

Community succession following massive ice-scour on a rocky intertidal shore: recruitment, competition and predation during early, primary succession

L. J. McCook*, A. R. O. Chapman

Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada

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Abstract. The importance of species interactions and recruitment variability was examined during the first year and a half of primary succession (1988–1989) on an exposed rocky seashore near Halifax, Nova Scotia. Previous work suggested that emergent rock on these shores is normally dominated by fucoid rockweeds because predatory whelks control the sessile animal competitors, mussels and barnacles, and because herbivorous littorinids control ephemeral algal competitors. Abundances of all species except seasonal ephemeral algae were very small throughout this experiment and we found no significant effects of carnivory, herbivory, plant-animal competition or plant-plant competition. A slight facilitation of *Fucus* recruitment is attributed to a thin mat of ephemeral, blue-green algae. Very few other studies have directly manipulated intertidal ephemeral algae. As primary succession may be very rare in this assemblage, these results may be specific to these circumstances, but they highlight the varying importance of species interactions with variable recruitment. In particular, it appears that variations in recruitment success may be important to community structure, even when recruitment is not limited by propagule supply. The scale of the study also provides insight into successional processes occurring after the recent, extensive ice-scour of exposed seashores in this region.

Introduction

On exposed rocky seashores in the Halifax region of Nova Scotia, Canada, emergent rock in the mid-shore is usually dominated by lush canopies of the rockweeds, *Fucus spiralis*, *F. vesiculosus* and *F. evanescens*, at progressively lower zones. Much of the substrate under these canopies is occupied by filter-feeding barnacles

(*Semibalanus balanoides*) and mussels (*Mytilus edulis*), and by crustose algae, especially *Hildenbrandia rubra*. Cleared space in these canopies is often occupied by ephemeral algae. Fucoid rockweeds compete for primary space with both ephemeral algae and filter-feeding sessile invertebrates. Extensive work here and in nearby New England suggested that persistence of the fucoid canopies was largely due to predation by whelks (*Nucella lapillus*) on filter feeders, and to herbivory by littorinid snails on ephemeral algae (see McCook and Chapman 1991 Fig. 1; also Menge 1976, 1978, 1991 a, b, Lubchenco 1978, 1982, 1983, 1986, Lubchenco and Menge 1978, Petraitis 1987, 1990, Chapman and Johnson 1990). In the present paper, we refer to *F. vesiculosus* and *F. evanescens* collectively as *Fucus*.

In April of 1987, sea-ice from the Gulf of St. Lawrence severely scoured large areas of exposed seashores in this area, removing virtually all canopy and understory species from the extreme supralittoral to more than a metre below mean low water. Following the scour, intertidal shores were dominated by a successional sequence of diatoms, ephemeral filamentous green algae, and fucoid rockweeds. Mussels reappeared as understory, but did not generally replace the rockweeds (McCook and Chapman 1991, McCook 1992).

These events gave us an opportunity to study successional interactions among perennial species, at unusually large-scales. Ice-scour of such extent (> 50 km of shoreline, McCook 1992) and intensity (1 to 3 m thick) is extremely rare in this region, and may not have occurred for at least 25 yr (Bedford Institute of Oceanography 1987; also Dinsmore 1972, Markham 1980). The more frequent scour reported in New England is much less extensive (Markham 1980) and less severe (since it does not remove fucoid canopies; Wethey 1985). Minor scours occur in sheltered bays in Nova Scotia and New England, where thin ice may form annually. Further north, ice-scour is a regular occurrence but perennial species are consequently rare.

Previous studies of intertidal successions have generally concentrated on smaller scales, often as patches creat-

* Current address and address for correspondence: Australian Institute of Marine Science, PMB#3, Townsville MC, Q1d, 4810, Australia

ed in established communities (e.g. Lubchenco and Menge 1978, Murray and Littler 1978, Sousa 1979, 1984a, Lubchenco 1983, Turner 1983, Van Tamelen 1987, Buschmann 1990, Farrell 1991). However, the recruitment of sessile species and the foraging of mobile species may be distinctly different at different scales (Sousa 1984a, b, 1985, Foster and Sousa 1985, Farrell 1989).

During succession, patterns of species abundance depend on interactions between sessile species, since early occupants may facilitate, tolerate or competitively inhibit later species (Clements 1928, Connell and Slatyer 1977). Some authors have suggested that species abundances (and interactions) are understood better in terms of propagule availability, and species' life-history traits (e.g. Egler 1954, Drury and Nisbet 1973, Tilman 1985, 1990, Huston and Smith 1987, McCook in press). Clearly, herbivory and predation may have important but varying effects, depending on the nature of interactions between sessile species (Farrell 1991). We have attempted several studies of these species interactions during this unusually large-scale succession (see also McCook and Chapman 1991, 1992, McCook 1992).

The experiments reported here were designed to examine the effects of post-settlement biological interactions on the first 18 mo of primary succession on an exposed rocky shore. We considered the community in terms of five guilds: carnivores, specifically whelks; herbivores, specifically littorinid snails, and amphipods if present; sessile invertebrate "filter feeders", specifically barnacles and mussels; ephemeral algae, including blue-green and eukaryotic algae; and furoid canopy algae. By removing or thinning each of these guilds we hoped to gauge the importance of predation, herbivory, and competitive interactions, between filter feeders and plants, and between plant guilds. However, interpretation of these effects was strongly influenced by the extremely low recruitment and immigration of most species during these experiments.

Experimental design, study site and methods

The effects of ephemeral algae and filter feeders were tested using a two-factor complete factorial design, with both guilds present or removed, in all possible combinations (Fig. 1, open plots). Each treatment combination was replicated five times in plots open to natural densities of herbivores and whelks, although these densities were very low. The effects of ephemeral algae, of barnacles and mussels, and of herbivores were tested with a three-factor design, with herbivore densities controlled by mesh cages (Fig. 1, caged plots, ten replicates each). The experiment was intended to be a single design, including the inclusion and exclusion of whelks, but whelks did not occur, and so were dropped from the design. Further, caged plots were analyzed separately to open plots, since there were substantial differences in successional processes between them (see below).

To test the effects of *Fucus* on other species, we intended to use a one factor comparison of open plots with *Fucus* at natural densities, half natural densities and one quarter natural densities. However, recruitment of *Fucus* in open plots was too small for useful comparison during this period.

The experimental site was on an exposed, south-facing granite shore at the Aquaculture Research Station, National Research Council Institute for Marine Biosciences, Sandy Cove, Halifax County, Nova Scotia (44°28'N, 63°33'W). This area had complete

Fucus canopy before the scour and recovered that canopy after this experiment. The experiment was begun in February 1988, ca. 1 yr after the original ice-scour. Since some quite uneven recovery had taken place, an artificial succession was initiated to ensure homogeneous starting conditions. All non-crustose species were removed from ca. 15 × 10 m of emergent shore in the *F. vesiculosus* zone, and 150 plots, 15 × 15 cm, were positioned at least 50 cm apart. The rock surface was heated with a flame thrower, dislodging flakes of rock until new rock was exposed over each entire plot. This ensured primary succession, but resulted in unusually smooth substrate. Plots were marked with wedge anchor bolts, randomly assigned to open and caged treatments, and then cages were attached to the bolts where appropriate.

Cages, 15 × 15 cm on the base and 10 cm high, were constructed from aluminium angle frames and 1-mm Nitex nylon monofilament mesh, with silicone caulking, and foam rubber gaskets to seal the base. Small drains, made of folded 1-mm stainless steel mesh, were placed under the lowest corner of the foam gaskets. Cages were wire-brushed when necessary to remove fouling algae and barnacles.

Abundances of sessile species were measured every few months, weather permitting, for ca. 18 mo, at which time cages were restricting *Fucus* growth in some plots. Abundances were measured as density and/or percent cover, in 10 × 10 cm quadrats centred on the plots to limit edge effects. Percent cover of sessile species was estimated by identifying all species present at 30 random points on a 100-point strung grid. Density of *Fucus* was counted as shoots or stipes, using jeweller's magnifying glasses when necessary. It was not possible to identify juvenile *Fucus* to species. Manipulated species were removed, as necessary, after data collection. Barnacles and mussels were removed with forceps. Ephemeral algae were removed as far as possible using scalpels or paint scrapers, but a thin layer usually remained attached to the rock. Considerable care was required to avoid damaging *Fucus* recruits when removing the ephemeral algae.

Densities of mobile species in open plots were counted every 2 to 4 wk, always in damp weather (fog and rain are modal weather in this area). Night-time and/or high tide censuses did not indicate large diurnal or tidal differences in density of these species. After each census, the littorinid snails, *Littorina obtusata* and *L. rudis*, were included in appropriate cages to mimic densities and size classes in open quadrats, but these densities were very small. Because no whelks, amphipods or other littorinids were found in open plots during the entire experiment, these species were not included in cages. Surveys of the whole site verified the small densities of mobile species. Birds, fish, crabs, starfish and sea urchins are rare in this zone of exposed shores in this area (personal observations).

Potential loss of *Fucus* recruits during ephemeral algae removal was minimized during the first summer by delaying the second ephemeral removal until after the peak period of *Fucus* settlement. Although increasing the chance of not detecting an effect of ephemeral algae (type II error), this strategy minimizes the chance of confounding the effects of ephemeral algae and procedural artifact (type I error). During later ephemeral algae removals, artifactual loss of *Fucus* recruits was estimated by collecting all removed ephemerals from randomly selected quadrats, and using a dissecting microscope to count casualties among *Fucus* recruits. This number was expressed as a percentage of the recruits counted in that quadrat before the removal. *Fucus* settlement was also monitored for almost 1 yr, using microscopic examination of natural substrate in the field, and of textured ceramic tiles in the lab. Ten 50 cm² areas of rock and ten of tile were placed in herbivore-proof cages randomly located throughout the experimental site. Rock and tiles were sterilized before each settlement period, using a blowtorch and an autoclave, respectively.

Cages strongly influenced the recruitment and/or growth of *Fucus*. Density of *Fucus* shoots was generally more than an order of magnitude greater in caged quadrats than in open quadrats. *Fucus* cover appeared earlier and was nearly complete in cages after 18 mo, compared with ca. 20% in open plots. [MANOVA on transformed density and cover of *Fucus* gave highly significant

	Ephemeral Algae	Filter Feeders	Herbivores	
Open Plots:				
Untreated Controls	+	+	+	
Ephemeral Removal	-	+	+	
Barnacle (& Mussel) Removal	+	-	+	
Ephemeral & Barnacle (& Mussel) Removal	-	-	+	
<hr/>				
Caged Plots				
	Herbivore Inclusions (<i>L. obtusata</i> & <i>L. rudis</i>)	+	+	(+)
		-	+	(+)
		+	-	(+)
<hr/>				
Herbivore Exclusions				
		+	+	-
		-	+	-

Fig. 1. Experimental design to test for effects on succession of ephemeral algae, barnacles and mussels, and herbivores. Open plots allowed mobile herbivores (and whelks) free access at natural densities. Herbivores were included in herbivore inclusion cages at approximately the same densities found in the analogous open plots; in practice, only a few *Littorina obtusata* and *L. rudis* were present and included in cages. Thus, there is little real difference between herbivore inclusions and exclusions, but the factor was retained in analyses as a precaution. The design originally involved inclusion and exclusion of whelks in combination with other factors, but whelks were never found in open plots, and so were not included in cages or analyses. Comparison of herbivore inclusion caged plots with open plots indicated significant and large caging artifacts (see “Experimental design, study site and methods”), so that caged and open plots were analyzed separately. Each open plot treatment combination was replicated five times, and each caged treatment ten times. +: species present at natural densities; (+): species included in cages at approximately natural densities; -: species removed or excluded

effects of cages and nearly significant interactions of cages and ephemeral removal, $P \leq 0.01$ and $P = 0.059$, mean % total sum of squares (SST) = 40 and 4%, respectively]. Further, the variances of (transformed) cover and density were significantly larger in caged treatments than open plots (F -tests generally $P \leq 0.01$; similar tests of variance effects for ephemeral or filter-feeder treatments were not significant $P > 0.42$). Finally, inspection of mature plants, 9 mo after the end of the experiment, indicated that most plants in cages plots were *F. evanescens*, whereas those in open plots were *F. vesiculosus*.

Because the successional process appeared different in open and caged plots and because caged plots outnumbered open plots by a factor of four, caged plots were analyzed separately. This avoids bias in estimating residual variance for open plots, but has a large cost in experimental power, since most of the effort was allocated to caged plots. (It also emphasizes the value of procedural controls). Although the results for caged treatments refer only to the unnatural conditions inside cages, these results were generally consistent with trends found in the open plots. The caged experiment, with greater power, can thus be very usefully compared to results of the open treatments, to provide information about the system under different conditions of humidity and shade, etc. Although herbivore densities were very low, the factor was retained in analyses as a precaution.

Measurements of the same response variable at different times are not independent and therefore were analysed as multivariate measures of that variable. The principal components (PC) of these measures are simply overall measures of the variable in time. Variance/covariance principal components analyses (PCA) showed that most ($\approx 90\%$) of the variability in the multivariate abundance could be described in terms of one (or at most two) principal components. Thus species abundances were analyzed by univariate ANOVA on the first principal component (see Table 1). For example, the cover of *Fucus* throughout the 18-mo experiment is described by eight counts or variables, but since the (non-zero) values of these counts are highly correlated, they can be effectively summarized by one variable, ‘overall abundance’. This variable is the first PC, and differences in the value of that PC indicate differences in overall cover. This approach has the benefits of increased protection against type I errors, compared to multiple ANOVAs for each date, and compared to MANOVA with higher dimensionality (Johnson and Field in press). As effects of treatments were generally consis-

tent in time in these experiments, the loss of temporal resolution is not a problem. (Note that we are not testing for changes through time.) Where the first PC described less than 90% of the variability, MANOVA was used to verify significance of effects for $>90\%$ of variability.

MANOVA preceded by PCA assumes that the same, linear dimensions can be used to describe abundance under different treatments. Support for this assumption stems from the effectiveness of the first PC in accounting for overall variance, and from MANOVA on the original multivariables, which verified consistent partitioning of variance for the two approaches. The (transformed) original data were also examined graphically for linearity, although non-linearity would be unlikely to contribute to type I errors. Both the original variables and PCs were checked for univariate homoscedasticity (Cochran’s test, $P > 0.05$) and normality and independence of residuals. Some minor violations of Cochran’s test were accepted where variance heterogeneity clearly would not lead to false conclusions. Repeated measures ANOVA was not used since the assumption that the highest-order interaction is zero may not be justified for repeated measures from the same quadrats. Note that statistical analyses of caged plots omit the last date, when some cages were clearly restricting *Fucus* growth.

Data were analyzed using Microsoft Excel™ and Systat 5.1™ (Macintosh). Significance of MANOVAs was based on F approximations to Wilks’ Lambda, Pillai Trace and Hotelling-Lawley trace statistics (Wilkinson 1989) and on univariate ANOVAs.

Results

General observations and effects of predation

The most immediate observation from this experiment is that colonization of control, open plots by perennial species was very small, during the first 18 mo of succession (Fig. 2). Final mean cover of *Fucus* was only ca. 20%, compared to ca. 90% in caged plots (Fig. 2A cf. 3A), and in similar sites during the natural succession after a similar period (see McCook and Chapman 1991). Rate of

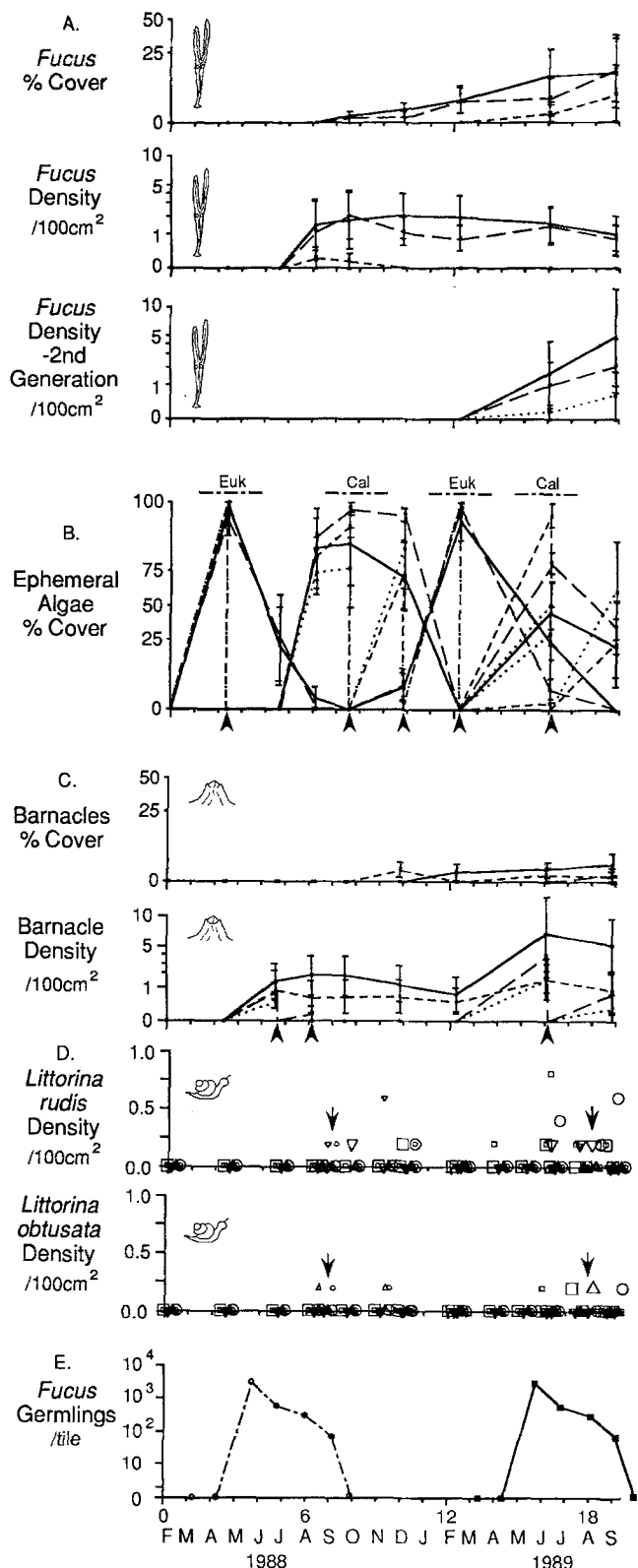


Fig. 2. Time courses of species abundance in open plots during primary succession. (—) Control, unmanipulated quadrats; (---) ephemeral algae removal quadrats; (- - -) barnacle/mussel removal quadrats; (· · · · ·) ephemeral algae and barnacle/mussel removal quadrats. (A) Cover and density of *Fucus*. (B) Ephemeral algae plotted as two groups: winter eukaryotic algae (Euk), and summer blue-green algae, predominantly *Calothrix* spp. (Cal). Experimental removal of ephemeral algae shown by vertical lines and arrows. Estimates of ephemeral algal thickness showed that ephemeral algae were generally thinner in ephemeral removals than

canopy recovery also varied within the site, apparently influenced by small differences in drainage, elevation, etc. Mussel recruitment was sufficiently small to be ignored [largest mean (SE) density in any treatment at any date ≤ 0.8 (0.8) 100 cm^{-2} ; no mussel reached > 5 mm in length]. Primary space was largely occupied by eukaryotic (protistan) ephemeral algae in the winter and spring, and an ephemeral mat of blue-green algae in the summer and fall (Fig. 2 and 3). Predominant eukaryotic ephemeral algae were the filamentous green algae *Ulothrix flacca* and *Urospora penicilliformis*, along with *Bangia atropurpurea*, *Porphyra* species, *Elachista fucicola* (as an epiphyte), *Enteromorpha intestinalis*, *Ulva lactuca* and diatoms. The blue-green algae, mainly a mixture of *Calothrix contarenii* and *Lyngbya majuscula*, formed a cohesive sheet or mat several mm thick, often only loosely attached to the rock substrate.

The effects of predation during this experiment were negligible. Whelks were essentially absent from the entire site for the duration of the experiment, probably because their prey were very scarce and because there was very little shelter from waves. Certainly, the small densities of mussels cannot be attributed to whelk predation.

Similarly, herbivore abundance in open plots was small enough to discount any biologically significant effect. Amphipods were virtually absent from the open plots, since the only common amphipod in this zone, *Hyale nilssoni*, is rarely found in such exposed conditions. The only herbivores found were *Littorina rudis* and *L. obtusata*, and the maximum combined density measured was less than 1 snail 100 cm^{-2} quadrat (Fig. 2D). We consider these densities representative, since similar or even smaller densities of mobile species were counted at high tide, night, and under various weather conditions and seasons. Inclusion of snails in cages did not have significant effects on *Fucus* (see Table 2). Although there was a significant difference in barnacle density between grazer treatments (see Table 3), this is unlikely to represent

controls, even when cover was similar (data not shown). (C) Cover and density of barnacles. Vertical lines and arrows show experimental removals. (D) Density of herbivorous periwinkle snails, *Littorina rudis* and *L. obtusata*. □/□: Mature/small snails in control, unmanipulated quadrats; ▽/▽: mature/small snails in ephemeral algae removal quadrats; △/△: mature/small snails in barnacle/mussel removal quadrats; ○/○: mature/small snails in ephemeral algae and barnacle/mussel removal quadrats. Night and/or high tide censuses of herbivores are combined and are indicated with arrows. Data in A–D are mean (\pm SEM) of five replicates. For clarity, SEMs not shown on herbivore density plots, but were generally equal to the mean. Cover data transformed to arcsine $\sqrt{(\% \text{ cover } 100^{-1})}$, density to $\ln(\text{density} + 1)$ for *Fucus*, and $\sqrt{\text{density}}$ for barnacles. (E) Settlement period of *Fucus*, as indicated by the density of microscopic *Fucus* embryos (continuous line) on textured ceramic tiles (see “Experimental design, study site and methods”). Values are mean of ten tiles. Settlement data only gathered in the second year, but we have indicated the same period for the previous year (dashed line) with data extrapolated back from 1989

a real effect. Grazer densities were very small, and univariate ANOVAs on the different dates showed that the difference was present before any grazers were included. The effect probably represents the failure of randomization to prevent consistent differences between sites allocated to the two treatments.

Effects of competition

Effects of barnacle and ephemeral algae on Fucus abundance

The cover and density of *Fucus* in open plots was generally so small that any effects were small and difficult to detect (Fig. 2). Abundance of barnacles was also small, so it is not surprising that no significant effects of barnacles on *Fucus* were found in either open plots or cages (Tables 1 and 2, Figs. 2 and 3).

However, ephemeral algae appear to have slightly facilitated *Fucus* recruitment and/or growth. Mean cover and density of *Fucus* were consistently small or zero where ephemeral algae were experimentally thinned and consistently non-zero otherwise (Fig. 2). Removal of ephemeral algae accounted for much of the variability in *Fucus* cover and density (respectively, 13 and 32% of variability in 1st PC), although the effect on cover was not statistically significant (Table 1). A similar, but non-significant, trend is seen in the second generation of *Fucus* recruits (Fig. 2 and Table 1). Although zero variance for some treatments compromises the assumption of homogeneity of variance, the consistency of treatment differences in time strongly supports the conclusions.

The effects of ephemeral removal on *Fucus* cover and density is strongly reinforced by very similar, but highly significant effects in caged plots (respectively, 17 and 25% of variability in 1st PC, Table 2 and Fig. 3; note *Fucus* in open plots and cages may have been different species, as mentioned above). The facilitation of *Fucus* by ephemeral algae is also suggested by several observations on *Fucus* recruitment. Density of *Fucus* recruits was much lower in naturally bare patches in the mat of ephemeral blue-green algae than on the adjacent algal mat. Extensive, systematic searches using a dissecting microscope found no embryos or germlings on bare rock, even when large numbers were simultaneously settling on sterilized, ceramic tiles. (The texture of these tiles apparently provided far better recruitment conditions for *Fucus* than the bare rock.) Microscopic observations showed that small *Fucus* recruits (≤ 2 mm) were generally attached to the surface of the algal mat, and progressively larger recruits were attached within the algal mat, or through it onto the rock. This suggests that *Fucus* was recruiting successfully to the surface of the algal mat and growing through it onto the rock. Attempts to quantify these observations with microscopic removal of ephemeral algae were not successful, owing to low recruitment of *Fucus* in the second summer.

These observations suggest that our experimental results are indeed due to facilitation of *Fucus* by ephemeral algae, and not to a procedural artifact, i.e., the removal

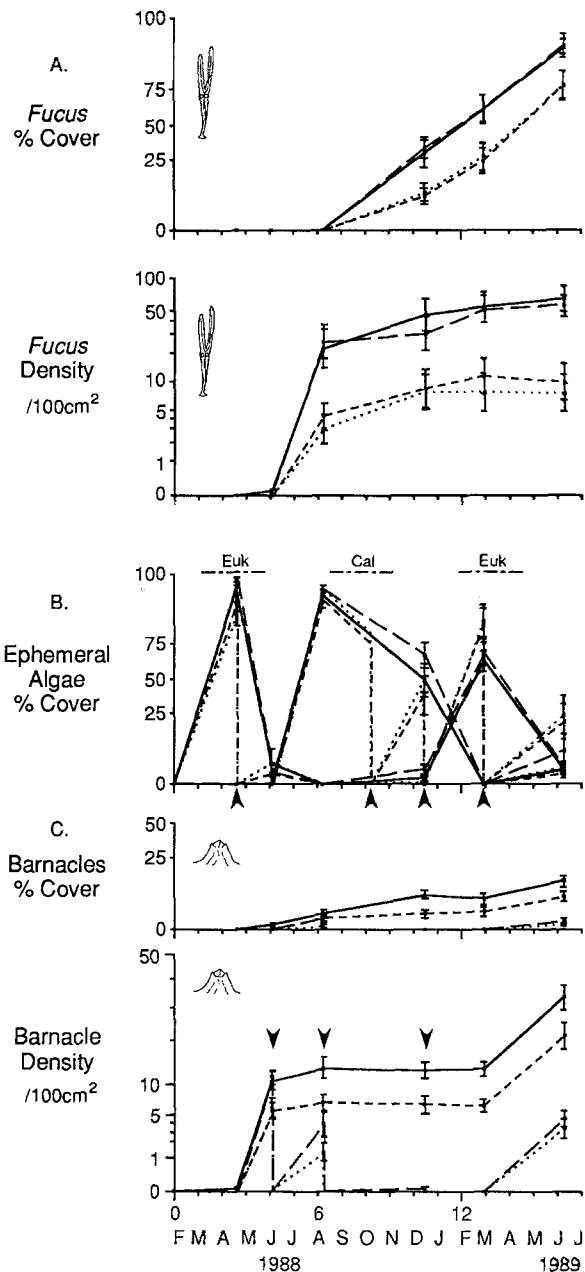


Fig. 3. Time courses of species abundance in caged plots during primary succession. (—) Control, unmanipulated quadrats; (---) ephemeral algae removal quadrats; (---) barnacle/mussel removal quadrats; (· · · · ·) ephemeral algae and barnacle/mussel removal quadrats. Data for grazer treatments shown pooled to simplify graphs, since grazing herbivores did not appear important (see "Results", Tables 2 and 3). Data therefore graphed as mean (\pm SEM) of 20 replicates, abbreviations and transformations as for Fig. 2

of *Fucus* recruits with ephemeral algae. Certainly, some microscopic recruits would have been removed with the ephemeral algae, but this alone cannot explain our results. Univariate ANOVAs show significant effects of ephemeral removal on *Fucus* recruitment (in cages $P < 0.001$) in August and September 1988. This is prior to any possible procedural artifacts, since ephemeral algae had only been removed once, before any substantial *Fucus* recruitment (personal observations, see also

Table 1. Analysis of effects of ephemeral algae and filter feeders on *Fucus* abundance in open plots. The first principal components (PCs) represent summary variables of abundance over time, since they account for most of the variance in abundance. Data were analyzed using ANOVA on the first PC, or, if the first PC accounted for less than 90% of variance, MANOVA was used on the first two PCs. %SST: % of total sum of squares explained by each factor; *P*: significance of each factor; and Multivariate *P*: significance of the

multivariate test on both factors, where 2 PCs were analyzed. Data were transformed, as indicated, before principal components analyses. Cochran's *C*: Cochran's statistic for principal components; * indicates data failed Cochran's test ($C_{crit.} = 0.629$). Bottom part of table indicates the % total variance accounted for by each PC and the component loadings of the original data counts. A blank component loading indicates that the cover or density was considered too low for meaningful analysis at that date

Source	df	<i>Fucus</i> % cover		<i>Fucus</i> density				2nd generation recruit density 1st PC		
		1st PC		1st PC		2nd PC		Multi-variate <i>P</i>	1st PC	
		%SST	<i>P</i>	%SST	<i>P</i>	%SST	<i>P</i>		%SST	<i>P</i>
Ephemerals (E)	1	13%	0.140	32%	0.014	7%	0.293	0.024	18%	0.079
Barnacles (B)	1	1%	0.608	0%	0.745	0%	0.838	0.917	0%	0.927
E × B	1	1%	0.758	0%	0.918	4%	0.396	0.681	3%	0.464
Residual	16	85%		67%		89%			80%	
Cochran's <i>C</i>		0.455		0.630*		0.707*			0.663*	
Transformation		$y = \text{Arcsine}(\sqrt{\text{cover}})$		$y = \ln(\text{density} + 1)$					$y = \ln(\text{density} + 1)$	
Principal components analyses										
% total variance:		93%		88%		9%		97%		97%
Date	Count No.	Component loadings								
Jul 1988	2									
Aug	3			0.875				-0.435		
Sep	4			0.981				-0.136		
Dec	5			0.757				0.217		
Feb 1989	6	0.127		0.678				0.301		
Jun	7	0.281		0.705				0.163		0.954
Sep	8	0.467		0.609				0.050		1.495

Table 2. Analysis of effects of ephemeral algae, filter feeders and grazing littorinid snails on *Fucus* abundance in caged plots. Where interaction effects were near significant ($0.1 > P > 0.05$), analyses were repeated within levels of grazers. In each case, conclusions were consistent with those of the three-way analysis presented here and

did not indicate important effects of grazers – note low %SST. * indicates data failed Cochran's test ($C_{crit.} = 0.293$). (Data were not collected for the fourth date for caged plots). Abbreviations as for Table 1

Source	df	<i>Fucus</i> % cover				<i>Fucus</i> density						
		1st PC		2nd PC		Multi-variate <i>P</i>	1st PC		2nd PC		Multi-variate <i>P</i>	
		%SST	<i>P</i>	%SST	<i>P</i>		%SST	<i>P</i>	%SST	<i>P</i>		
Ephemerals (E)	1	17%	0.000	1%	0.398	0.001	25%	0.000	2%	0.305	0.000	
Barnacles (B)	1	0%	0.850	0%	0.639	0.880	0%	0.608	0%	0.567	0.761	
Grazers (G)	1	0%	0.547	2%	0.161	0.318	0%	0.499	0%	0.096	0.187	
E × B	1	0%	0.975	0%	0.886	0.989	0%	0.861	2%	0.267	0.526	
E × G	1	2%	0.240	0%	0.612	0.443	3%	0.099	1%	0.471	0.218	
B × G	1	0%	0.929	5%	0.059	0.170	0%	0.989	3%	0.102	0.264	
E × B × G	1	4%	0.075	3%	0.153	0.080	1%	0.289	0%	0.903	0.562	
Residual	72	78%		89%			71%		92%			
Cochran's <i>C</i>		0.192		0.192			0.179		0.326*			
Transformation		$y = \text{Arcsine}(\sqrt{\text{cover}})$				$y = \ln(\text{density} + 1)$						
Principal components analyses												
% Total variance:		89%		9%		97%		89%		8%		96%
Date	Count No.	Component loadings										
Jul 1988	2											
Aug	3			0.114				0.881		-0.466		
Dec	5	0.356		0.114				0.932		0.268		
Feb 1989	6	0.470		0.058				0.980		0.070		
Jun	7	0.383		-0.177				0.968		0.096		

Table 3. Analysis of effects of ephemeral algae and grazing littorinid snails on barnacles. Abbreviations as for Table 1. * indicates data failed Cochran's test ($C_{crit.}=0.906$). ¹ Univariate analy-

ses of cage plots indicate that the apparent effect of grazers was present prior to inclusion of grazers, and thus probably represents artifacts from treatment allocations to sites

Source	df	Barnacle density-open plots					Barnacle density-cages				
		1st PC		2nd PC		Multi-variate <i>P</i>	1st PC		2nd PC		Multi-variate <i>P</i>
		%SST	<i>P</i>	%SST	<i>P</i>		%SST	<i>P</i>	%SST	<i>P</i>	
Ephemerals (E)	1	11%	0.347	6%	0.513	0.529	18%	0.004	2%	0.440	0.011
Grazers (G)	0,1						11%	0.023 ¹	0%	0.760	0.078
E × G	0,1						3%	0.238	0%	0.902	0.502
Residual	8,16	89%		94%			68%		98%		
Cochran's <i>C</i>		0.555		0.953			0.334		0.442		
Transformation		$y = \sqrt{(\text{density})}$					$y = \sqrt{(\text{density})}$				
Principal components analyses											
% Total variance:		77%		18%		96%	80%		10%		90%
Date	Count No.	Component loadings									
Jul 1988	2	1.003		0.600			1.028		0.189		
Aug	3	1.097		0.511			1.241		0.481		
Sep	4	1.123		0.524							
Dec	5	1.020		0.478			1.106		0.196		
Feb 1989	6	0.906		0.329			0.993		0.212		
Jun	7	1.810		-0.759			1.608		0.758		
Sep	8	1.411		-0.823							

Fig. 2). Later removal of ephemeral algae was timed so that most recruits would be visible to the naked eye. Finally, few *Fucus* recruits were found in microscopic examination of samples of removed ephemeral algae (casualty rate estimated over all ephemeral algae removal procedures was 4.3%, SE = 2%).

Effects of ephemeral algae removal on barnacles

Barnacle density was lower when ephemeral algae were experimentally thinned. In the open plots, this effect was not significant and, given the low recruitment, was unlikely to be biologically important. However, the effect was significant and perhaps more biologically important in caged plots, where overall barnacle density was higher (Figs. 2, 3, Table 3).

Effects of furoid algae

The effects of furoid algae in open plots were presumably negligible, since the density of *Fucus* was so low. However, several observations indicate that settlement or growth of ephemeral algae may be generally higher where cover of *Fucus* was lower. For example, in March and June 1990, ephemeral cover was higher for caged treatments with lower cover of *Fucus* (ironically the ephemeral removal treatments Fig. 3) and ephemeral cover in cages was less than in open plots (which had less *Fucus*; Fig. 2A, B cf. 3A, B). In general, ephemeral algae did not recruit under *Fucus* throughout the site (see also McCook and Chapman 1991, McCook 1992).

Discussion

The present study was intended to test the widely accepted view of community structure on these shores that where *Fucus* persists as a canopy, this is because whelk predation controls plant-animal competition, and herbivory by littorinid snails controls plant-plant competition (references in "Introduction"). Our results show that, during this stage of this (artificially) primary succession, none of these factors was an important determinant of species composition, because of the low recruitment of most species. The only important influence on species composition appeared to be variations in *Fucus* recruitment, which was facilitated by the presence of ephemeral blue-green algae or cages.

Three factors limit the generality of our results, without invalidating them. First, the conclusion that competition and predation were unimportant depends on the low recruitment and immigration of most species. This conclusion is nonetheless valid (see also Underwood and Denley 1984), and such circumstances may not be uncommon. During the early natural succession, extensive areas of shore were beyond the reach of whelks and littorinids, which tended to graze outward from crevices in the rock. Recruitment of mussels to these areas was also quite low (McCook 1992). Second, the use of newly exposed substrate limits the generality of the conclusions, but enabled tests of the hypothesized structure that are not confounded by initial differences in remnant biota. Critically, this procedure avoided differences in amounts of remnant *Fucus* holdfasts. Since *Fucus* can regenerate from minute amounts of holdfast (McCook and Chapman 1992), such differences may lead to distinctly differ-

ent successional processes. Third, the results from caged plots really refer only to the artificial conditions in the cages, given the strong artifact of cages on *Fucus* recruitment. The parallel treatment effects in open plots and cages imply that the caged plots still provide valuable information, despite this artifact. Nonetheless, this artifact indicates that these cages are not a suitable means of excluding mobile species from bare, emergent rock on these shores. This contrasts with results from tidal pools and established *F. spiralis* canopy (Parker 1987, Chapman 1989, 1990).

Predation, plant-animal competition, and recruitment

It is valuable to consider why recruitment and immigration were so slow in this experiment. Whelk density was also low during early stages of the natural succession. The absence of whelks is presumably due to the lack of prey and/or of shelter, and contrasts with areas or successional stages where mussels are more abundant, and whelks more important (e.g. Menge 1976, 1978, 1991 b, Menge and Sutherland 1976, Petraitis 1987, McCook and Chapman 1991). Petraitis (1990) argued that whelks may be unimportant even when they and their prey are present, although Menge (1991 b) considers this to be due to low recruitment of mussels.

The poor recruitment of mussels in our study is particularly interesting, since it was not caused by predators, nor affected by the removal of ephemerals. Mussel recruitment at a range of sites on the surrounding shore was much more prolific, even a few metres from this experiment, suggesting that larval supply was not restricting mussel recruitment. We believe that poor recruitment of mussels was due to the combination of exposure and the lack of suitable attachment sites. The rock surface in these plots was exceptionally smooth, and mussels settle predominantly around surface heterogeneities, such as rock crevices, barnacles or furoid holdfasts (McCook and Chapman 1991, McCook 1992; also Menge 1976, Grant 1977, Petraitis 1987, 1990). In this sense, the poor mussel recruitment may be an artifact of our preparation of the site. Other workers have found that attachment of mussels is facilitated by filamentous algae (e.g. Seed 1976, Petraitis 1990), yet we did not find evidence for this. Perhaps the impact of waves outweighed any facilitation by these algae. The blue-green algal mat, whilst microscopically filamentous, was superficially very smooth.

No effect of barnacles on *Fucus* or mussels was detected in this experiment or during the natural succession (McCook 1992) but this may only reflect their low recruitment. Other work suggests that, at higher densities, barnacles influence recruitment of both algae and mussels, and the grazing efficiency of littorinids (Menge 1976, Grant 1977, Lubchenco 1983, Petraitis 1987, 1990, Chapman and Johnson 1990). In this context, it is interesting that ephemeral algae may have slightly enhanced recruitment of barnacles. This contrasts with Minchinton and Scheibling's (in press) results for the same period and area, and with Petraitis' (1983) finding that settlement of barnacles was inhibited by *Enteromorpha* spp. This dif-

ference probably depends on the type of ephemeral algae, as discussed below for *Fucus*. These differences in effects of barnacles on other species and of other species on barnacles, emphasize the variable role of barnacles in the community structure.

Herbivory and plant-plant competition

The low densities of grazing littorinids and amphipods during this experiment are probably due to the lack of shelter rather than food, since ephemeral algae were abundant throughout most of the experiment. Littorinids grazed heavily on eukaryotic and blue-green ephemeral algae near rock crevices and other shelter, but all quadrats in this experiment were beyond their reach, as were large areas of substrate during the early natural succession (McCook 1992). The importance of littorinid and amphipod herbivores may vary with successional stage, since they are more abundant after canopy establishment (e.g. McCook and Chapman 1991, McCook 1992). Several other studies have found that grazing by amphipods or littorinids did influence species composition or abundance during colonization or succession (e.g. Lubchenco and Menge 1978, Lubchenco 1983, 1986, Petraitis 1983, 1987, Parker 1987, Chapman and Johnson 1990). However, these studies usually involved either small patches in established canopy, sheltered sites or tide pools, and usually focussed on *Littorina littorea*, which is larger, and has a different distribution and diet (Barker and Chapman 1990). This incidentally serves to emphasize the importance of patch size to studies of herbivory during succession (see also Sousa 1984 a), and of ensuring that herbivore effects are not artifacts of adjacent successional stages or microhabitats.

Plant-plant competition between *Fucus* and ephemeral algae did not significantly affect abundances of either group in open plots in the present study or in the early natural succession (McCook 1992). *Fucus* is certainly more important at higher abundances, and later in succession (see observations in "Results", and e.g. Menge 1976, Lubchenco 1986, Chapman 1989, 1990, Chapman and Johnson 1990, McCook and Chapman 1991, McCook 1992). More importantly, during this study, success of *Fucus* did not depend on control of ephemeral competitors by herbivores or by waves, as concluded by Lubchenco (1986). Lubchenco's conclusion was based on results from sites in which *Fucus* propagules were assumed rare, in which case competition with ephemerals is unlikely. Like Lubchenco (1986), we did not directly test the effects of wave exposure on ephemeral algae. However, ephemeral growth in open plots was similar to that in cages or in similar sheltered areas near this site. This makes it unlikely that ephemeral growth was limited by waves.

Fucus recruitment and facilitation by ephemeral blue-green algae

We consider that variations in *Fucus* recruitment are important to primary succession in this assemblage. The

only significant factors in this experiment, cages and ephemeral algae, both affected *Fucus* recruitment and *Fucus* abundance is important to the assemblage in general (e.g. McCook and Chapman 1991).

The small abundance of *Fucus* in open plots is not due to herbivory, or to limited propagule supply. Herbivores were essentially absent and settlement was dense in cages, and prolific on ceramic tiles. Recruitment of *Fucus* onto rock was generally poor. We conclude that ephemeral algae and cages facilitate the settlement or recruitment of *Fucus*. (Alternatively, if *F. evanescens* propagules were plentiful but *F. vesiculosus* propagules were not, we conclude that cages affected settlement of *F. evanescens* and ephemerals affected that of both species. The conclusions are similar.)

The facilitation of recruitment of *Fucus* probably stems from the amelioration of physical conditions for attachment or survival of zygotes. Higher humidity provided by the mat of blue-green algae and by the cages may prolong survival of embryos during development. In cages, this effect is probably compounded by protection from waves, since unprotected, newly-settled embryos are often removed by a single wave (Vadas et al. 1990). Indeed, compared to the exceptionally smooth rock in these sites, the tangled mat of microscopic filaments in the blue-green algae may also provide some shelter and/or better attachment for furoid zygotes that settle amongst them. It was clear from our observations that *Fucus* embryos attached first to the ephemeral algal mat, and later to the underlying rock. Furoid zygotes attach by means of a mucilage pad and primary rhizoid, which adhere to the microscopic texture of the substratum (Moss 1975, 1981).

The conclusion that ephemeral algae facilitated *Fucus* is particularly interesting, since it contrasts with the conclusions of Lubchenco [1982, 1983, 1986, Lubchenco and Cubit (1980)] and Sousa (1979, for the Pacific coast). These are the only other studies we have found that directly manipulated intertidal ephemeral algae in the field, despite the widely accepted importance of these algae. Based on observations alone, ephemeral algae had no detectable effect on *Fucus* during the natural succession (McCook 1992) whereas Knight and Parke (1950) suggested that *Fucus* recruited faster amongst ephemeral algae than on bare rock. Brawley and Johnson (1991) found that short-term survival of furoid embryos was better amongst algal turfs or under canopy than in exposed sites. Hruby and Norton (1979) found in laboratory experiments that *Enteromorpha intestinalis* inhibited attachment of ephemeral algal spores to glass slides but enhanced survival of previously attached spores.

The facilitation of *Fucus* recruitment by ephemeral algae is also significant as one of very few examples of direct, plant-plant facilitation on rocky intertidal shores. Turner (1983) found obligate facilitation of surfgrass recruitment by turfing red algae, which provided attachment sites for the seeds. Whilst facilitation of *Fucus* by ephemerals, and the facilitation of algae or mussels by barnacles (e.g. Menge 1976, Chapman 1989) are not obligate, it is noteworthy that these examples all involve recruitment, rather than later growth.

The effects of ephemeral algae on *Fucus* may be very important to the structure of the assemblage. Very different successional processes may occur when later dominants are inhibited or facilitated by earlier species, depending on the strength of those effects (Connell and Slatyer 1977, Turner 1983, Connell et al. 1987, McCook in press). This is particularly true when considering the potential importance of factors such as herbivory (Farrell 1991). Removal of ephemeral algae by herbivores may slow down or even redirect succession when the ephemeral algae facilitate *Fucus* growth, whereas herbivory on inhibitory ephemeral algae would speed up the successional dominance by *Fucus* (e.g. Lubchenco 1983, see also Farrell 1991). Further, when herbivory is patchy, as around crevice refuges, the effects of facilitation or inhibition on *Fucus* growth may also be patchy.

Experimental context and variability in community structure

The importance to assemblage structure of ephemeral algal effects on *Fucus* depends heavily on the context of the interaction. We have found an overall facilitation of *Fucus* recruitment by ephemeral algae, but we believe this facilitation stems from enhanced recruitment on a very thin, cohesive mat of blue-green algae, present during the summer recruitment period of *Fucus*. There was no evidence for facilitation during the natural succession (McCook 1992), nor did we directly observe such effects with the much thicker growth of winter, filamentous green algae, although *Fucus* settlement during this period was low. Such thick growth may inhibit *Fucus* success (Hruby and Norton 1979, Lubchenco 1982, 1983, 1986 but cf. Knight and Parke 1950). Our results do not conflict with the earlier work, but underscore the variability in these interactions. This, in turn, emphasizes the value of viewing successional effects as interactions between species' life-history traits and individual circumstances, rather than as simple inhibition or facilitation. Our results refer only to this combination of species, seasonality, exposure, substratum texture, and especially to primary succession. Primary succession is almost certainly rare on these shores, and furoid recruitment may be less important than vegetative regeneration during natural succession, even after severe disturbances (McCook and Chapman 1992, McCook 1992, see also Cousens 1985, Vadas et al. 1990).

Variations in supply of propagules may strongly influence intertidal community structure (Underwood and Denley 1984, Gaines and Roughgarden 1985, Underwood and Fairweather 1989). Our results for *Fucus* and mussels indicate that, even when propagule supply is not limiting, variations in recruitment success may still be important, and may be very dependent on other species. Further, our results demonstrate the need for information about the 'supply-side ecology' of canopy algae (but see Reed et al. 1988, Reed 1990). Little is known about causes of variation in availability of macroalgal propagules, yet these are almost certainly important and quite different to those acting on the better studied benthic

invertebrates, such as barnacles (e.g. Connell 1985, Gaines and Roughgarden 1985, Menge and Sutherland 1987, Menge 1991 a). Indeed, recruitment from planktonic zygotes may be relatively unimportant (McCook and Chapman 1992, McCook 1992).

In a recent retrospective analysis, Menge (1991 a, also Menge and Farrell 1989) concluded that, compared to competition and predation, recruitment accounted for relatively little variation in community structure during his previous studies in New England. However, this interpretation essentially refers only to possible relationships between spring recruitment and adult populations the following autumn, only during his studies, and only to barnacles and perhaps mussels. His evidence for effects on *Fucus* is not strong, since any effects of *Fucus* recruitment on community structure are unlikely to be felt the same year. Menge considers that the low importance of recruitment is due to the high recruitment in this assemblage (relative to Panama or to Petraitis' 1990 sheltered site in New England, Menge 1991 a, b). Our present results support the idea that competition and predation are less influential when recruitment is low (Gaines and Roughgarden 1985, Menge and Sutherland 1987, Menge and Farrell 1989, Menge 1991 a, b), but indicate that Menge's (1991 a) description of New England shores is not regionally and/or historically general (see also Petraitis 1987, 1990, Menge 1991 b).

In summary, during an exceptional, early primary succession, competition and predation did not significantly affect abundance of most species, owing to the very low recruitment of these species. Ephemeral algae slightly facilitated recruitment of the usually dominant *Fucus* rockweed, perhaps by improved survival of embryos on a thin mat of ephemeral blue-green algae. These conclusions are probably quite specific to these conditions, but underscore the potential variability in structure amongst very similar assemblages of species.

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