \pm 1.1\%$, respectively; Fig. 9A). All other subdominants at each exposure, including “*Hymenena*,” “*Dilsea*,” and *Constantinea* at wave-exposed sites, and *Neorhodomela*, *Odonthalia* and *Mazzaella* at the intermediate and wave-protected sites, were much more likely to be displaced by surfgrass than they were to displace surfgrass.

These data suggest a paradox. If surfgrass displaces almost all other species at relatively high rates, and if it is a superior competitor (see Section

A. EXPOSED SITES



B. INTERMEDIATE SITE



C. PROTECTED SITES

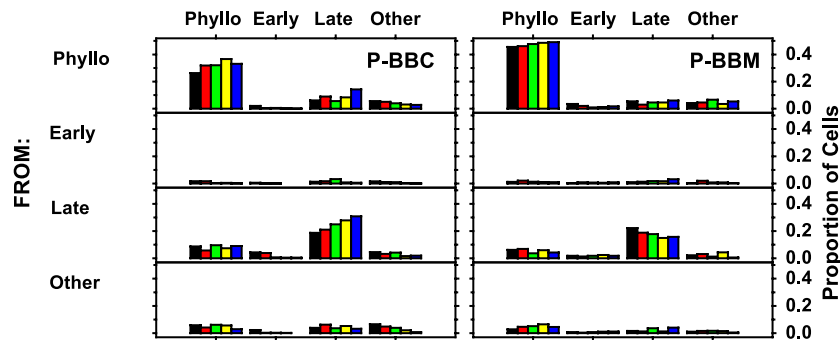


Fig. 8. Annual transition probabilities among functional groups, including surfgrass (*Phyllospadix*), early and late successional species, and all other space occupants aggregated (“other”). Categories from which the change occurs are listed on the ordinate, categories to which the change occurs are listed on the abscissa. All probabilities total to 1.0 in each year at each site. Persistence (i.e., no change) is the most frequent “transition” at all sites. The focus of our analysis was on the transitions involving change.

3.4.1) why does not it eliminate them? As detailed below, the answer lies in changes in susceptibility to disturbance and competitive ability of surfgrass along the wave-exposure gradient: both are high at wave-exposed sites and low at wave-protected sites.

3.3. Disturbance regime

Physical disturbance is evidently the primary deterrent to the potential dominance of *Phyllospadix*, especially at wave-exposed sites. Examination of the

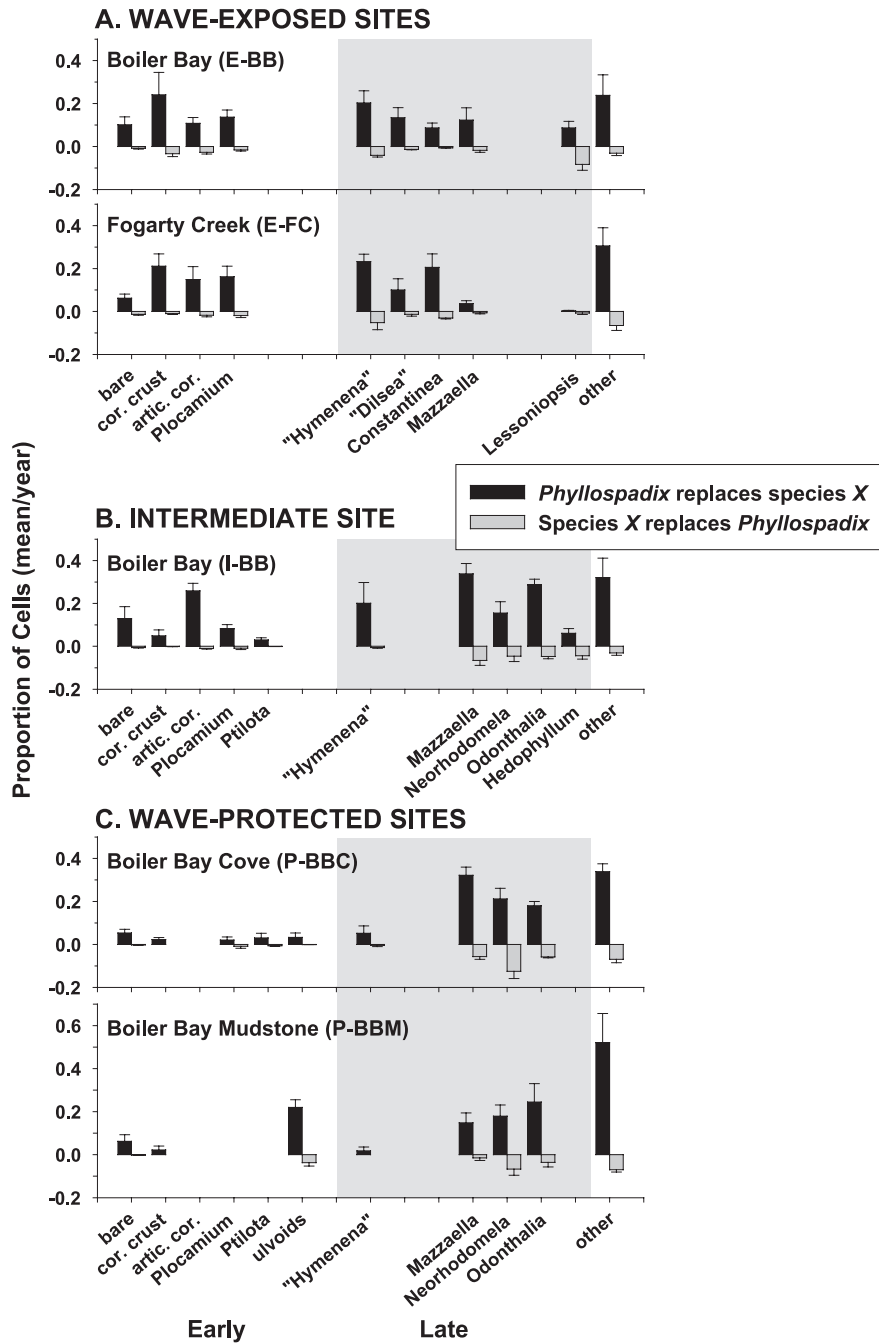


Fig. 9. Annual transition probabilities (mean+1 S.E. of per-plot means, averaged across years) for the main components of the macrophyte matrix, focusing on transitions involving *Phyllospadix* (i.e., surfgrass overgrowing other species and other species overgrowing surfgrass). Most change involves surfgrass overgrowing its neighbors.

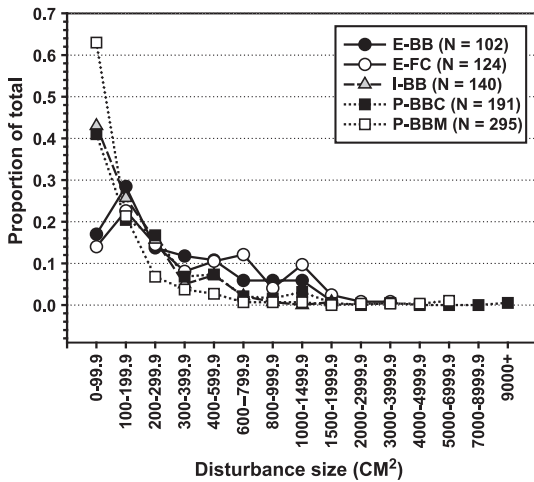


Fig. 10. Size frequency of disturbances by site, totalled over 1985–1990 (*n* is the total number of disturbances for each site). The majority of disturbances at wave-protected sites were small (0–99.9 cm²); those at wave-exposed sites were larger on average, with the most frequent size in the next-to-smallest category (100–199.9 cm²).

edges of surfgrass patches frequently revealed rhizomes that had been broken along segments of the edge. Further, surfaces next to these areas of broken rhizomes were often bare, covered with encrusting coralline algae, or occupied by algal species that are known to be rapid colonizers of vacated space. Rapid colonizers include ulvoids, diatoms, and various species of red and brown algae (see description of “other” category under Section 3.1). These clear markers of disturbance allowed us to quantify the disturbance regime as described in Methods. This analysis also aimed at understanding another seeming paradox. What was the cause of disturbances in wave-protected areas where the magnitude of wave turbulence is very much less than at wave-exposed areas?

Most disturbances were small (<200 cm²) in area (Fig. 10), although they occasionally reached much larger sizes (maximum sizes: E-BB, 1876 cm²; E-FC, 3310 cm²; I-BB, 1598 cm²; P-BBC, 26,418 cm²; P-BBM 6169 cm²). Disturbance size frequencies varied

DISTURBANCE REGIME

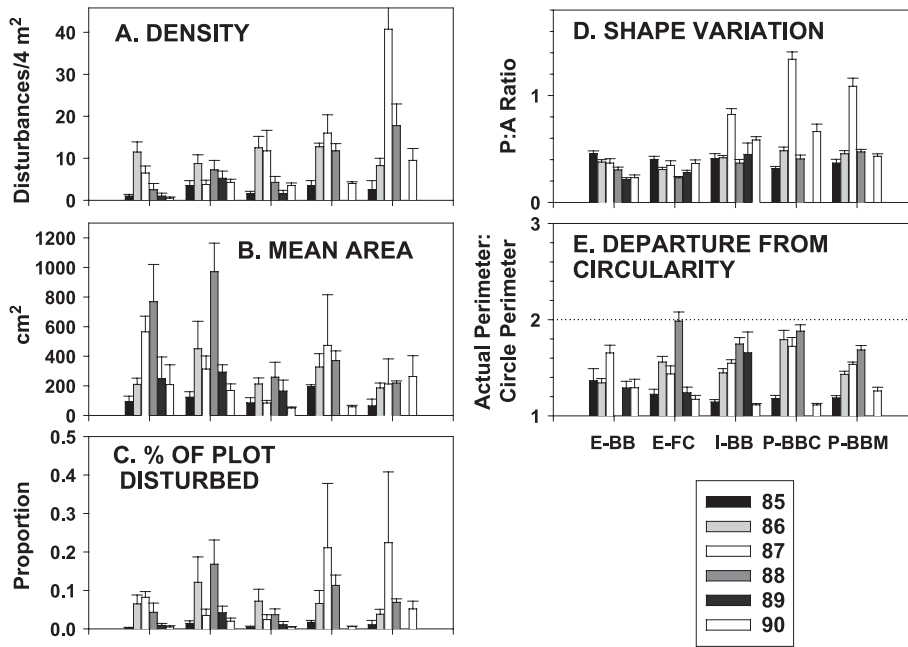


Fig. 11. Components of the disturbance regime, including per year (A) density (number/4 m²), (B) area (cm²), (C) percent of total area of each 4m² plot disturbed, (D) variation in shape as indicated by perimeter/area ratios, and (E) departure from circularity as indicated by ratios of actual perimeter/perimeter of a circle. All data are mean+1 S.E.

with wave-exposure (Fig. 10). At wave-exposed sites, disturbances 100–200 cm² were most numerous, while at the intermediate and wave-protected sites, disturbances 0–100 cm² were most common. Further, wave-exposed sites tended to have more disturbances at intermediate size ranges (200–1000 cm²) while wave-protected sites tended to have more very large disturbances (>4000 cm²).

Disturbance regimes varied substantially in space and time (Fig. 11). The number of disturbances per year/plot, or rate of disturbance, varied with wave exposure and year (Table 2A, wave exposure×year interaction term; *p*=0.048). Overall, the rate of

generation of disturbances at wave-protected sites was 2.5× (95% confidence interval: 1.8× to 3.3×) the rate at wave-exposed sites, and 1.8× (1.2× to 2.5×) the rate at the intermediate site (Table 2A, effect size). Disturbance rate varied among years (rank order: 86>87>88>90>85). Rates in 1986 (highest rate) were 4.6× (2.9× to 7.2×) those in 1985 (lowest rate).

Disturbance size (mean area in cm²) also varied with wave exposure and year (Table 2B, main effects; wave exposure *p*=0.0003, year *p*<0.0001). As suggested by the size frequency patterns (Fig. 10), mean disturbance size at wave-exposed sites was 2.3× (1.6× to 3.3×) larger than at the intermediate site and

Table 2
Effect of year and wave-exposure on disturbance regime

Disturbance metric	Source of variation	<i>df</i>	MS	<i>F</i>	<i>P</i>	R ²	Pairwise comparisons	Effect size (95% CI)
(A) Disturbance density (no./plot)	Wave exposure	2	1.473	16.0	<0.0001	0.58	P>I=E	P>E: 2.5× (1.8× to 3.3×) P>I: 1.8× (1.2× to 2.5×)
	Year	4	1.240	13.5	<0.0001		86 87 88 90 85	86>85: 4.6× (2.9× to 7.2×)
	Wave exposure×year	8	0.192	2.08	0.048			
	Error	78	0.092					
(B) Mean disturbance area	Wave exposure	2	0.866	9.23	0.0003	0.50	E>I=P	E>I: 2.3× (1.6× to 3.3×) E>P: 1.6× (1.2× to 2.2×)
	Year	4	0.877	9.34	<0.0001		88 86 87 85 90	88>90: 4.0× (2.5× to 6.2×)
	Wave exposure×year	8	0.179	1.91	0.07			
	Error	78	0.094					
(C) Proportion of plot disturbed	Wave exposure	2	0.060	2.64	0.08	0.36		
	Year	4	0.149	6.54	0.0001		87 88 86 90 85	87>85: 12.2× (5.2× to 22.2×)
	Wave exposure×year	8	0.027	1.20	0.31			
	Error	85	0.023					
(D) Shape variation (perimeter/area)	Wave exposure	2	0.191	14.3	<0.0001	0.71	P=I>E	P>E: 1.36× (1.22 to 1.52) I>E: 1.34× (1.17× to 1.54×)
	Year	4	0.223	16.8	<0.0001		87 90 86 85 88	87>88: 2.0× (1.69× to 2.36×)
	Wave exposure×year	8	0.144	10.8	<0.0001			
	Error	78	0.013					
(E) Departure from circularity	Wave exposure	2	0.004	1.70	0.2	0.71		
	Year	4	0.095	40.3	<0.0001		88 87 86 85 90	88>90: 1.49× (1.39× to 1.6×)
	Wave exposure×year	8	0.003	1.16	0.34			
	Error	78	0.002					

Pairwise comparisons on main effects (by wave exposure with years combined, by year with exposures combined) were made using linear contrasts. E=exposed; I=intermediate; P=protected. Lines in pairwise comparisons overlap levels that do not differ; levels are ordered by magnitude with largest values listed first. When a factor was statistically significant, effect size and 95% confidence intervals were calculated for wave exposure comparisons and for comparisons between the largest and smallest annual values using estimates from linear contrasts. Disturbance density, mean area, shape variation, and departure from circularity were log₁₀-transformed, and the proportion of the plots disturbed and CV of disturbance area were arcsin-transformed. Cochran's *C* test (Winer et al., 1991) indicated that all variances were homoscedastic after transformation except for the proportion of the plots disturbed. Significant values are shown in boldface. 1989 data were dropped from the analysis because no data were available from P-BBC and P-BBM.

1.6× (1.2× to 2.2×) larger than at the wave-protected sites (Table 2B, effect size). The largest average disturbance sizes occurred at E-BB in 1987 and 1988 and at E-FC in 1988 (Fig. 11B). Disturbance size variation across years, by rank, was 88>86>87>85>90, and 1988 disturbances (the largest) were 4.0× (2.5× to 6.2×) larger than 1990 disturbance (the smallest) (Table 2B, linear contrasts and effect sizes). Note that in 1987 at P-BBM, the site×year combination with the highest observed rate of disturbance, average disturbance size was relatively small, around 200 cm². In contrast, in 1988 at E-FC, the site×year combination with the largest disturbances, the rate of disturbance was relatively small, about seven per plot (Fig. 11A,B).

The percent of the total area of the plot disturbed can serve as an indication of the relative extensiveness of the damage from disturbance. The extensiveness of disturbance damage varied strikingly among years, but not among wave-exposures (Fig. 11C, Table 2C). As suggested by the patterns of disturbance rate and size, the most extensive loss was in 1987 and 1988 (rank order: 87>88>86>90>85). Percent damage in 1987 (highest level) was 12.2× (2.2× to 22.2×) greater than in 1985 (lowest level).

Disturbed patches were typically ovoid in shape, but in some years shape varied dramatically, including

extensive lobes with corridor-like attachments. We examined this pattern by calculating the ratio of perimeter to area (P/A ratio) and an index of the extent to which the disturbances departed from a circular shape independent of area (the ratio of the actual perimeter to the perimeter of a circle of the same area) (Fig. 11D,E). Shape variation varied greatly with wave exposure and year (Table 2D, wave exposure×year interaction). Thus, shape varied little through time at the wave-exposed sites but at sites of low turbulence, large P/A ratios occurred in 1987 and 1990 (Fig. 11D), suggesting that at low turbulence sites (intermediate and wave-protected) disturbances tended to be more irregular in shape. This comparison is confounded, however, by the fact that mean disturbance size was greater at wave-exposed sites than at the intermediate and wave-protected sites (Table 2B). If disturbance size is factored out by examining the actual to circle perimeter ratio, shape varied primarily through time (Table 2E, year as a main effect: rank order, 88>87>86>85>90). Disturbances were more irregular during years of high frequency, size, and proportion disturbed (1986–1988) and more circular in years of low overall disturbance (1985, 1990) (Fig. 11E, Table 2E; linear contrasts). Disturbance shape ratios in 1988 were 1.5× (1.4× to 1.6×) larger (more irregular) than those in 1990.

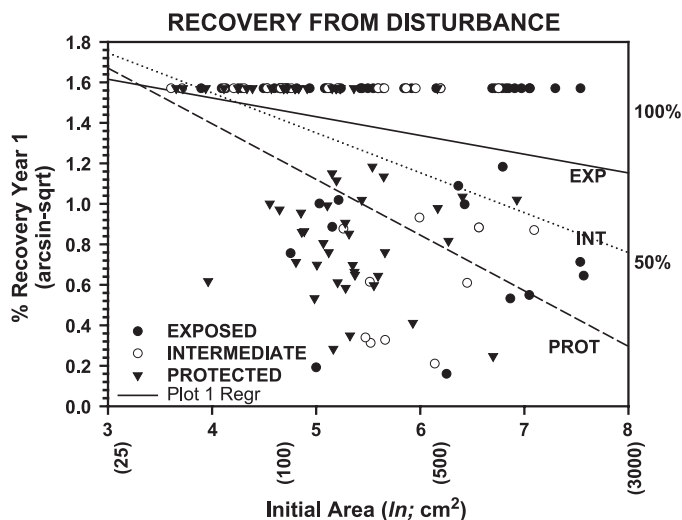


Fig. 12. Recovery from disturbance (i.e., rate of return to surfgrass) during the first post-disturbance year by wave-exposure, 1986–1988. For reference, approximate actual area (non-transformed) of initial disturbance is shown at intervals in parentheses along the abscissa and approximate percent (non-transformed) recovery is shown on the right ordinate. Each symbol represents one disturbance.

3.3.1. Recovery from disturbance

As suggested by a plot of initial area vs. percent recovery in the first year (Fig. 12), disturbances recovered differentially by exposure and initial size (Table 3; log-linear model analysis; likelihood-ratio $\chi^2=31.0$, 8 *df*, $p<0.0001$). Large (>500 cm²) disturbances recovered at a disproportionately higher rate at wave-exposed sites than did those at wave-protected sites. Of the 44 wave-exposed disturban-

ces undergoing >90% recovery, 11 (25%) were large, while of the 22 wave-protected disturbances undergoing >90% recovery, 0 were large. Small disturbances tended to recover more quickly at wave-exposed sites as well. Of the 38 small disturbances at wave-exposed sites, 33 (86.8%) underwent >90% recovery while of the 53 small disturbances at wave-protected sites, only 22 (41.5%) recovered nearly fully. The largest disturb-

Table 3
Recovery and expansion of disturbances to surfgrass

(A) Recovery analysis

I. Regressions of initial disturbance area (cm ²) vs. percent recovery in the following year				
Exposure	Linear regression	<i>n</i>	<i>p</i>	<i>r</i> ²
Wave-exposed (two sites)	% recovery=1.89–0.093 (area)	58	0.025	0.087
Intermediate (one site)	% recovery=2.34–0.197 (area)	29	0.09	0.102
Wave-protected (two sites)	% recovery=2.50–0.275 (area)	57	0.0009	0.182
II. Loglinear model analysis (best fit model: exposure+initial size+rate of closure+exposure×initial size+initial size×rate)				
Observed (expected) Frequencies (number of disturbances falling in each exposure×size×rate category)				
Exposure	Initial size (cm ²)	Rate of closure (% recovered/year)		
		<50	51–90	>90
Exposed	<500	2 (7.8)	3 (6.6)	33 (23.6)
	>500	5 (4.8)	3 (5.4)	11 (8.8)
Intermediate	<500	6 (5.2)	2 (4.3)	17 (15.5)
	>500	1 (1.3)	2 (1.4)	2 (2.3)
Protected	<500	16 (11.0)	15 (9.1)	22 (32.9)
	>500	1 (1.0)	3 (1.1)	0 (1.9)
Statistic	Value	<i>df</i>	<i>p</i>	
Pearson χ^2	28.2	8	0.00046	
Likelihood-ratio χ^2	31.0	8	0.00014	

(B) Expansion analysis

I. Regressions of initial disturbance area (cm ²) vs. percent expansion in the following year						
Exposure	Linear regression	<i>n</i>	<i>p</i>	<i>r</i> ²		
Wave-exposed (two sites)	% increase=9.22–0.838 (area)	32	0.01	0.20		
Intermediate (one site)	% increase=9.13–0.969 (area)	14	0.01	0.41		
Wave-protected (two sites)	% increase=7.86–0.796 (area)	27	0.047	0.15		
II. Analysis of covariance						
Source	<i>df</i>	MS	<i>F</i>	<i>p</i>	<i>r</i> ²	Effect size
Exposure	2	8.620	4.58	0.01	0.22	E>P: 3.3×
Initial area	1	33.483	17.8	<0.0001		(1.6× to 5.2×)
Error	69	1.881				

Percent recovery data were arcsin-transformed, and initial area was ln-transformed. In A and B II, the assumption of homogeneity of slopes (parallelism) was met; interactions between initial area and exposure were not significant (A II: $F=1.73$, $p=0.18$, 2, 138 *df*; B II: $F=0.04$, $p=0.96$, 2, 67 *df*). Linear contrasts indicated that for the expansion analysis, the regression for the wave-exposed site differed from that for the wave-protected site, but that the intermediate site did not differ from either.

ance to recover fully in the first year at wave-exposed sites was 1880 cm² in area, almost four times larger than the largest disturbances to recover fully at wave-protected sites (476 cm²). As expected, disturbance recovery at the intermediate site tended to be intermediate between recovery rates at more and less wave-exposed sites.

3.3.2. Expansion of disturbances

When disturbances increased in size during the second year, smaller clearances expanded proportionately more than did larger ones (Fig. 13), and wave-exposed clearances expanded at a rate 3.3× (1.6× to 5.2×) greater than wave-protected clearances (Table 3B). Thus, expansion in size of disturbances seemed primarily to be a function of the wave-exposure regime.

3.4. Effect of biotic interactions on patch boundaries

3.4.1. Grazer effect

In general, macrograzers are sparse in low zone turf mosaics (Turner, 1985; Menge, personal observations), and at wave-exposed areas the main macrograzers in surfgrass-dominated areas were limpets (*Lottia* spp.), chitons (*Katharina tunicata*, *Tonicella lineata*), and isopods (*Idotea wosnesenskii*). The most obvious evidence of a herbivore effect were the rare occasions where a *Katharina* or *Tonicella* could be observed residing in, and presumably

maintaining a small clearing in the turf (see, e.g., the 1990 photo in Fig. 6). Nonetheless, because abundance does not necessarily reflect impact, we tested the effects of limpets and chitons on boundaries between *Phyllospadix* and both *Constantinea* and “*Dilsea*” (Fig. 14). Results after 38 months showed that as expected, herbivores did not influence the boundaries between these species pairings (Fig. 14; one-way ANOVA; $p=0.74$ and 0.45 , respectively, 2, 9 *df*). Surfgrass overgrew its neighbors at about the same rate in both +Grazer and –Grazer treatments. Further, the presence of a stainless-steel fence did not seem to influence this pattern. Surfgrass growth in +Grazer +Fence and +Grazer –Fence plots did not differ for either pairing.

3.4.2. Spatial interactions among established patches

Experiments at the wave-exposed sites yielded results consistent with those in the spatially explicit analyses. Surfgrass appeared to be the dominant competitor for space among the turf species in the mosaic. As indicated earlier, mosaic co-dominants at the wave-exposed sites included *C. simplex*, “*Dilsea*” complex, and “*Hymenena*” complex. Thus, with *Phyllospadix*, six species pairings among these taxa were possible in pairwise border competition experiments. Of these, only *Phyllospadix* vs. “*Hymenena*” was not done due to lack of sufficient border space in the experimental area between patches of these species for at least four replicates.

Surfgrass grew into neighboring patches of both “*Dilsea*” and *Constantinea* regardless of whether or not the algal neighbor was removed (Fig. 15A,B). During the 38-month run of the experiment, surfgrass grew on average 20 cm (0.53 cm/month×38) into the neighboring +“*Dilsea*” plot and 13 cm into the –“*Dilsea*” plot, rates sufficient to fully displace (or nearly so) all the algae in the 15×15-cm neighboring plot. Similarly, surfgrass nearly completely displaced *Constantinea* as well (14.4 cm in +*Constantinea* plots, 10.7 cm in –*Constantinea* plots). Note that there was a trend towards slower growth by surfgrass when its competitor was absent, suggesting that neighbors facilitate surfgrass overgrowth. Finally, although we were unable to carry out experiments with the *Phyllospadix*–“*Hymenena*” pairing, “*Hymenena*” was displaced by surfgrass at a very high rate in the overgrowth

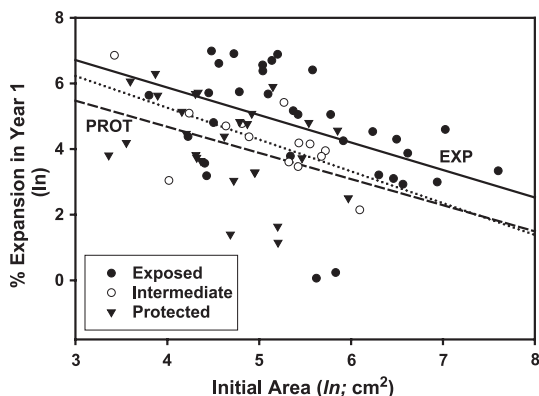


Fig. 13. Rate of further expansion of disturbances that continued to enlarge, by wave exposure, from 1986 to 1988. Wave-exposed disturbances (EXP, solid line) enlarged faster than did wave-protected disturbances (PROT, dashed line).

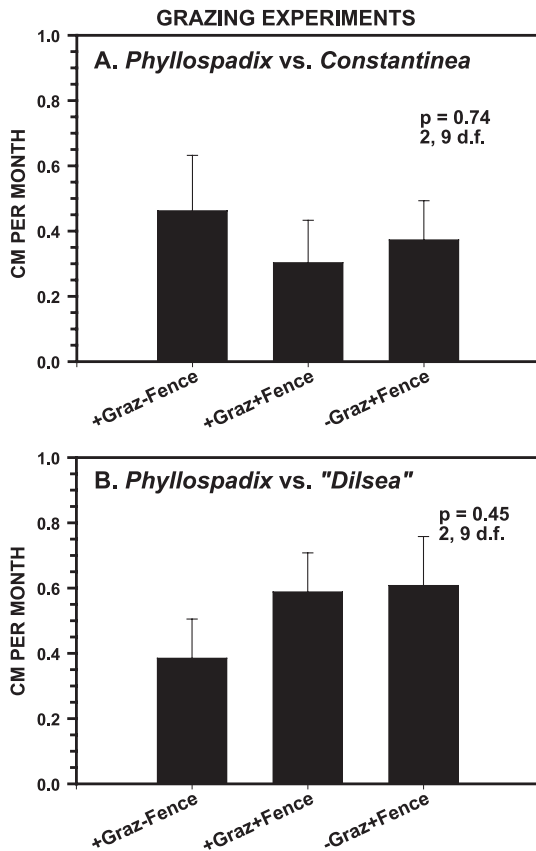


Fig. 14. Results of grazing experiments at E-BB. (A) Outcome of interaction at boundary between *Phyllospadix* and *Constantinea* and (B) outcome of interaction at boundary between *Phyllospadix* and "*Dilsea*." See text and Fig. 3 for explanation of treatments. Surfgrass overgrew its neighbors regardless of the presence or absence of grazers or an exclosure fence.

analysis using transition matrices (Fig. 9), suggesting that this species was also a subordinate competitor to *Phyllospadix*.

Interactions among the other wave-exposed mosaic turf species were slower. Growth patterns in "*Dilsea*"–"*Hymenena*," and *Constantinea*–"*Hymenena*" interactions suggested that when a neighbor is absent, the remaining species moves into the vacated space (Fig. 15C,D). In these two pairings, "*Hymenena*" tended to overgrow its neighbor when both neighbors were present as well as when both neighbors were absent, suggesting that "*Hymenena*" may dominate in competition amongst red algal turfs. In *Constantinea*–"*Dilsea*" pairings, the interaction appeared to be a virtual standoff (Fig. 15E). After

38 months, *Constantinea* had grown towards its neighbor in both its presence and absence, but only 3 to 4 cm.

In the wave-protected experiments at P-BBM, little change occurred at the pairwise species boundaries regardless of the presence or absence of neighbors (Fig. 16). Neither surfgrass nor its main co-occupants of space, *Neorhodomela* and *Odonthalia*, grew much in any treatment, and although surfgrass and *Odonthalia* tend to move into vacated space, the changes were not significant. For example, in the absence of *Neorhodomela*, surfgrass grew only 2.2 cm into the vacated space in 38 months. Similarly, *Odonthalia* grew only 3.7 cm into –*Phyllospadix* space and surfgrass grew only 1.1 cm into –*Odonthalia* space. Thus, in contrast to the wave-exposed results, where surfgrass almost completely displaced neighbors or fully occupied vacated space within 3+ years, macrophytes barely grew at the wave-protected site over the same time interval.

3.4.3. Recruit–adult interactions: *Phyllospadix* vs. *Neorhodomela*

The growth of surfgrass recruits (seedlings) was affected by *Neorhodomela*, but the effect varied through time (Fig. 17, Table 4, month \times *Neorhodomela* interaction, univariate $p=0.016$). At both upper and lower levels of the low zone, *Phyllospadix* grew more slowly in the presence of *Neorhodomela* from August through November 1987, and then grew more rapidly in the presence of *Neorhodomela* from January through May 1988. The drop in percent cover that occurred in August 1988, plus the slower growth in the presence of *Neorhodomela* during the previous summer to early autumn, suggests that growth of surfgrass recruits may vary with seasonal changes in environmental stress. Air temperatures reach a peak during July and August, and each year since 1985 we have observed that surfgrass bleaches and desiccates during this time. The slower growth observed in the upper low zone experiments (Fig. 17A, Table 4, Height effect, $p=0.04$) is consistent with this possible affect of thermal stress on surfgrass. These fluctuations suggest the hypothesis that growth of surfgrass recruits is inhibited by its co-dominant during more stressful times of the year and is facilitated during less stressful times of the year (late autumn through spring).

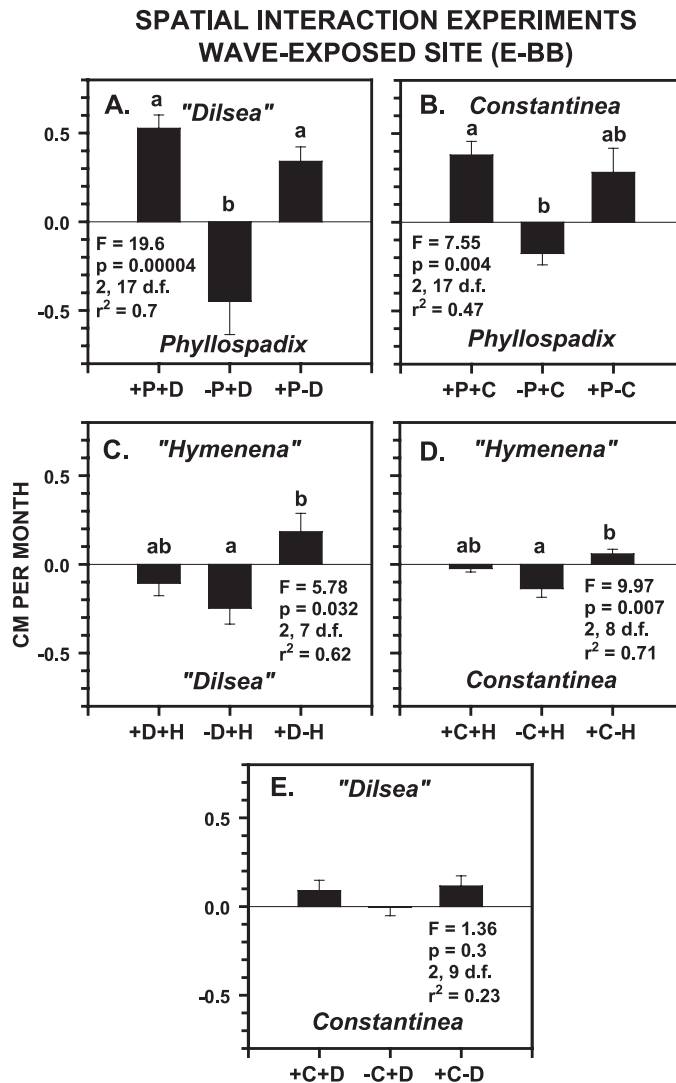


Fig. 15. Results of competition experiments at E-BB. In each panel, the 0.0 axis represents the border between the two interactors. For example, in (A), the surfgrass patch occupied the negative half of the panel and "Dilsea" occupied the positive half of the panel. Histograms show the distance into each patch that the boundary between the species moved under conditions of presence or absence of each (see Fig. 3 for explanation of treatments). The analyses shown in each panel were a one-way ANOVA on the distance ($\ln(\text{cm}+1)$) advanced or retreated by the border/month based on results taken on the final sample date. In (A) and (B), for added statistical power, the analysis included +*Phyllospadix* +*Dilsea* and +*Phyllospadix* +*Constantinea* plots from the grazer effect experiment. Analyses without these additional plots gave the same results but with larger p -values: *Phyllospadix* vs. *Dilsea*; $F=11.23$, $p=0.0036$, $df=2, 9$ and *Phyllospadix* vs. *Constantinea*; $F=6.55$, $p=0.018$, $df=2, 9$.

In contrast, *Neorhodomela* recruits (clumps with only two to five branches) were clearly inhibited by the presence of established *Phyllospadix* (Fig. 18, Table 5). In the presence of surfgrass, overall abundance of *Neorhodomela* declined while in the absence of surfgrass, overall abundance of *Neorhodomela* increased. These trends varied through time, as *Neo-*

rhodomela abundance declined through fall into winter in all plots, regardless of surfgrass presence, and recovered differentially through spring and summer (Table 5, within-subjects; month \times *Phyllospadix* interaction, $p=0.017$). The seasonal trend reflects the fact that *Neorhodomela* perennates, meaning that the thalli (upright portion of the alga) mostly die back during

**SPECIES INTERACTION EXPERIMENTS
WAVE-PROTECTED SITE (P-BBM)**

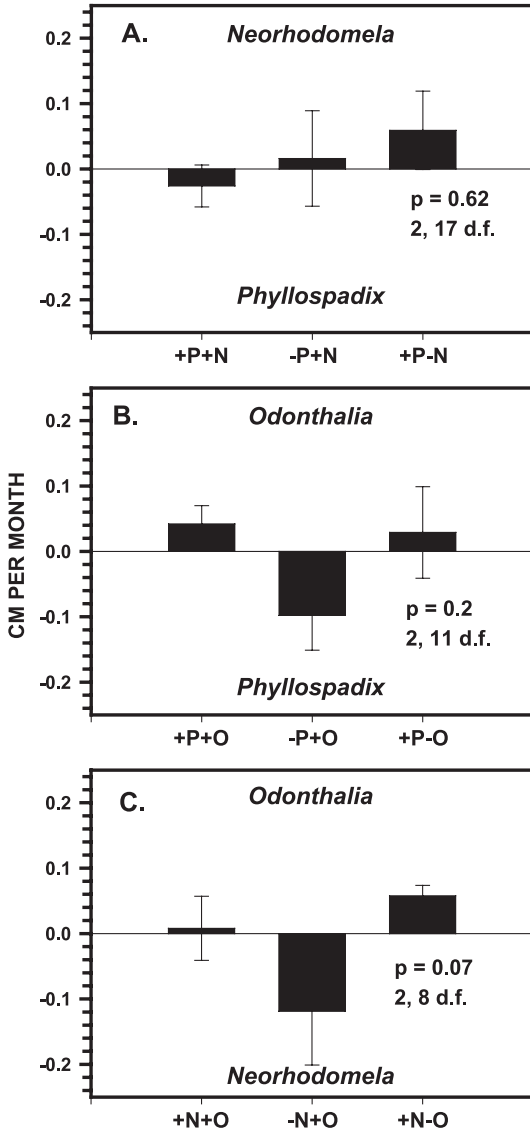


Fig. 16. Results of competition experiments at P-BBM. See Fig. 15 caption for interpretation of results.

winter leaving the basal crust holdfast to regrow new thalli in spring. Together, these results suggest that in adult–recruit interactions, surfgrass recruits are capable of gradual expansion while surrounded by *Neorhodomela*, but that *Neorhodomela* recruits will gradually be overwhelmed and displaced when surrounded by surfgrass. These patterns suggest that surfgrass is the

dominant competitor at the I-BB site, although competition is likely to proceed slowly as at the more protected site in which the pairwise experiments were done.

4. Discussion

This study demonstrates that, in contrast to the “mean-field” impression of relatively unchanging macrophyte abundances, when viewed in a spatially explicit manner, the picture is one of constant change. In addition to generating new understanding of the dynamics of macrophyte-dominated low rocky intertidal assemblages along the eastern Pacific coast, we suggest that our results make several additional

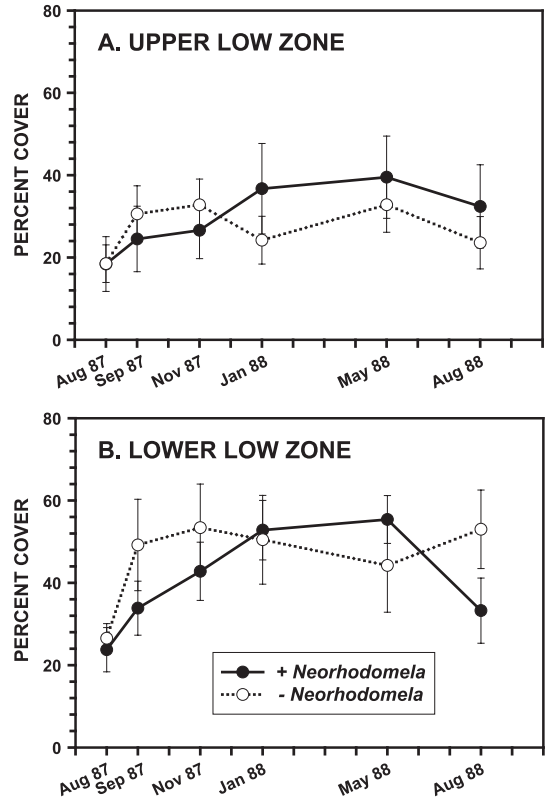


Fig. 17. Results of experiments testing change in abundance of *Phyllospadix* recruits in the presence and absence of *Neorhodomela* in the upper low zone (A) and lower low zone (B). From August to November 1987, surfgrass recruits tended to expand in size faster in the absence of *Neorhodomela*, suggesting release from competition. From January to May 1988, *Phyllospadix* expanded faster in the presence of *Neorhodomela*, suggesting facilitation.

Table 4

Test of effect of height on the low shore and established *Neorhodomela larix* on growth (ln of percent cover) of *Phyllospadix scouleri* recruits

Univariate analysis				
Source of variation	df	Mean square	F	p
<i>Between subjects</i>				
Height on the shore	1	0.9802	5.17	0.04
<i>Neorhodomela</i>	1	0.0617	0.33	0.58
Height× <i>Neorhodomela</i>	1	0.1226	0.65	0.44
Error	13	0.1896		
<i>Within subjects</i>				
Month	5	0.1287	12.6	≪ 0.000001
Month×Height	5	0.0134	1.31	0.27
Month× <i>Neorhodomela</i>	5	0.0311	3.04	0.016
Month×Height× <i>Neorhodomela</i>	5	0.0097	0.95	0.45
Error	65	0.0102		

Multivariate analysis

Source	Wilk's Lambda	df	F	p
Month	0.1392	5, 9	11.13	0.0012
Month×Height	0.5153	5, 9	1.69	0.23
Month× <i>Neorhodomela</i>	0.3183	5, 9	3.86	0.038
Month×Height× <i>Neorhodomela</i>	0.5958	5, 9	1.22	0.37

Analysis employed repeated measures analysis of variance (RM-ANOVA) because the same plots were sampled repeatedly through time. The assumption of compound symmetry was met (Mauchly criterion=0.133, $\chi^2=22.4$, 14 df, $p=0.07$) so we present unadjusted probabilities. Statistically significant probabilities are shown in boldface.

advances. First, our work offers insight into the dynamics of a common but relatively unstudied pattern, plant-dominated mosaics, whether marine or non-marine. Second, this study expands our understanding of the factors structuring low zone communities in general, and of the dynamics of rocky intertidal communities as a whole. Third, this study provides a case study that is relevant to the theory of spatial dynamics. We address each of these issues in turn below.

4.1. Macrophyte mosaic dynamics along a wave-exposure gradient

The dynamics of these macrophyte mosaics are primarily a function of processes focused on the

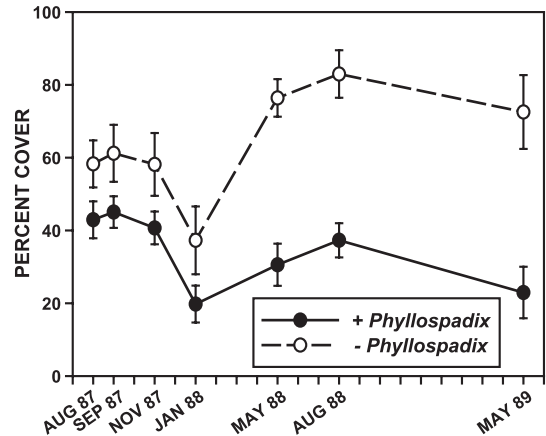


Fig. 18. Results of experiments testing change in abundance of *Neorhodomela* “recruits” (small clumps) in the presence and absence of *Phyllospadix*. *Neorhodomela* expanded in area in the absence of surfgrass and shrank in area in its presence, suggesting competition.

surfgrass *P. scouleri*. At wave-exposed sites in particular, this angiosperm is affected by forces that disturb the spatial pattern of the mosaic, and disturbance combined with patterns of growth of surfgrass dictates the structure of the mosaic. The composition of the mosaic varies with wave exposure, presumably because dispersal ranges or the tolerance ranges to

Table 5

Test of effect of established *Phyllospadix scouleri* on growth (ln percent cover per plot) of *Neorhodomela larix* recruits

Univariate analysis				
Source of variation	df	Mean Square	F	p
<i>Between subjects</i>				
<i>Phyllospadix scouleri</i>	1	3.6426	15.13	0.0013
Error	16	0.2407		
<i>Within subjects</i>				
Month	6	0.2738	9.02	≪ 0.000001
Month× <i>Phyllospadix</i>	6	0.1777	5.85	0.00003
Error	96	0.0304		
Multivariate analysis				
Source of variation	Wilk's Lambda	df	F	p
Month	0.1764	6, 11	8.56	0.0013
Month× <i>Phyllospadix</i>	0.2966	6, 11	4.35	0.017

Analysis employed RM-ANOVA. The assumption of compound symmetry was met (Mauchly criterion=0.2624, $\chi^2=18.4$, 20 df, $p=0.56$) so unadjusted probabilities are presented. Statistically significant probabilities are shown in boldface.

wave exposure-related factors of the mostly red algal co-occupants of the mosaic are narrower than the range of conditions present. Surfgrass, in contrast, spans the entire range of conditions, although our results suggest that optimal growth conditions exist toward the wave-exposed end of the environmental gradient. In the following, we organize our comments following the three stages of the dynamics of the mosaic, *clearance*, *colonization*, and *succession*, and on the processes involved in each.

4.1.1. Clearance

Disturbance regimes clearly varied through time, with several disturbance metrics suggesting that the highest rates of loss occurred in 1986–1988 while lower rates occurred in 1985 and 1989–1990 (Fig. 11, Table 2). To our surprise, disturbance regimes were roughly similar across the wave exposure gradient. For example, the average number of disturbances per 4 m² plot was similar at wave-exposed, intermediate, and wave-protected sites in 1985, 1986, 1989 and 1990 (Table 6). Average disturbance size differed with exposure only in 1988, and the total proportion of each plot disturbed did not vary with exposure in any year of the 6-year study. Proportional losses/year averaged over years were (mean±95% confidence interval) 6.5±2.3% (wave-exposed), 3.3±4.7% (inter-

mediate) and 9.4±2.3%. Thus, contrary to expectation, mosaics in wave-protected areas appear to be disturbed about as much as do mosaics in wave-exposed areas. Further, in those few cases where disturbance did vary with wave-exposure, patterns were still not entirely as expected. Some measures indicated that in some years disturbance was greater at wave-exposed sites (e.g., average disturbance size in 1988; Fig. 11B) but for others disturbance was greater in wave-protected areas (e.g., average number of disturbances per plot, proportion of plot disturbed; Fig. 11A,C).

4.1.2. Role of substratum

What was the basis of these patterns, particularly the unexpectedly high disturbance in wave-protected areas? Our estimates of rock hardness and of sediment depth suggest that disturbance in these mosaics is an integrated result of the combination of wave impact, which diminishes from wave-exposed to wave-protected areas (e.g., Menge et al., 1996), variable substratum strength, and variable sedimentation (Appendix 1). Wave-exposed sites, with basaltic rock composition, presumably have substrata that are less prone to failure than substrata at wave-protected sites, which are mudstone or mudstone under a thin layer of basalt. Thus, although wave impact is less in wave-sheltered sites, plants attached to the weaker substratum

Table 6

Analysis of variation (one-way ANOVA) in disturbance regime (number per year, average disturbance area and proportion of total area disturbed) across the wave exposure gradient by year from 1985 to 1990

Characteristic	Year	MS	MSE	df	F	p	r ²
Number per year	1985	3.15	6.6176	2, 17	0.48	0.63	0.053
	1986	7.93	18.3456	2, 17	0.43	0.66	0.048
	1987	1121.1	124.32	2, 17	9.02	0.002	0.51
	1988	244.5	34.65	2, 17	7.06	0.006	0.45
	1989	7.04	8.588	1, 10	0.82	0.39	0.076
	1990	40.09	11.79	2, 17	3.40	0.057	0.29
Mean area	1985	2758.7	6501.0	2, 17	0.42	0.66	0.048
	1986	21,219	42,417	2, 17	0.50	0.62	0.056
	1987	169,442	132,207	2, 17	1.28	0.30	0.13
	1988	829,319	131,828	2, 17	6.29	0.009	0.425
	1989	30,146	35,737	1, 10	0.84	0.38	0.078
	1990	26,312	33,236	2, 17	0.79	0.47	0.085
Proportion disturbed	1985	0.00013	0.00016	2, 17	0.82	0.46	0.088
	1986	0.0034	0.0055	2, 17	0.61	0.55	0.067
	1987	0.071	0.044	2, 17	1.60	0.23	0.159
	1988	0.0065	0.0060	2, 17	1.09	0.36	0.113
	1989	0.00057	0.00067	1, 10	0.85	0.38	0.079
	1990	0.00093	0.00061	2, 17	1.53	0.24	0.153

tum in these areas presumably are more susceptible to wave forces. By weakening surfgrass rhizomes, burial by sediment may exacerbate plant detachment during even modest wave action. We suspect that both softer substratum and sedimentation underlie the unexpectedly high disturbance rates in wave-protected areas, but have no information with which to evaluate this expectation or its alternatives (i.e., that one or the other factor is the more important one).

4.1.3. Annual variation

Why did disturbance vary so dramatically among years? The most obvious possibility is that the winters preceding summer measurements of low disturbance had less severe wave action than did winters preceding summer measurements of high disturbance. Unfortunately, the technology to quantify wave forces directly at each of these sites during the study period was unavailable at the time. A less direct measure is to examine patterns of significant wave height (h_s) recorded by NOAA's array of offshore data buoys which measure h_s , defined as the highest one-third of all of the wave heights during each hourly 20-min sampling period (see <http://www.ndbc.noaa.gov>). Using buoy data and disturbance rates in Paine and Levin (1981), Denny's (1995) analysis successfully used h_s to predict the range of rates of mussel dislodgement. Denny (Table 4 in Denny, 1995) provided annual estimates for h_s for Coquille River, OR, about 200 km south of our sites. Comparing these estimates of yearly average h_s (in meters) to estimates of the percentage of our 2×2-m plots that was disturbed (mean±95% confidence interval) from 1985 to 1990 yields:

1985— $h_s=2.202$, % disturbed= $0.97\pm0.4\%$;
 1986— $h_s=2.272$, % disturbed= $10.8\pm0.4\%$;
 1987— $h_s=2.090$, % disturbed= $11.9\pm0.4\%$;
 1988— $h_s=2.410$, % disturbed= 10.9 ± 0.4 ;
 1989— $h_s=2.061$, no data for % disturbed; and
 1990— $h_s=2.359$, % disturbed= 1.8 ± 0.4 .

Although high h_s and high disturbance occurred in 1986 and 1988, no such relationships are evident in 1985, 1987 and 1990. We conclude that the evidence is insufficient to attribute the annual variation in the macrophyte mosaic disturbance regime to annual variation in storminess. Similar non-correspondence between disturbance loss and storminess has more

recently been observed in our studies of mid-zone mussel bed disturbance at this and other sites along the Oregon coast (G. Allison, P. Halpin, B. Menge unpublished data). Other alternatives, such as variation in susceptibility to disturbance due to annual differences in wintertime surfgrass physiological condition (e.g., due to periods of exceptional thermal stress) cannot be discounted on the basis of present information.

4.1.4. Colonization

Although the patterns of disturbance help explain why surfgrass monocultures do not replace the mosaic, the explanation of why the turf is composed of many algal species rather than few is less clear. One hypothesis, that propagules of algal turf species have dispersal limited to the immediate vicinity of reproductive plants (e.g., (Sousa, 1984a), may help explain variation in recolonization of clearances at wave-exposed sites, but not at wave-protected sites. Specifically, while the red alga *C. simplex* exhibited variation in density of recruitment at different distances from propagule sources at a wave-exposed site, no variation in recruit density with distance from propagule source was observed for *O. floccosa* or *N. larix* (Menge et al., 1993). Large differences in average recruit density were observed, however, with *Neorhodomela* settling at much lower densities than *Odonthalia*.

Nonetheless, our observations during this research and the studies of Turner (1983a, 1985) make it clear that recolonization of disturbed areas was not predictable. Turner's (1983a) studies of succession in wave-protected mosaics suggested that colonization and successional pathways varied with the season of clearance. Spring clearances were colonized and initially dominated by different species than were observed in autumn clearances.

Studies of algal phenology suggest that life history differences are likely to also play a key role in maintaining the mosaic structure (Menge et al., 1993), at least at wave-exposed areas. The red algae *C. simplex* and *Hymenena flabelligera* were reproductive for relatively brief periods in spring and summer, for example, meaning spores for colonization of disturbances would be available only during this time period. At wave-protected areas, phenological observations indicated that the two most common mosaic algae, *Odonthalia* and *Neorhodomela* were reproduc-

tive during all months but January and February and thus were likely to be able to colonize disturbances almost year-round. With respect to *Odonthalia* and *Neorhodomela*, we suspect that *Odonthalia*'s advantage in colonization ability is offset by a persistence-competitive advantage by *Neorhodomela*, but this possibility has not been investigated.

These differences in phenology and in apparent dispersal distance with wave exposure are consistent with the differences in mosaic diversity along the environmental stress gradient. Higher diversity at wave-exposed sites, for instance, may be a function of high variation in the identity of invaders of disturbed patches due to brief periods of spore dispersal and localized dispersal. Lower diversity at wave-protected sites may result from more predictable patch colonization due to lengthy periods of reproduction (by *Odonthalia* and *Neorhodomela*) and wider-ranging dispersal of spores (by *Odonthalia*).

4.1.5. Succession

The structure of the macrophyte mosaic was remarkably stable at each site over the 6 years of this study (Fig. 4). Based on these quantitative results, and qualitative observations begun in 1980, this pattern of seeming constancy has persisted for >20 years. Intensive research involving at least monthly visits continues to the present (summer 2004) at Boiler Bay and Fogarty Creek, and, with the exception of a sharp reduction in the abundance of laminarians (e.g., *Lessoniopsis*, *Hedophyllum*) during the El Niño of 1997–1998 (Menge et al., personal observations; Freidenburg et al., unpublished data), algal mosaic structure has remained unchanged.

4.1.6. Overgrowth interactions

The study of spatially explicit changes in the permanently marked plots, however, demonstrated that this apparent constancy is illusory (e.g., Figs. 6–9). Large shifts occurred within the mosaic on an annual basis at wave-exposed, intermediate and wave-protected areas. With field observations of overgrowth of algal neighbors by surfgrass, the competition and grazer-effect experiments indicate that in the absence of disturbance, all sites would eventually become surfgrass monocultures. With the exception of *Lessoniopsis*–*Phyllospadix* interactions, all surfgrass–algal interactions were strictly hierarchical: surfgrass was

never overgrown by any algal turf species. Although we did not quantify epiphytic algae, field observations indicated that epiphytic cover of *Phyllospadix* blades was minimal. The *Lessoniopsis*–*Phyllospadix* interaction appears to have been a standoff, at least under normal conditions. Although each exchanged space at the expense of the other, at least at Exposed Boiler Bay (Fig. 9A), these changes appeared to balance out, at least during 1985–1990. Expansion of the temporal scale of these studies to include severe El Niños, such as that in 1997–1998, would have been interesting because during this time *Lessoniopsis* virtually disappeared from E-BB while surfgrass appeared unaffected (Menge et al., personal observations). By summer 2000, however, this kelp had recovered to abundances that qualitatively appeared comparable to those observed previously. The mechanisms underlying the reduction of the kelp appeared to include nutrient depletion and thermal stress (Freidenburg et al., unpublished data) while the mechanisms underlying its rapid recovery are unknown.

4.1.7. Experimental evidence

The experimental and marked plot results suggest that *P. scouleri* is a dominant competitor for space in this mosaic, but that the rate of displacement of competitors by surfgrass varies with wave exposure. In the wave-exposed competition experiments, surfgrass almost completely overgrew its neighbors in adjacent plots, meaning that in 3 years the edge of the surfgrass patch grew ~15 cm (in terms of mean area or percent area covered $\pm 95\%$ confidence interval: 4.91 ± 1.0 cm²/month or $3.7 \pm 1.6\%$ /month) (Fig. 15). In terms of % area overgrown annually in the 2×2-m plots at wave-exposed sites, this growth rate translates into about 19.6% of a plot being overgrown by surfgrass in a year. At this rate, in the absence of disturbance it would take about 5 years for surfgrass to occupy 100% of the space in an initially clear plot. Note that this rate is about 3× higher than the rate of disturbance in the marked plots (range of area lost to disturbance across wave exposures was 3.3 to 9.4/year; see above). We believe that this difference is related in part to the disturbance plots being somewhat higher (by about 0.3 to 0.6 m) on the shore than were the experimental plots. Surfgrass higher on the shore is likely to grow slower due to lesser immersion time,

and thus shorter exposure to nutrients and longer exposure to thermal and desiccation stress.

Growth in experiments at wave-protected sites was far less than at wave-exposed sites (Fig. 16). Monthly growth rate (area covered) was $0.32 \pm 1.0 \text{ cm}^2$ or $0.75 \pm 0.8\%$ (and thus statistically undetectable from zero growth), or about 1.4% of a plot being overgrown by surfgrass in a year. At this rate, in the absence of disturbance, it would take about 70 years for surfgrass to occupy 100% of the space in an initially clear plot. This rate of growth is substantially lower than the rate of disturbance at wave-protected sites ($9.4 \pm 1.3\%$), suggesting that recovery from disturbance is more a reflection of processes influencing colonization and growth of the macroalgae than of processes influencing surfgrass growth. These between-exposure differences in growth also seem most likely due to thermal and desiccation stress, both of which increase towards more wave-sheltered parts of the shore. Stress effects were often observed in the field; during late spring and summer the distal portions of blades of surfgrass commonly die, turn brown or white and eventually slough off at wave-protected areas while such effects are seen far less often at wave-exposed areas. It seems likely that the energy devoted to replacing such losses in surfgrass is likely to come at the cost of slower rhizome growth. Macroalgae such as *Neorhodomela* and *Odonthalia* in contrast seem less affected by stress.

We thus postulate that the processes underlying mosaic structure at wave-exposed sites are disturbance, surfgrass overgrowth and competition for space, and variable algal life histories. Disturbance focused primarily on *Phyllospadix* clearly prevents surfgrass, the dominant competitor for space in this system, from eliminating its turf-forming algal neighbors. As suggested by our experiments and observations, grazing appears of minimal importance in either causing gaps in the mosaic or in maintaining patches. This result was expected: limpets and chitons, the most likely macrograzers to have a potential effect on surfgrass or turfy algae, are sparse in the algal mosaic (e.g., Turner, 1985; Menge, personal observations), probably because of the almost total lack of open space (Fig. 4). At wave-protected sites, in contrast, disturbance, persistence and standoff competition, and differential colonization among the macroalgae seem to be the primary processes. Disturbance seems less

focused on any particular species, and overgrowth competition for space seems of minimal importance. New disturbances are occupied rapidly by ephemeral algae such as ulvoids, which are soon replaced by *Odonthalia*, also a rapid colonist. Surfgrass appears to be a co-dominant with *Neorhodomela*, and both are slow colonists.

4.2. Dynamics of macrophyte-dominated intertidal zones

Macrophyte-dominated mosaic dynamics have been studied in a number of locations globally (e.g., Lubchenco and Menge, 1978; Sousa, 1979a; Underwood and Jernakoff, 1981; Dethier, 1984; Hartnoll and Hawkins, 1985; Stewart, 1989; Hawkins et al., 1992; Williams, 1993; Airoidi et al., 1995; Johnson et al., 1997; Burrows and Hawkins, 1998; Dudgeon et al., 1999; Airoidi, 2000; Benedetti-Cecchi, 2000; Benedetti-Cecchi et al., 2000), but with the exception of the Isle of Man studies (Hartnoll and Hawkins, 1985; Hawkins et al., 1992; Johnson et al., 1997; Burrows and Hawkins, 1998), incorporation of spatially explicit approaches remains rare. Below, we examine similarities and differences between the present study and several other investigations of the dynamics of macrophyte-dominated assemblages in rocky intertidal regions.

In Washington State, the intertidal kelp *H. sessile* dominated space at moderate wave exposures due to competitive exclusion of other potential canopy-forming macroalgae (Dayton, 1975). Combining all wave exposures, the shade provided by *Hedophyllum* facilitated the persistence of an assemblage of “obligate” understory species (20 species, some of which are components of the algal mosaic studied here). *Hedophyllum* inhibited the abundance of another assemblage of “fugitive” species (33 species). The dominance of *Hedophyllum* was diminished towards more wave-sheltered areas by thermal and desiccation stress, and towards more wave-exposed areas by competition with *Lessoniopsis* and *Laminaria setchellii*. Thus, as with *Phyllospadix*, growth and competitive ability of *Hedophyllum* varied along a wave-exposure gradient, with diminished abundance being associated with heightened stress. Interestingly, surfgrass was not abundant at Dayton’s (1975) sites, even though wave-exposures and other physical

environmental characteristics at outer coast Washington and central Oregon coast sites are similar (Menge, personal observations).

In the San Juan Islands of Washington State, a more wave-sheltered region, surfgrass was an abundant component of low zone macrophyte assemblages (Dethier, 1984). Studies focused in tidepool assemblages showed that surfgrass was a dominant competitor. As we have observed in the present study, when surfgrass dominated a tidepool it was invulnerable to competitive displacement, and surfgrass seemed to be a primary target of wave-caused disturbance (Dethier, 1984).

A study of surfgrass (*P. torreyi*)–macroalgal turf interactions in Southern California also suggested that surfgrass was competitively dominant on the lower shore and a primary target of disturbance (Stewart, 1989). Further, Stewart (1989) indicated that temporal variation in the border between *P. torreyi* and the turf was a dynamic response of growth to variable disturbance intensity from wave forces, environmental stress, and substratum strength.

In New England, algal turf, consisting primarily of *Chondrus crispus* and *Mastocarpus stellatus*, dominates space in the low intertidal zone of moderately wave-exposed to wave-sheltered areas (Lubchenco and Menge, 1978; Dudgeon et al., 1999). Mussels (*Mytilus edulis*), which can overgrow and smother these red algae under natural conditions at wave-exposed areas or in the experimental absence of predators at more sheltered areas, are the only species capable of displacing *Chondrus* (Lubchenco and Menge, 1978). Recently, Dudgeon et al. (1999) investigated the interaction between *Chondrus* and *Mastocarpus* and demonstrated that the nature of the interaction varies with increasing height on the shore. At lower elevations, *Chondrus* was fast-growing and dominated in competition with *Mastocarpus*. The latter had low recruitment on the lower shore, and persisted at this level primarily as a prostrate encrusting holdfast. Disturbance from waves during winter storms was the only deterrent to the development of *Chondrus* monocultures. Higher on the shore, *Chondrus* grew slower and was differentially more susceptible to loss of tissue from thermal and desiccation stress in spring, summer and fall. Dudgeon et al. (1999) suggest that this differential tissue loss prevented competitive exclusion by *Chondrus* and is

therefore the most likely mechanism allowing these species to coexist in the upper low zone. Hence, as in our study, the competitive ability of the dominant varied along a gradient of environmental stress. Coexistence was maintained by a combination of disturbance, environmental stress, life history characteristics and competition.

The Isle of Man studies (Hartnoll and Hawkins, 1985; Hawkins et al., 1992; Johnson et al., 1997; Burrows and Hawkins, 1998) provide the clearest contrast with the disturbance-competition dominated dynamics summarized for the above studies. Dynamics of the mid-intertidal fucoid–barnacle–limpet mosaic are driven by the limpet–fucoid interaction. Bare rock surface is most likely to be colonized by barnacles, especially if limpets are sparse. A barnacle substratum inhibits limpet grazing and thus enhances fucoid settlement (juveniles of which settle on both barnacles and bare rock). Through time denser stands of juvenile fucoids coalesce into adult fucoid-dominated patches due to losses of fucoid plants attached to barnacles (from wave disturbance and barnacle mortality caused by whelks aggregating to the fucoid–barnacle patches) and to bare rock (from limpet grazers attracted by the fucoid canopy). Eventually, fucoid adults are lost to wave disturbance, partly as a consequence of thalli weakened by grazing, and bare rock is again exposed. Limpets, whose grazing inhibits barnacle settlement, gradually move away after the canopy is gone, starting the cycle anew. Such cycles last about 5 to 6 years (Burrows and Hawkins, 1998). Thus, although disturbance plays a role, the primary forces driving this system appear to revolve around limpets, their grazing effects on fucoids, and the facilitation of limpets by fucoid canopies. Competition for space also appears to play a relatively minor role.

4.3. Rocky intertidal community dynamics

How do the patterns we have documented in this macrophyte mosaic compare to other rocky intertidal systems? With a few exceptions, the number of rocky intertidal investigations that have characterized disturbance regimes is surprisingly small. All of the examples known to us that quantified at least some aspects of the disturbance regime in comparable units are listed in Table 7. These include three studies of

mussel beds, one of a fucoid/barnacle assemblage, and two studies of macrophyte beds (including the present study).

Despite the limited set of examples, there are some intriguing similarities among the studies. For example, disturbance rate, measured as percent of the area of the bed/year, is surprisingly similar for two mussel beds, a fucoid/barnacle bed, and a macrophyte mosaic (Table 7). Although maximum “rotation” (years for 100% turnover) can vary by almost an order of magnitude (35 to 250 years, a 7-fold difference), minimal rotation was more similar among these very different types of assemblages (4.6–13.9 years, a 3-fold difference).

On the other hand, striking differences also occurred. Disturbance size in the mussel beds reached much greater sizes than in the macrophyte-dominated assemblages (maxima of 25 vs. 2.6 m²; Table 7).

Recovery rates also varied, ranging from ~1 cm/year advancement of the patch edge (California mussel bed) or ~1–5%/year (surfgrass beds) to 20 cm/year or ~12%/year (Washington mussel bed), to 78%/year (Oregon mussel bed), and even 100%/year recovery (Oregon macrophyte mosaic). In the latter case, full recovery was commonly observed because most disturbed patches were small (Figs. 10 and 11), the minimum rates we observed in the mosaic (40%/year). Although expansion rates of already existing disturbances are even less often reported, the minimum rates we observed in the mosaic (40%/year) were higher but still relatively comparable to those observed by Dayton (1971) for mussels at Portage Head, Washington (24%). In contrast, our respective maximum rates differed by an order of magnitude (529%/year for the mosaic; 4884% for mussels). Dayton (1971) did not report the duration of his

Table 7
Comparison of disturbance dynamics in marine intertidal habitats

Community location (citation)	Pattern	Disturbance size (range, m ²)	Disturbance rate (% of area/year)	Recovery rate (cm ² /year; %/year)	Expansion rate	Rotation (year for 100% turnover)
(1) Mussel bed, Tatoosh I., WA (Paine and Levin, 1981)	Patches in bed	1. 0.003–21.6 2. 0.013–11.0 3. 0.19–5.8 4. 0.21–25.0 5. 0.04–4.5	2.9–12.3	20 cm/year ×8 years to recover	nd	8.1–34.7
(2) Mussel bed, Northern California (Sousa, 1984a,b)	Patches in bed	0.0075–1.125 (80–81)	nd	2.7–7.7%/year; 1–1.44 cm/year	nd	nd
(3) Mussel bed, Central Oregon Coast (Guichard et al., 2003)	Patches in bed	nd	BB: 9–25% FC: 1–36% YB: 11–16%	1–12% 0.25–6% 10–78%	nd nd nd	nd nd nd
(4) Fucoid/Barnacle beds, Oregon Coast (Farrell 1989)	Patches in bed	0.0002–0.064	2.2–10.6	nd	nd	9.5–45.5
(5) Surfgrass, Oregon Coast (Turner, 1983a,b, 1985)	Patches in bed	nd	nd	0.9–5.3%/year (experimental plots)	nd	nd
(6) Macrophyte Mosaic (Menge et al., 1993, this study)	Mosaic elements	0.0001–2.6	0.8–10.6 (exp) 0.4–7.2 (int) 1.3–21.7 (prot)	135–484 cm ² /year (exp) 61–267 cm ² /year (int) 119–139 cm ² /year (prot) 76–100%/year (exp) 70–100%/year (int) 66–90%/year (prot) (natural disturbances)	417–684 cm ² /year 90–170 cm ² /year 40–167 cm ² /year 176–529%/year 40–176%/year 51–166%/year	9.4–125 13.9–250 4.6–77

nd, no data. Exp=wave-exposed; int=intermediate; prot=wave-protected. Data are ranges of annual means, or overall averages. Numbers 1–5 in study 1 indicate different locations on the island. Site codes (disturbance and recovery rates) in study 3: BB, Boiler Bay; FC, Fogarty Creek; YB, Yachats Beach (see citation for details).

observation period for these data (probably <3 years). Nonetheless, these comparisons, and our field observations at both Washington and Oregon sites, indicate that disturbed patches in mussel beds can reach far greater sizes, and are likely to expand at higher rates than in macrophyte mosaics.

Because of the small sample size, little more can be made of these comparisons. It does seem clear, however, that the dynamics of mussel beds and macrophyte mosaics share a common feature that is independent of phyletic considerations. Both mussels and surfgrass were dominant competitors, and both were the most susceptible species to disturbance in their respective systems. A similar set of tradeoffs has been documented for kelp bed mosaics (Dayton et al., 1984). The kelp beds off central and southern California consist of a diverse assemblage of species of differing morphologies, ranging from tall canopy-forming perennials to mid-level understory kelps to substratum-hugging prostrate canopy species to algal turfs. Field observations and experiments demonstrated that the dominant kelp *Macrocystis pyrifera* was both the dominant competitor for light and was the most susceptible member of the mosaic to disturbance from storm-generated waves.

4.4. Comparison to non-marine communities

Mosaics are common in terrestrial habitats, particularly in grasslands, prairies, meadows, pastures and old fields (e.g., Turkington et al., 1979; Turkington and Harper, 1979; Grubb, 1986; Turkington and Mehrhoff, 1990; Lavorel et al., 1994). Disturbance is an important process in these environments, and the disturbance regime has been quantified in a variety of studies (e.g., Goldberg and Gross, 1988). Interestingly, in many of these the annual disturbance rate is similar to the rates observed in mussel beds, fucoid/barnacle beds, and macrophyte turfs (Table 7). In examples of prairie, coastal dunes, and old fields, average % area disturbed/year was commonly in the range of 0.1–10% (Table 8 in Goldberg and Gross, 1988), which is similar to the ranges listed in Table 7. Most disturbances in terrestrial environments were due to biotic sources (pocket gophers, moles, ants, mice, ground squirrels, badgers) rather than physical disturbance. These similarities are intriguing and may suggest that the ecological principles underlying

regimes of disturbance share commonalities regardless of the habitat.

4.5. Community theory

The influence of spatial structure on species coexistence has a long history in ecology (Skellam, 1951; Huffaker, 1958; Levins and Culver, 1971; Horn and MacArthur, 1972; Armstrong, 1976). The dramatic increase of computing power during the past few decades has facilitated a major expansion of theory in this area, and helped to foster a variety of approaches including patch models, reaction diffusion equations, interacting particle systems, and cellular automata (Lavorel et al., 1993; Durrett and Levin, 1994a,b; Tilman and Kareiva, 1997; Wilson and Nisbet, 1997).

At the community level, incorporation of spatial structure has offered new insight into the question of species coexistence (Tilman, 1994). As indicated by Tilman (1994), the incorporation of spatial structure frees models from the unrealistic restriction that the number of coexisting species is limited by the number of discrete limiting resources. His models indicated that under certain conditions, there is no limit to the number of species that can coexist on a single limiting resource. His basic model assumed a spatially subdivided, infinitely large and physically homogeneous habitat with random colonization and no dispersal from outside the habitat, and that species differed systematically in competitive ability, colonization ability, and mortality rate. In addition, the model also assumes a trade-off between competitive ability and colonization ability and possibly between competitive ability and longevity. In this case, limitation of species number would result from the imposition of finite boundaries on the habitat, demographic stochasticity, or evolutionary limits to dispersal or longevity. Other factors that presumably could enhance diversity are a physically heterogeneous environment and disturbance.

The appropriateness of surfgrass communities for testing such a model appears mixed. We can quantify competitive ability, colonization ability and rate, mortality and change in occupancy of space in a spatially explicit manner, but the surfgrass system is open to dispersal, not closed, so this aspect of the model would need modification. For example, although some algae have very limited dispersal distances (Sousa,

1984a), others disperse tens to hundreds of kilometers (Reed et al., 1988; Kinlan and Gaines, 2003). Surfgrass seeds seem likely to disperse distances of at least kilometers, and thus also to have open populations. In “mean field”-type models (e.g., Lotka-Volterra competition and predation models), the outcomes of open vs. closed models are dramatically different (Gaines and Lafferty, 1995), so it is likely that similar changes would occur in open vs. closed spatially explicit models.

In marine rocky intertidal systems, cellular automata approaches have begun to provide valuable insights. In a study of mussel beds on Tatoosh Island, Washington, Wootton (2001) showed that the natural pattern of patchiness and diversity in a mussel bed mosaic was well mimicked by a cellular automata model, predicting 92.5% of the variance in composition. He concluded that such accuracy required considerable detail, including specifics of interactions among species, size structure of the mussels, neighbor–neighbor interactions, and the disturbance regime. In a second mussel bed study at Bamfield, British Columbia, the cellular automata model of Robles and Desharnais (2002) accurately reproduced the two-dimensional layout of a mussel bed across vertical tidal and horizontal wave exposure gradients. Their model included mussel size, mussel recruitment rate, predation rate and mussel growth rate and how these varied across the two environmental gradients. Finally, in a mussel bed study on the Oregon coast, Guichard et al. (2003) demonstrated that processes acting locally, such as neighbor–neighbor interactions and disturbance, and globally acting forces such as phytoplankton productivity interacted to produce pattern in the bed, and that locally generated pattern scaled to large-scale pattern in a scale-invariant manner.

The macrophyte mosaic study reported here is highly amenable to cellular automata and similar spatially explicit analysis. In fact, Keymer (2003) has begun modeling efforts based on the algal mosaic system presented here. His efforts embed the algal mosaic dynamic in a broader array of theoretical possibilities, ranging in complexity from a monospecific dominant (such as surfgrass or mussels), to algal metapopulations within a surfgrass matrix, to a mosaic. Such efforts, combining the greater detail of an empirical study with the broader generality of a theoretical study warrant further attention.

5. Conclusions

We conclude that the structure of this mosaic is primarily a consequence of disturbance, competition for space among neighboring mosaic elements, life history differences, colonization ability, and how these vary with wave exposure. Surfgrass is the dominant competitor but appears to be a poor colonizer, at least to surfgrass beds, and is the most susceptible to disturbance from storm-generated waves. Coexisting algal species are inferior competitors, and include species with a range of dispersal capabilities, including fast-colonizing “fugitive” species such as *Ulva* spp., *Enteromorpha* spp., *Corallina officinalis*, *P. irregulare*, and *O. floccosa*, as well as slower colonizers. Disturbance, from waves (wave-exposed areas) and sedimentation and substratum weakness (wave-protected areas), varies primarily through time but surprisingly little across the wave-exposure gradient. Differences in species composition with wave-exposure regime undoubtedly reflect differences in physiological tolerances and for some species, probably dispersal limitation. Life history differences, including morphological characteristics such as whether or not a species has an encrusting, spreading holdfast system, also seem to play a role in determining whether or not an alga is a common component of the algal mosaic. Many of these characteristics seem to characterize other systems, both marine and non-marine.

Many aspects of this system would seem to make it useful for interactive tests of spatial theory. Recent advances in understanding of dispersal patterns of macrophytes and invertebrates in relation to coastal oceanography (Sponaugle et al., 2002; Kinlan and Gaines, 2003; Siegel et al., 2003) raise the expectation that a more inclusive set of models can be developed that would be appropriate for open as well as closed systems.

Acknowledgements

We thank M. Bracken, J. Burnaford, T. Freidenburg, B. Grantham, P. Halpin, C. Krenz, H. Leslie, J. Lubchenco, K. Nielsen, and C. Reimer for comments and critiques on this research. Constructive comments by S. Shumway and R. Osman improved the final

version of the manuscript. We thank Betsy Abbott and the late Alice Abbott King for access to the Fogarty Creek site. Thanks also to D. Schiel and B. Davison of the University of Canterbury, Christchurch, New Zealand, for providing space and facilities for the first author to write and analyze while on sabbatical. The research was funded by NSF grants OCE84-15609 and OCE88-11369. Analysis and writing were

supported by grants from the A.W. Mellon Foundation, the David and Lucile Packard Foundation, Robert and Betty Lundeen, and an endowment from the Wayne and Gladys Valley Foundation. This is contribution number 159 from PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans: A Long-Term Ecological Consortium funded by the David and Lucile Packard Foundation. [SS]

Appendix 1. Characterization of study sites

Site location (site code)	Substratum					Macrophytes	
	Slope (aspect)	Rock type	Rock hardness index ¹ (mean ± S.E.M.)	Sediment deposition	Sediment depth ² (range, cm)	Taxon richness ³ mean (range)	Dominant elements of macrophyte mosaic
Wave-exposed sites							
Fogarty Creek (E-FC)	<15° (~SW)	basalt	9.8 ± 0.3 ^a	none	0	5.7 (2–10)	<i>Phyllospadix</i> spp., <i>Lessoniopsis littoralis</i> , “ <i>Hymenena</i> ” complex 4, articulated coralline algae
Boiler Bay (E-BB)	11° (~SW)	basalt	9.6 ± 0.2 ^a	none	0	6.8 (3–11)	<i>Phyllospadix</i> spp., “ <i>Hymenena</i> ” complex, <i>Constantinea simplex</i> , <i>Plocamium cartilagineum</i> , “ <i>Dilsea</i> ” complex
Wave-intermediate site							
Boiler Bay (I-BB)	10° (~SW)	basalt	11.2 ± 0.4 ^b	infrequent	0–0.62	5.6 (2–9)	<i>Phyllospadix</i> spp., <i>Mazzaella</i> spp. 6, <i>Odonthalia floccosa</i> , <i>Neorhodomela larix</i> , <i>Hedophyllum sessile</i>
Wave-protected sites							
Boiler Bay <i>Neorhodomela</i> Cove (P-BBC)	10° (~SW)	mudstone overlain by basalt	3.3 ± 0.1 ^c	common	0.38–1.46	4.8 (2–9)	<i>Phyllospadix scouleri</i> , <i>larix</i> , <i>Mazzaella</i> spp., <i>Odonthalia floccosa</i>
Boiler Bay <i>Neorhodomela</i> Mudstone (P-BBM)	0° (undef.)	mudstone	3.7 ± 0.1 ^c	common	0.93–2.62	4.3 (1–9)	<i>Phyllospadix scouleri</i> , <i>larix</i> , <i>Odonthalia floccosa</i>

¹ An index of rock hardness was estimated by using a stopwatch to record the time required to drill a hole of 6.35-mm diameter to a standard depth of 76 mm, under the weight of our gasoline-powered rotohammer. Twenty holes were drilled at haphazardly located places at each of the five sites. Values with different superscripts (a–c) are significantly different at the $\alpha=0.05$ level (Bonferroni-corrected post hoc test of differences among means). Measurable sediment at I-BB occurred only once, in August 1987.

² Sediment depth was sampled in eight 0.5 × 0.5 m quadrats in each grid (see Methods) at each site from 1986 to 1988 by placing a quadrat frame, subdivided by nylon cord into 25 squares (each 10 × 10 cm), over each mosaic quadrat. Sediment depth was measured at each of the 4 × 4 (16) cord intersections, in November 1986, January, May, August, and November 1987, and January and September 1988. Data shown are the maximum and minimum monthly means for each site.

³ Number of macrophyte taxa per 0.25-m² quadrat, $n=32$ quadrats per year per site.

^a *H. flabelligera*, *H. multiloba*, *Polymeura latissima*, and *Cryptopleura* spp.

^b *Dilsea californica*, *Schizymenia pacifica*, and *Halymenia schizymenioides*.

^c Mostly *M. splendens*, but occasionally *M. flaccida* and *M. heterocarpa*.

References

- Airoldi, L., Rindi, F., Cinelli, F., 1995. Structure, seasonal dynamics and reproductive phenology of a filamentous turf assemblage on a sediment influenced, rocky subtidal shore. *Botanica Marina* 38, 227–237.
- Airoldi, L., 2000. Effects of disturbance, life histories, and overgrowth on coexistence of algal crusts and turfs. *Ecology* 81, 798–814.
- Allison, G.W., 2004. The influence of species diversity and stress intensity on community resistance and resilience. *Ecological Monographs* 74, 117–134.
- Armstrong, R.A., 1976. Fugitive species: experiments with fungi and some theoretical considerations. *Ecology* 57, 953–963.
- Beisner, B.E., Haydon, D.T., Cuddington, K., 2003. Alternative stable states in ecology. *Frontiers in Ecology and Evolution* 1, 376–382.
- Benedetti-Cecchi, L., 2000. Predicting direct and indirect interactions during succession in a mid-littoral rocky shore assemblage. *Ecological Monographs* 70, 45–72.
- Benedetti-Cecchi, L., Bulleri, F., Cinelli, F., 2000. The interplay of physical and biological factors in maintaining mid-shore and low-shore assemblages on rocky coasts in the northwest Mediterranean. *Oecologia* 123, 406–417.
- Blanchette, C.A., 1996. Seasonal patterns of disturbance influence recruitment of the sea palm, *Postelsia palmaeformis*. *Journal of Experimental Marine Biology and Ecology* 197, 1–14.
- Blanchette, C.A., Worcester, S.E., Reed, D.C., Holbrook, S.J., 1999. Algal morphology, flow, and spatially variable recruitment of surfgrass *Phyllospadix torreyi*. *Marine Ecology. Progress Series* 184, 119–128.
- Burrows, M.T., Hawkins, S.J., 1998. Modelling patch dynamics on rocky shores using deterministic cellular automata. *Marine Ecology. Progress Series* 167, 1–13.
- Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111, 1119–1144.
- Crowder, M.J., Hand, D.J., 1990. *Analysis of Repeated Measures*. Chapman and Hall, London, UK.
- Dayton, P.K., 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41, 351–389.
- Dayton, P.K., 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs* 45, 137–159.
- Dayton, P.K., Currie, V., Gerrodette, T., Keller, B.D., Rosenthal, R., Ven Tresca, D., 1984. Patch dynamics and stability of some California kelp communities. *Ecological Monographs* 54, 253–289.
- Denny, M.W., 1995. Predicting physical disturbance: mechanistic approaches to the study of survivorship on wave-swept shores. *Ecological Monographs* 65, 371–418.
- Dethier, M.N., 1984. Disturbance and recovery in intertidal pools: maintenance of mosaic patterns. *Ecological Monographs* 54, 99–118.
- Dudgeon, S.R., Steneck, R.S., Davison, I.R., Vadas, R.L., 1999. Coexistence of similar species in a space-limited intertidal zone. *Ecological Monographs* 69, 331–352.
- Durrett, R., Levin, S.A., 1994a. The importance of being discrete (and spatial). *Theoretical Population Biology* 46, 363–394.
- Durrett, R., Levin, S.A., 1994b. Stochastic spatial models: a user's guide to ecological applications. *Philosophical Transactions of the Royal Society of London. B* 343, 329–350.
- Farrell, T.M., 1989. Succession in a rocky intertidal community: the importance of disturbance size and position within a disturbed patch. *Journal of Experimental Marine Biology and Ecology* 128, 57–73.
- Farrell, T.M., 1991. Models and mechanisms of succession: an example from a rocky intertidal community. *Ecological Monographs* 61, 95–113.
- Gaines, S.D., Lafferty, K.D., 1995. Modeling the dynamics of marine species: the importance of incorporating larval dispersal. In: McEdwards, L. (Ed.), *Ecology of Marine Invertebrate Larvae*. CRC Press, Boca Raton, FL, pp. 389–412.
- Goldberg, D.E., Gross, K.L., 1988. Disturbance regimes of midsuccessional old fields. *Ecology* 69, 1677–1688.
- Grubb, P.J., 1986. Problems posed by sparse and patchily distributed species in species-rich plant communities. In: Diamond, J., Case, T.J. (Eds.), *Community Ecology*. Harper and Row, New York, NY, pp. 207–225.
- Guichard, F., Halpin, P., Allison, G.W., Lubchenco, J., Menge, B.A., 2003. Mussel disturbance dynamics: signatures of oceanographic forcing from local interactions. *American Naturalist* 161, 889–904.
- Hawkins, S.J., Hartnoll, R.G., 1983. Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology Annual Reviews* 21, 195–282.
- Hartnoll, R.G., Hawkins, S.J., 1985. Patchiness and fluctuations on moderately exposed rocky shores. *Ophelia* 24, 53–63.
- Hawkins, S.J., Hartnoll, R.G., Kain, J.M., Norton, T.A., 1992. Plant–animals interactions on hard substrata in the north-east Atlantic. In: John, D.M., Hawkins, S.J., Price, J.H. (Eds.), *Plant–Animals Interactions in the Marine Benthos*. Oxford University Press, Oxford, England, pp. 1–32.
- Horn, H.S., MacArthur, R.H., 1972. Competition among fugitive species in a harlequin environment. *Ecology* 53, 749–752.
- Huffaker, C.B., 1958. Experimental studies on predation: dispersion factors and predator–prey oscillations. *Hilgardia*, 343–383.
- Johnson, M.P., Burrows, M.T., Hawkins, S.J., Hartnoll, R.G., 1997. Spatial structure on moderately exposed rocky shores: patch scales and the interactions between limpets and algae. *Marine Ecology. Progress Series* 160, 209–215.
- Johnson, M.P., Burrows, M.T., Hawkins, S.J., 1998. Individual based simulations of the direct and indirect effects of limpets on a rocky shore *Fucus* mosaic. *Marine Ecology. Progress Series* 169, 179–188.
- Keymer, J.E. 2003. Competition for space and intertidal community structure. PhD Princeton University, Princeton, NJ.
- Kinlan, B.P., Gaines, S.D., 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84, 2007–2020.

- Lavorel, S., Gardner, R.H., O'Neill, R.V., 1993. Analysis of patterns in hierarchically structure landscapes. *Oikos* 67, 521–528.
- Lavorel, S., Lepart, J., Debussche, M., Lebreton, J.-D., Befly, J.-L., 1994. Small scale disturbances and the maintenance of species diversity in Mediterranean old fields. *Oikos* 70, 455–473.
- Levin, S.A., 1992. The problem of pattern and scale in ecology. *Ecology* 73, 1943–1967.
- Levin, S.A., Pacala, S.W., 1997. Theories of simplification and scaling of spatially distributed processes. In: Tilman, D., Kareiva, P. (Eds.), *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*. Princeton University Press, Princeton, New Jersey, pp. 271–295.
- Levins, R., Culver, D., 1971. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences of the United States of America* 68, 1246–1248.
- Lubchenco, J., Menge, B.A., 1978. Community development and persistence in a low rocky intertidal zone. *Ecological Monographs* 48, 67–94.
- Lundalv, T., 1971. Quantitative studies on rocky-bottom biocoenoses by underwater photogrammetry. A methodological study. *Thalassia Jugoslavica* 7, 201–208.
- Lundalv, T., 1986. Detection of long-term trends in rocky sublittoral communities: representatives of fixed sites. In: Moore, P.G., Seed, R. (Eds.), *The Ecology of Rocky Coasts*. Columbia University Press, New York, NY, pp. 329–345.
- MacArthur, R.H., 1972. *Geographical Ecology*. Harper and Row, Publishers, New York, NY.
- Menge, B.A., 1976. Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecological Monographs* 46, 355–393.
- Menge, B.A., Farrell, T.M., Olson, A.M., van Tamelen, P., Turner, T., 1993. Algal recruitment and the maintenance of a plant mosaic in the low intertidal region on the Oregon coast. *Journal of Experimental Marine Biology and Ecology* 170, 91–116.
- Menge, B.A., Daley, B.A., Wheeler, P.A., 1996. Control of interaction strength in marine benthic communities. In: Polis, G.A., Winemiller, K.O. (Eds.), *Food Webs: Integration of Pattern and Dynamics*. Chapman and Hall, New York, NY, pp. 258–274.
- Pacala, S.W., Levin, S.A., 1997. Biologically generated spatial pattern and the coexistence of competing species. In: Tilman, D., Kareiva, P. (Eds.), *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*. Princeton University Press, Princeton, New Jersey, pp. 204–232.
- Paine, R.T., Levin, S.A., 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs* 51, 145–178.
- Quinn, G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, UK.
- Ramsey, F.L., Schafer, D.W. 1997. *The statistical sleuth: a course in methods of data analysis*. Duxbury Press, Wadsworth Publishing, Belmont, CA.
- Reed, D.C., Laur, D.R., Ebeling, A.W., 1988. Variation in algal dispersal and recruitment: the importance of episodic events. *Ecological Monographs* 58, 321–335.
- Robles, C., Desharnais, R., 2002. History and current development of a paradigm of predation in rocky intertidal communities. *Ecology* 83, 1521–1536.
- Siegel, D.A., Kinlan, B.P., Gaylord, B., Gaines, S.D., 2003. Lagrangian descriptions of marine larval dispersal. *Marine Ecology. Progress Series* 260, 83–96.
- Skellam, J.G., 1951. Random dispersal in theoretical populations. *Biometrika* 38, 196–218.
- Sousa, W.P., 1979a. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60, 1225–1239.
- Sousa, W.P., 1979b. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* 49, 227–254.
- Sousa, W.P., 1984a. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. *Ecology* 65, 1918–1935.
- Sousa, W.P., 1984b. The role of disturbance in natural communities. *Annual Reviews of Ecology and Systematics* 15, 353–391.
- Sousa, W.P., 2001. Natural disturbance and the dynamics of marine benthic communities. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), *Marine Community Ecology*. Sinauer Associates, Sunderland, MA, pp. 85–130.
- Sponaugle, S., Cowen, R.K., Shanks, A.L., Morgan, S.G., Leis, J.M., Pineda, J., Boehlert, G.W., Kingsford, M.J., Lindeman, K.C., Grimes, C., Munro, J.L., 2002. Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. *Bulletin of Marine Science* 70, 341–375. Supplement.
- Steinberg, E.K., Kareiva, P., 1997. Challenges and opportunities for empirical evaluation of “spatial theory”. In: Tilman, D., Kareiva, P. (Eds.), *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*. Princeton University Press, Princeton, New Jersey, pp. 319–332.
- Stewart, J.G., 1989. Maintenance of a balanced, shifting boundary between the seagrass *Phyllospadix* and algal turf. *Aquatic Botany* 33, 223–241.
- Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75, 2–16.
- Tilman, D., Kareiva, P. (Eds.), *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*. Princeton University Press, Princeton, New Jersey.
- Tilman, D., Lehman, C.L., Kareiva, P., 1997. Population dynamics in spatial habitats. In: Tilman, D., Kareiva, P. (Eds.), *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*. Princeton University Press, Princeton, New Jersey, pp. 1–20.
- Torlegard, A.K.I., Lundalv, T., 1974. Under-water analytical system. *Photogrammetric Engineering* 40, 287–293.
- Turkington, R., Harper, J.L., 1979. The growth, distribution and neighbor relationships of *Trifolium repens* in a permanent pasture: I. Ordination, pattern and contact. *Journal of Ecology* 67, 201–218.

- Turkington, R., Mehrhoff, L.A., 1990. The role of competition in structuring pasture communities. In: Grace, J.B., Tilman, D. (Eds.), *Perspectives on Plant Competition*. Academic Press, New York, NY, pp. 307–340.
- Turkington, R., Cahn, M.A., Vardy, A., Harper, J.L., 1979. The growth, distribution, and neighbor relationships of *Trifolium repens* in a permanent pasture: III. The establishment and growth of *Trifolium repens* in natural and perturbed sites. *Journal of Ecology* 67, 231–243.
- Turner, T., 1983a. Complexity of early and middle successional stages in a rocky intertidal surfgrass community. *Oecologia* (Berlin) 60, 56–65.
- Turner, T., 1983b. Facilitation as a successional mechanism in a rocky intertidal community. *American Naturalist* 121, 729–738.
- Turner, T., 1985. Stability of rocky intertidal surfgrass beds: persistence, preemption, and recovery. *Ecology* 66, 83–92.
- Turner, T., Lucas, J., 1985. Differences and similarities in the community roles of three rocky intertidal surfgrasses. *Journal of Experimental Marine Biology and Ecology* 89, 175–189.
- Underwood, A.J., 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Annual Reviews of Oceanography and Marine Biology* 19, 513–605.
- Underwood, A.J., Jernakoff, P., 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. *Oecologia* (Berlin) 48, 221–233.
- Wilkinson, L., 1998. SYSTAT 8.0 Statistics. SPSS, Chicago, IL.
- Williams, G.A., 1993. Seasonal variation in algal species richness and abundance in the presence of molluscan herbivores on a tropical rocky shore. *Journal of Experimental Marine Biology and Ecology* 167, 261–275.
- Wilson, W.G., Nisbet, R.M., 1997. Cooperation and competition along smooth environmental gradients. *Ecology* 78, 2004–2017.
- Winer, B.J., Brown, D.R., Michels, K.M., 1991. *Statistical Principles in Experimental Design*. 3rd ed.
- Wootton, J.T., 2001. Local interactions predict large-scale pattern in empirically derived cellular automata. *Nature* 413, 841–844.