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COMMUNITY-WIDE EFFECTS OF NONINDIGENOUS SPECIES ON TEMPERATE ROCKY REEFS

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Abstract. Ecological interactions among invading species are common and may often be important in facilitating invasions. Indeed, the presence of one nonindigenous species can act as an agent of disturbance that facilitates the invasion of a second species. However, most studies of nonindigenous species are anecdotal and do not provide substantive evidence that interactions among nonindigenous species have any community-level effects. Here, using a combination of field experiments and observations we examine interactions among introduced species in New England kelp forests and ask whether these interactions have altered paradigms describing subtidal communities in the Gulf of Maine. The green alga *Codium fragile* was observed at the Isles of Shoals, Maine, USA, in 1983 and has since replaced the native kelp as the dominant seaweed on leeward shores. Experiments manipulating kelp and *Codium* reveal that *Codium* does not directly inhibit growth or survival of kelp. *Codium* does, however, successfully recruit to gaps in the kelp bed and, once established, inhibits recruitment of kelp. A second nonindigenous species, *Membranipora membranacea*, grows epiphytically on kelp, and experiments reveal that the presence of *Membranipora* reduces growth and survival of kelp, resulting in defoliation of kelp plants and gap formation in kelp beds. In the absence of *Codium*, kelp recolonizes these gaps, but when present, *Codium* colonizes and prevents kelp recolonization. Manipulations of herbivores demonstrate that herbivory will reinforce *Codium* dominance. Thus, the demise of New England kelp beds appears to result from one invasive species facilitating the spread of a second nonindigenous species.

Key words: Codium; *Gulf of Maine, USA; herbivory; indirect effects; introduced species; Isles of Shoals, Maine, USA; kelp recruitment and nonindigenous species;* Membranipora; *nonindigenous species; recruitment; species interactions;* Tautogolabrus adspersus.

INTRODUCTION

Natural barriers to species dispersal are now routinely defeated by human activities, and as a result, the introduction of species outside their natural range has become a common occurrence. Accidental and deliberate species introductions are presently occurring at rates rivaling those of the last tens of millions of years. These introductions may constitute the most severe environmental threat the world now faces (Kareiva 1996, Vitousek et al. 1997). Although as few as 10% of introduced species become established (Williamson 1996), nonindigenous species have the potential to severely alter the structure and function of native communities (e.g., Byers 2000, Grosholz et al. 2000). The potential impact of biological invasions on terrestrial and freshwater communities has been recognized for decades (Elton 1958); however, the mechanisms by which introduced species impact native communities are often unknown (Parker et al. 1999). The task of identifying the impacts of biological invaders becomes increasingly difficult when we consider the potential for complex interactions, including direct effects, indirect effects, and cumulative impacts (Simberloff and Von Holle 1999).

When organisms are transported from their native ranges to a new locale, they only rarely proliferate, spread, and persist (Mack et al. 2000). Identifying the mechanisms that allow a nonindigenous species to become invasive is of immense scientific and practical interest. Successful invaders are frequently associated with human disturbance such as livestock grazing, intensive agriculture, changes in fire regime, and alterations to wetlands (Mack et al. 2000). In a recent review of interactions among nonindigenous species, Simberloff and Von Holle (1999) intimate that the presence of nonindigenous species may act as an agent of disturbance that facilitates the invasion of other species. However, most studies of nonindigenous species are anecdotal and do not provide substantive evidence that interactions among nonindigenous species have any population effects (Parker et al. 1999, Simberloff and Von Holle 1999).

Here we examine the direct and indirect effects of nonindigenous species on rocky reefs in the Gulf of

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Maine where, in recent years, numerous species have been introduced and are now established. Recent introductions include a European nudibranch *Tritonia plebeia* (Allmon and Sebens 1988), California tunicates *Styela clava* and *Botrylloides* spp. (Carlton 1989), a western Pacific crab *Hemigrapsus sanguineus* (Gerard et al. 1999), a bryozoan from Europe, *Membranipora membranacea* (Berman et al. 1992), an Asian green alga *Codium fragile* (Carlton and Scanlon 1985), and a European flatworm *Convoluta convoluta* (Rivest et al. 1999). *M. membranacea* and *C. fragile* have become particularly abundant in the Gulf of Maine. We ask if the presence of these invasive species has significantly altered the structure of New England subtidal communities and, if so, whether the impacts have been synergistic. In doing so, we explicitly examine the hypothesis that the presence of one nonindigenous species facilitated the expansion of a second introduced species.

STUDY SYSTEM

Diverse and productive forests of kelp fringe many temperate rocky coasts throughout the world, including the Gulf of Maine. The productivity of these complex habitats rivals even the most productive terrestrial habitats, fixing up to 3 kg $C \cdot m^{-2} \cdot yr^{-1}$ (Witman 1988). Typically, kelp forests have a three-tiered structure with the top tier consisting of a canopy rising above the bottom. Shading by the kelp canopy results in a middle tier of shrubby, shade-tolerant understory composed of red and smaller brown seaweeds (Johnson and Mann 1988). A bottom tier of encrusting coralline algae covers most of the rocky surfaces.

In the Gulf of Maine, as in other locales, grazing by sea urchins (*Strongylocentrotus droebachiensis*) can convert diverse, productive kelp forests to an alternate, low productivity community dominated by urchins and herbivore-resistant coralline algae (Witman 1987, Keats 1991). Physical factors acting on urchin populations appear to trigger shifts between community states. Although the occurrence of important physical processes is unpredictable in time or space, the outcome following a physical disturbance (kelp forest or urchin-dominated community) was thought to be highly predicable in the Gulf of Maine (Johnson and Mann 1988).

FOCAL NONINDIGENOUS SPECIES

Codium fragile *ssp.* tomentosoides

During the early 1900s, the green alga *Codium fragile* ssp. *tomentosoides* (hereafter referred to as *Codium*) dispersed from the northwest Pacific to northern Europe, where it expanded its range over the next 50 years. In 1957, *Codium* was discovered along the east coast of the United States on Long Island. It arrived via transplantation of oysters either from Washington State or The Netherlands, and quickly spread south to North Carolina and north to Cape Cod, Massachusetts (Fralick and Mathieson 1972, Carlton and Scanlon 1985). The species was first observed on Appledore Island in the Isles of Shoals (central Gulf of Maine) in 1983 and was abundant throughout all the islands of the Isles of Shoals archipelago by 1991 (Prince 1988, P. S. Levin, J. A. Coyer, R. Petrik, and T. P. Good, *personal observations*). By late 1992, *Codium* had spread throughout the Northwest Atlantic, including Nova Scotia (Bird et al. 1993).

This rapid range expansion was facilitated by the ability of *Codium* to reproduce by both fragmentation and sexual reproduction. *Codium* undergoes extensive fragmentation in winter when intact individuals are often reduced to their basal holdfast. New fronds can grow from the residual holdfast, and drifting fragments can reattach on open substrata (Fralick and Mathieson 1972, Mathieson 1989). Most sexual reproduction occurs in summer in New England (Prince 1988). Biflagellated swarmers are released from macroscopic plants and germinate directly into heterotrichous germlings (Fralick and Mathieson 1972). The spread of *Codium* has also been accelerated by transplantation of oysters, entrapment in fishing nets, and attachment to ship hulls (Bird et al. 1993). *Codium* is consumed worldwide by a variety of urchins and other herbivores (Prince and LeBlanc 1992, Trowbridge 1995), but it does not appear to be a preferred food source for *Strongylocentrotus droebachiensis* in the Gulf of Maine (Prince and LeBlanc 1992, Scheibling and Anthony 2001).

Membranipora membranacea

The encrusting cheilostome bryozoan *Membranipora membranacea* (hereafter referred to as *Membranipora*) grows epiphytically on kelp blades both in Europe (Ryland 1970, Eggleston 1972) and along the North American Pacific coast (Osburn 1953, Yoshioka 1982). It was first observed in the Gulf of Maine in 1987 (Lambert 1990) and has since become the dominant epibiont of laminarian kelps in this region (Berman et al. 1992). In the Gulf of Maine, *Membranipora* grows and reproduces during the summer, and colonies senesce in the fall (Ellison and Harvell 1989, Berman 1994). *Membranipora* has been reported to occur on up to 85% of kelp individuals (Berman et al. 1992), and kelp blades with heavy encrustations of the senesced bryozoan are susceptible to storm damage (Dixon et al. 1981, Lambert et al. 1992). In southern Maine, for example, winter storms of average intensity resulted in the defoliation of a kelp bed that had persisted for >25 yr (Lambert et al. 1992). Similar defoliation events have been observed in Nova Scotia (Scheibling 2000). Although fishes and nudibranchs consume *Membranipora* elsewhere (Bernstein and Jung 1979, Harvell 1984), it does not appear to have significant predators in the Gulf of Maine (Lambert et al. 1992).

METHODS

Study site

Field experiments and descriptive investigations were conducted on rocky reefs at the Isles of Shoals, 10 km offshore of Portsmouth, New Hampshire, USA (42°59′ N; 70°37′ W). The Isles of Shoals consist of nine small granitic islands with subtidal rock-ledge habitats that are typical of the Gulf of Maine (Witman 1987). All work was conducted in water 4–7 m deep at low tide. For the past two decades, we have studied these sites intensively (Levin 1991, 1993, 1994*a*, 1996, Levin and Mathieson 1991, Levin et al. 1997, Rivest et al. 1999) as have others e.g., (Witman 1985, 1987, Mathieson and Hehre 1986). Thus, it is possible to place results of our study in a longer term temporal context.

General approach

Our general approach in this project was to first describe the pattern of change in the algal assemblages on rocky reefs at the Isles of Shoals. We then performed a series of field and laboratory experiments to elucidate the mechanisms underlying the potential impacts of *Codium* and *Membranipora* on native seaweeds as well as the organisms that use seaweed beds as habitat.

Changes in the structure of algal assemblages

In 1990–1992 and 1996–1998, we quantified the algal habitat on Appledore Island as part of ongoing work on fish recruitment (Levin et al. 1997). Algae were grouped as kelps (mostly *Laminaria saccharina*), filamentous (mostly *Ceramium* spp. and *Polysiphonia* spp.), and *Codium* (Levin 1991, 1994*b*). The percent cover of each algal group was estimated by recording the type of alga at 50-cm intervals along randomly placed 15-m transects. A minimum of 10 transects was sampled at each site, and thus, we sampled at least 300 points in each site. We enumerated algal cover only in August in each year because this is when the fish that we were investigating settled from the plankton to macroalgal habitat (Levin 1994*a*). Because we report only algal cover (not bare cover) this should be viewed as a relative measure of algal abundance. One-way analysis of variance (ANOVA) was used to determine if the percent cover of each of the three algal groupings changed among years.

Impacts of Codium *and* Membranipora *on kelp*

Does Codium *inhibit recruitment of kelp?*—Because of the dense cover of *Codium* we observed at our study sites and that has been reported elsewhere (Chapman 1999, Scheibling and Anthony 2001), we reasoned that *Codium* may inhibit kelp recruitment (see also Scheibling 2000). To test the hypothesis that increases in *Codium* cover have occurred because *Codium* outcompetes kelp by inhibiting recruitment of juvenile kelp, we performed an experiment in which algal cover was manipulated. In June 1997 we established eight circular experimental plots (9 m^2) in three sites along the western (leeward) shoreline of Appledore Island at 4–7 m depth. Following a randomized block design, we either removed all *Codium* or removed no algae (i.e., the control). In order to ensure that all experimental treatments were independent, we separated experimental plots within experimental blocks by 10 m, with blocks separated by $>$15 m. Divers removed *Codium* by hand, placed all algae in mesh bags, and disposed of the algae several meters downcurrent from the study site. Control plots received similar diver disturbance, but no algae was removed. In addition, two cement slabs (27 cm long × 18 cm wide × 2.25 cm tall) were placed within plots to evaluate recruitment of algae.

In September 1997 and March, May, and August 1998, we estimated the percent cover of algae on cement slabs by enumerating the presence of species beneath a 27 × 18 cm grid of 50 points. As *L. saccharina* produces unilocular sporangia through the winter (Mathieson et al. 1981), and young kelp sporophytes are apparent in spring, we quantified kelp cover before, and for varying periods after, the recruitment of juveniles. We used repeated-measures ANOVA to test for differences in kelp cover in the presence or absence of *Codium* (main effect) and among sampling dates (repeated measure).

Do Codium *or* Membranipora *affect kelp growth or survival?*—Embedded within the experiment described above, we evaluated the effect of both *Codium* and *Membranipora* on survival and growth of kelp. Within the central 4.5-m^2 area of each experimental plot, we randomly attached two kelp plants (length: 30.1 ± 1.3 cm [mean ± 1 SE]) to the substratum by weaving the holdfast of kelp into polypropylene line attached to the bottom with epoxy. On one kelp individual within each plot we removed all *Membranipora* growth by gently removing colonies using a fingernail (Harvell et al. 1990). These kelp individuals were paired with a second individual that had at least 50% cover of *Membranipora*. All kelp individuals subsequently were tagged with sequentially numbered plastic cable ties fastened loosely around the stipe of the plant. Previous work had indicated that tag chafing would be minimal and that this method would have minimal effects on kelps (Coyer and Zaugg-Haglund 1982).

We revisited each plant five times over 19 d and recorded the presence/absence of tagged individuals. We also measured kelp growth by following the movement of a small hole, 0.8 cm in diameter and 5 cm from the blade–stipe junction, punched into the blade. A new hole was punched on each visit to the plant; the distance between the newly and previously punched holes represented simple linear growth (Coyer and Zaugg-Haglund 1982). Differences in kelp growth were assessed using a two-way ANOVA with the presence or absence of *Codium* and *Membranipora* as main effects. Differences in the proportion of individuals surviving to the end of the experiment were assessed with a likelihood-ratio chi-square test. It was possible to unambiguously determine if a plant survived, since in all cases where an individual was missing, its holdfast remained.

Mechanisms underlying shifts in algal assemblage structure

Is kelp with or without Membranipora *more susceptible to herbivory?*—Because *Membranipora* may increase the nutritional value of kelp (Nestler and Harris 1994), we also tested the relative palatability of kelp (*L. saccharina*) with and without *Membranipora* to herbivory by offering a sea urchin (*Strongylocentrotus droebachiensis*) or a snail (*Lacuna vincta*) a choice between the two. Kelp pieces were damp-dried to remove excess water, weighed to the nearest milligram, and offered to an individual herbivore held in a 1.6-L tub with flow-through seawater. Each herbivore was offered a choice between similar-sized (damp-dried mass = 285 ± 15.6 mg [mean ± 1 SE] per piece) kelp pieces. Pieces with and without *Membranipora* came from the same individual kelp, and each kelp plant, as well as herbivore, was used in only one replicate. Paired kelp pieces (i.e., from the same individual kelp) were also set up without herbivores to control for autogenic changes in mass (Peterson and Renaud 1989, Renaud et al. 1990). After ~76 h the pieces were reweighed and the amount consumed was calculated using the equation

$$\left(H_0 \times \frac{C_f}{C_0}\right) - H_f$$

where H_0 and H_f were the initial and final masses, respectively, in the presence of herbivores, and C_0 and C_f were initial and final masses in the absence of herbivory (Cronin and Hay 1996). Differences in consumption were analyzed with a paired-sample *t* test.

Is Codium *or kelp more susceptible to herbivory?*—The relative palatability of *Codium* and kelp was first assessed by offering sea urchins a choice between the two algal species using the protocol described above. Algae were damp-dried, weighed to the nearest milligram, and offered to an individual sea urchin held in a 1.6-L tub with flow-through seawater. Each sea urchin was offered a choice between similar-sized pieces (damp-dried mass = 454 ± 12.1 mg [mean ± 1 SE] per piece). Again, each alga and sea urchin was used in only one replicate, and paired algal pieces were established without herbivores to control for autogenic changes in mass (Peterson and Renaud 1989, Renaud et al. 1990). After 48 h, the plants were reweighed, and the amount consumed was calculated as above.

We also assessed the palatability of *Codium* relative to kelp using a no-choice assay (sensu Cronin and Hay 1996) with either *S. drobachiensis* or *L. vincta* as herbivores. A piece of each alga was placed alone in a flow-through 1.6-L container with a randomly assigned herbivore. Herbivores were allowed to feed for 72 h. A paired piece of algal tissue (from the same plant) was placed in a similar tub without an herbivore to control for autogenic changes in mass. Treatments were arrayed in a sea table randomly. At the end of the assays, algae were reweighed and the amount each plant consumed was calculated as described above. Data were analyzed with a *t* test assuming unequal variances.

Our laboratory experiments used *S. droebachiensis* and *L. vincta* because these are the dominant herbivores at our sites (Witman 1985, 1987). Nonetheless, other herbivores exist in the system and may differentially consume algae. Therefore, we performed an additional experiment in which similar-sized pieces of *Codium* and kelp (damp-dried mass = 974 ± 9.9 mg) were attached to the sea floor by weaving their holdfasts into three-stranded polypropylene line that was epoxied to the substrate. We choose a location where urchins were locally abundant. Pairs of *Codium* and kelp ($N = 20$ pairs) of each species were placed at ~3-m depth and exposed to all herbivores (cf. Hay 1981). After 24 h we retrieved the algae, reweighed individual pieces, and calculated the amount consumed as the difference between the initial and final masses.

Potential community-level consequences of Codium/Membranipora *invasion*

Potential effects on the algal assemblage.—In 1997 and 1998 we sampled algae in seven sites around the Isles of Shoals archipelago. Using the same transect procedure described above, we sampled percent cover of *L. saccharina*, *Codium*, *Ulva lactuca*, *Chondrus crispus*, crustose coralline algae, and filamentous red algae (mostly *Ceramium* spp. and *Polysiphonia* spp.) along a minimum of 10 transects per site in both years. We selected these species and functional groups because previous work has demonstrated their importance to other species in kelp bed communities (Levin 1991, 1994*b*, Bologna and Steneck 1993, Tupper and Boutilier 1995*b*). We expressed the relative abundance of native kelp vs. nonindigenous *Codium* as the ratio

$$\frac{\%\text{kelp} + 1}{\%\textit{Codium} + 1}.$$

We then asked if differences in the algal assemblage were associated with the relative abundance of kelp vs. *Codium* using a general linear model (GLM). Percent covers of filamentous red algae, crustose corallines, *U. lactuca*, and *C. crispus* were dependent variables in the model, and the ratio of kelp to *Codium*, year, and wave exposure (windward vs. leeward side of the Isles of Shoals) were independent variables. Prior to analysis, we followed the procedures described by Wilkinson et al. (1996) to access multivariate normality. No patterns were evident that would indicate violation of the assumption of homogeneity.

To illustrate the association of the kelp and *Codium*

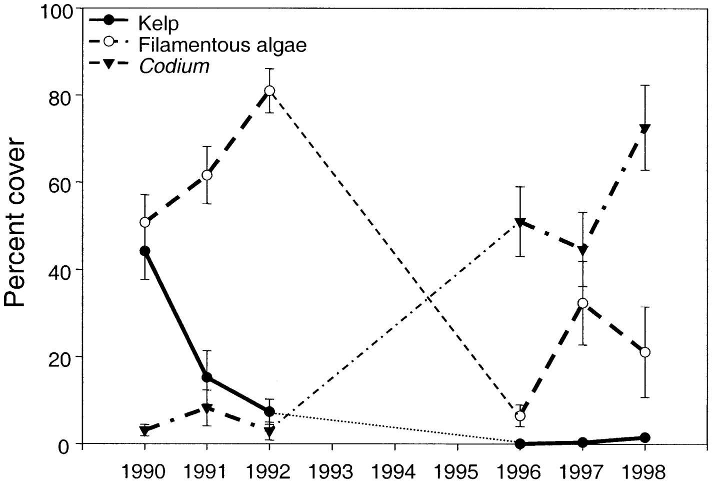

FIG. 1. Percent cover of algal functional forms at Appledore Island, Isle of Shoals, Maine, USA, 1990–1998. The thinner sections of the curves indicate years in which algal cover was not enumerated. Data are means ± 1 SE.

with the algal assemblage we performed correlations between the ratio of kelp to *Codium* with the algal species we identified in our surveys. We performed these correlations only to illustrate the results of the GLM above; significance was determined with the GLM.

Potential effects on mobile animals.—To determine if a shift in the algal assemblage from kelp to *Codium* domination might impact rocky-reef invertebrates and fishes, we conducted an experiment in which we created 1-m^2 patches of algae on otherwise barren substratum. Algal patches ($N = 6$ patches per algal species) were constructed in June 1998 by attaching 16 kelp or *Codium* plants to four 1-m-long ropes, which in turn were attached to two parallel pieces of chain separated by 1 m (Levin and Hay 1996). A density of 16 plants/m^2 was sufficient to create patches of 100% cover for both algal species. Replicates of each treatment were separated from each other and from natural reef by at least 10 m and arranged in blocks separated by at least 12 m.

Algal patches were sampled visually 5 times from 12 to 26 August 1998, during the peak settlement of the rocky-reef fish, cunner (*Tautogolabrus adspersus*) (Levin 1994*a*). Densities of newly settled cunner (<20 mm standard length [SL]) as well as other mobile animals (crabs, lobsters, snails, other fish species, etc.) were censused following procedures developed by Sale and Douglas (1981), and used with success in the Gulf of Maine by P. S. Levin (e.g., Levin 1994*a*). Specifically, a diver approached a patch and at a distance of 2 m slowly circled the patch while recording the number of active species within 1 m of the patch. The diver then moved closer and counted demersal species associated with the algae. Finally, the algae themselves were searched. We used the mean value of the five censuses as the response variable in a one-way ANOVA testing for differences in numbers of conspicuous animals between kelp and *Codium* patches.

RESULTS

Changes in the structure of algal assemblages

In 1990–1992 the subtidal community at Appledore Island (Isles of Shoals, Gulf of Maine) consisted of a kelp canopy with an understory of filamentous species. Since the early 1990s there has been a significant shift in the algal assemblage (Fig. 1, Table 1). In 1990, kelp coverage averaged 44 (±6.44)% (mean ± 1 SE), and percent cover of filamentous algae was >50 (±6.3)%. *Codium* was rare at the site with a cover of 3.1 (±1.3)%. Kelp declined as the decade progressed, and by the late 1990s, average kelp cover did not exceed 2%. Similarly, the cover of understory filamentous red algae declined from a peak of nearly 80% cover in 1992 to below 32% since 1996 (Fig. 1, Table 1). While kelp and associated understory species declined during the last decade, there was a marked increase in the coverage of *Codium* (Table 1). *Codium* cover at Appledore Island increased more than 20 fold by 1998, and is now the dominant seaweed at the site (Fig. 1).

Impacts of Codium *and* Membranipora *on kelp*

Does Codium *inhibit recruitment of kelp?*—We observed marked differences in kelp recruitment to plots in which we removed *Codium* vs. those left as controls (Fig. 2). Kelp recruits appeared on our cement slabs in March 1998, just after the peak period of kelp reproduction. The cover of kelp recruits peaked in May 1998 and averaged nearly 8-fold higher in plots in which *Codium* was removed vs. controls, although this was significant only at an α of 0.06 ($F_{1,9} = 4.496$, $P = 0.06$). By August 1998 no kelp recruits remained in control plots, while cover of kelp recruits averaged >4% in *Codium*-removal plots.

Do Codium *and* Membranipora *affect kelp growth or survival?*—Growth rates of kelp did not vary between experimental plots from which *Codium* was either removed or left intact as a control ($F_{1,41} = 0.52$;

TABLE 1. Results of a general linear model testing the hypothesis that major algal species or functional forms varied as a function of the relative abundance of kelp and *Codium*.

Source of variation†	SS	df	MS	F	P
Chondrus	9.061	1	9.061	2.135	0.149
Error	284.281	67	4.243		
Ulva	3.481	1	3.481	3.262	0.07
Error	71.486	67	1.067		
Algal crust	620.134	1	620.134	48.862	<0.001
Error	850.341	67	12.92		
Filamentous algae	297.177	1	297.177	11.524	0.001
Error	1727.789	67	25.788		

Notes: Results are shown only for the ratio of kelp to *Codium* effect. Multivariate test statistic, Wilks' lambda = 0.409, $F = 23.082$, df = 4, 64, $P < 0.001$.

† Percent covers of filamentous red algae, crustose corallines, *Ulva lactuca*, and *Chondrus crispus* were dependent variables in the model, and the ratio of kelp to *Codium*, year, and wave exposure (windward vs. leeward side of the Isles of Shoals) were independent variables.

$P = 0.48$). In the presence of *Codium*, kelp growth averaged 0.37 ± 0.06 cm/d (mean ± 1 SE) compared to growth in controls of 0.47 ± 0.08 cm/d (Fig. 3). In contrast, when we removed *Membranipora* from kelp blades, kelp grew a significant 3.5-fold faster (0.68 ± 0.05 cm/d vs. 0.19 ± 0.03 cm/d) than when we left *Membranipora* on kelp blades ($F_{1,41} = 59.93$; $P < 0.001$). However, we were unable to detect an interactive effect of *Membranipora* and *Codium* on kelp growth ($F_{1,41} = 2.18$; $P = 0.15$).

Survival of kelp varied significantly among our experimental treatments (Likelihood-ratio chi square = 10.46, df = 3, $P = 0.015$). At the end of the experiment, survival was >75% for kelp with *Membranipora* removed both in the presence and absence of *Codium* (Fig. 4). When we left *Membranipora* on kelp but removed *Codium*, survival decreased to 53%. In control plots in which both *Membranipora* and *Codium* were present, survival decreased further to 20%. Thus, it appeared the combined effect of *Membranipora* and *Codium* was greater than would be predicted by their individual impacts.

Mechanisms underlying shifts in algal assemblage structure

Is kelp with Membranipora *more susceptible to herbivory?*—Our laboratory feeding assays revealed that the relative palatability of kelp with and without *Membranipora* also varied. Sea urchins consumed more than twice as much kelp with vs. without *Membranipora* (68 ± 12.4% vs. 29.2 ± 11.8% (mean ± 1 SE); $t = 4.13$, df = 21, $P < 0.001$). Similarly, *Lacuna vincta* consumed 5 times more kelp with vs. without *Membranipora* (26.5 ± 16.0% vs. 5.1 ± 10.5%; $t = 2.95$, df = 17, $P = 0.008$).

Is Codium *or kelp more susceptible to herbivory?*—Given a choice between *Codium* and kelp, sea urchins consumed nearly 10-fold more kelp than *Codium* ($t = 2.31$, df = 18, $P = 0.03$; Fig. 5a). Additionally, evidence from no-choice feeding assays suggests *Codium* is not preferred by urchins. In both control and urchin-present treatments, *Codium* increased in mass and this increase did not vary significantly between treatments ($t = 1.85$, df = 18, $P = 0.08$; Fig. 5b). In contrast, the

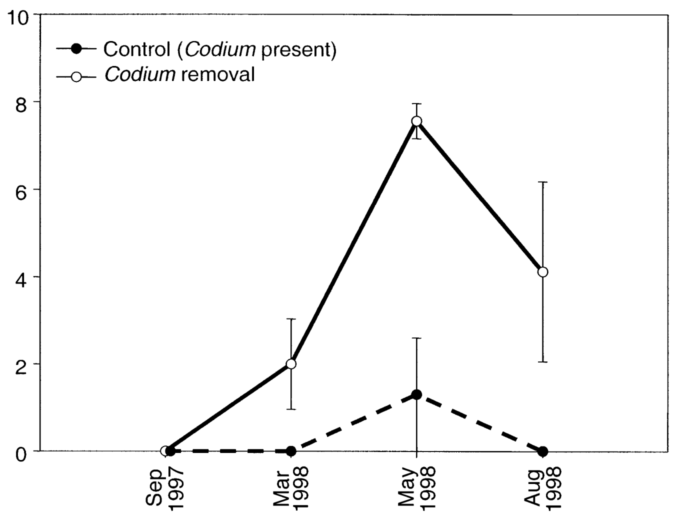

FIG. 2. Percent cover of kelp (*Laminaria saccharina*) on cement slabs placed within experimental plots in which *Codium* was removed or left intact (control). Data are means ± 1 SE.

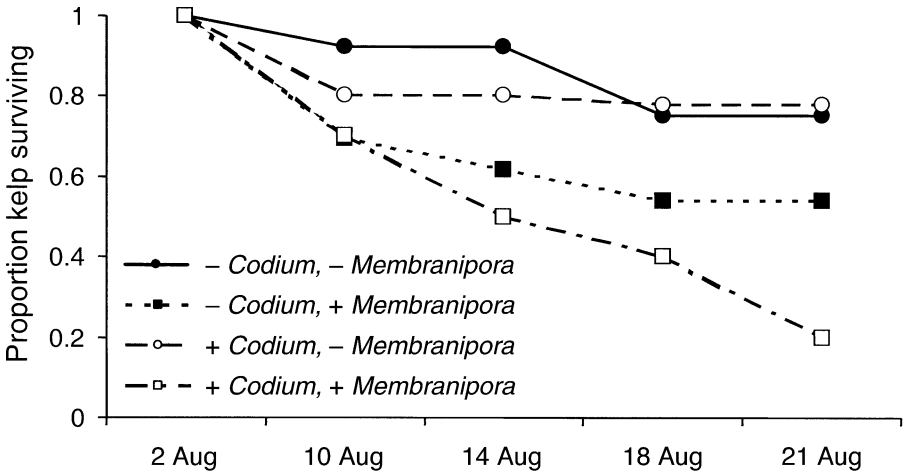

FIG. 3. Proportion of tagged kelp (*Laminaria saccorhina*) surviving within plots in which both *Codium* and epiphytic *Membranipora* were not manipulated (i.e., +*Codium*, +*Membranipora*), either *Codium* or *Membranipora* was removed, and both *Codium* and *Membranipora* were removed.

loss of kelp biomass was a significant 6-fold greater in the presence vs. absence of urchins ($t = 3.59$, df = 10, $P = 0.005$; Fig. 5b).

Results from no-choice feeding assays with *L. vincta* were qualitatively similar. We were unable to detect differences in the change in *Codium* biomass between *Lacuna*-present or control treatments ($t = 1.47$, df = 14, $P = 0.16$; Fig. 5c); however, we did observe greater biomass loss of kelp in the presence vs. the absence of *Lacuna* ($t = 8.00$, df = 13, $P < 0.001$; Fig. 5c).

When we placed kelp and *Codium* in the field exposed to ambient herbivores, our results were similar to our laboratory results. After 24 h, more than 3 times more kelp than *Codium* had been consumed (Fig. 5).

Potential community-level consequences of Codium/Membranipora *invasion*

Potential effects on the algal assemblage.—Our censuses around the Isles of Shoals revealed that *Codium* cover was nearly 10-fold greater on wave-protected than exposed shores (403.04% vs. 4.6 + 3.04% (means ± 1 SE); $t = 10.357$, $P < 0.001$). After statistically removing the effect of wave exposure (by including it in our general linear model) we found that the algal assemblage associated with kelp differed from that associated with *Codium* (Table 1). Generally, we observed a lower percent cover of *Ulva lactuca*, *Chondrus crispus*, crustose coralline algae, and filamentous red algae when the ratio of kelp to *Codium* was high (i.e., kelp dominance) (Table 2). However, the total percent cover of all algal species combined was positively associated with kelp dominance ($R = 0.47$, $P = 0.002$).

Potential effects on mobile animals.—When we created patches of kelp and *Codium* on an otherwise barren substratum, a number of adult decapods moved into the experimental plots. However, we were unable to detect differences in the densities of crabs (*Cancer irroratus* and *Carcinus meanas*) or lobsters (*Homarus americanus*) between kelp and *Codium* plots (Fig. 6).

The fish, cunner (*T. adspersus*), also occurred on experimental patches. Cunner on plots were small (<20 mm SL) and newly settled from the plankton. We observed nearly 6-fold more cunner on kelp than on *Codium* patches (Fig. 6).

DISCUSSION

The previously predictable dynamics of New England (USA) subtidal communities (Johnson and Mann 1988) have clearly been altered by biotic invasions. In addition to urchin- and kelp-dominated habitats, there now appears to be a new and third state—the nonindigenous *Codium*-dominated habitat. Although present at the Isles of Shoals since 1983, the occurrence of expansive *Codium* meadows was unknown until the mid-1990s, after a shift from kelp to *Codium* dominance. The replacement of kelp communities appears to be widespread within the Northwest Atlantic Ocean

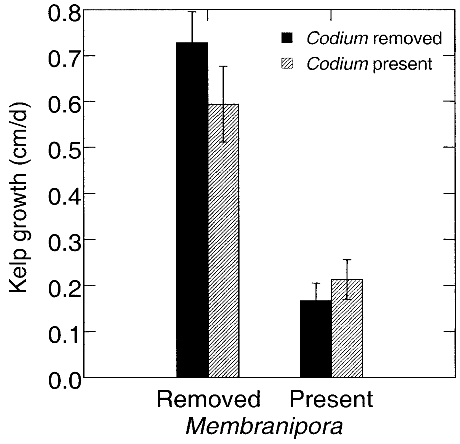

FIG. 4. Growth of kelp (*Laminaria saccharina*) on which *Membranipora* was removed or left on kelp blades within plots in which *Codium* was present or removed.

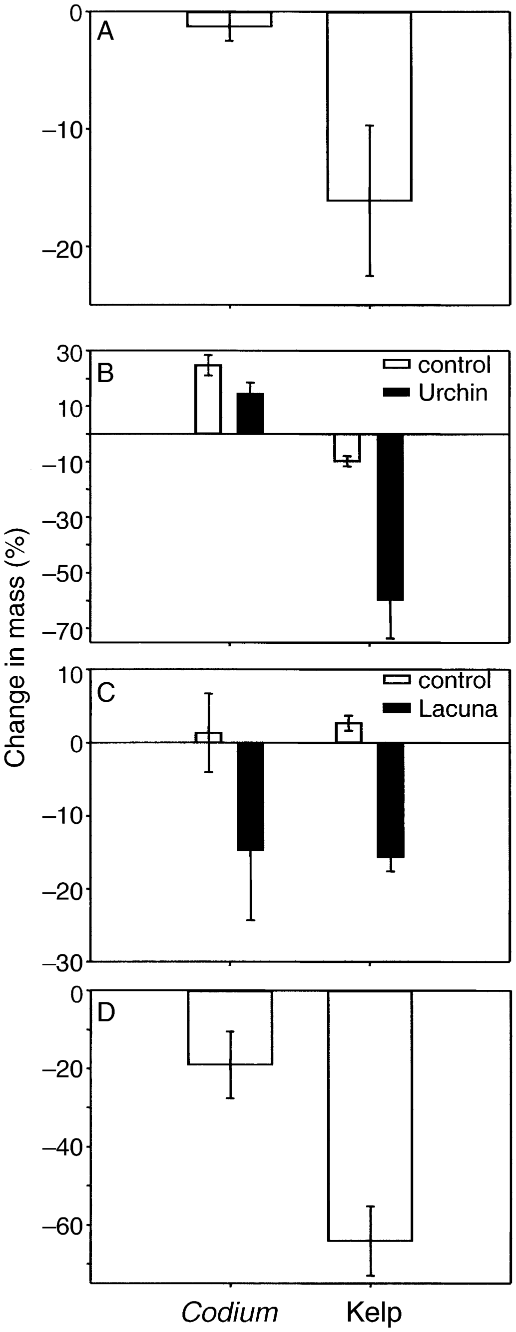

FIG. 5. Palatability of *Codium* compared to kelp (*Laminaria saccharina*) in various tests at Appledore Island in the Isles of Shoals, Gulf of Maine, USA. (A) A choice assay in which both *Codium* and kelp were offered to sea urchins in the laboratory. (B) A no-choice assay in which either *Codium* or kelp were offered to sea urchins in the laboratory. (C) A no-choice assay in which either *Codium* or kelp were offered to snails (*Lacuna vincta*). (D) A field assay in which *Codium* and kelp were exposed to all herbivores. Data are means ± 1 SE of the mass of seaweed consumed during the feeding assay (negative means it was eaten, 0 means no change, and positive means it grew).

TABLE 2. Pearson correlation of algal species or functional form with the ratio of kelp to *Codium* at the Isles of Shoals (Gulf of Maine, USA).

Algal species or functional form	Correlation with kelp: *Codium* ratio
Rhodophyta	
Ceramium rubrum	0.011
Chondrus crispus	−0.414
Corallina officinalis	−0.324
Phycodrys rubens	0.089
Polysiphonia spp.	−0.316
Algal crusts	−0.400
Phaeophyceae	
Agarum cribrosum	0.037
Desmarestia aculeate	−0.061
D. viridis	−0.084
Chlorophyta	
Enteromorpha spp.	−0.101
Ulva lactuca	−0.053
Total filamentous algae	−0.457
Total cover of algae	0.466

(Chapman 1999, Scheibling and Anthony 2001). We argue below that the transformation of *Codium* from a naturalized to invasive species was facilitated by the introduction of *Membranipora* (Fig. 7).

Established kelp forests can resist invasion by *Codium* by monopolizing primary space. Earlier work has demonstrated that the presence of established seaweed beds inhibits the recruitment of *Codium* (Fralick and Mathieson 1972, Mathieson 1989). *Codium* can, however, recruit to gaps in kelp forests after disturbances. Gap formation thus sets the stage for a shift from kelp to *Codium* dominance. Historically, grazing by sea urchins was the major source of biotic disturbance in New England kelp forests (Witman 1987, Johnson and Mann 1988, Keats 1991), and our feeding assays suggest they would avoid *Codium* in favor of kelp. However, recent overexploitation of urchins has greatly reduced their abundance in the Gulf of Maine (Vadas and Steneck 1995, Steneck 1997). Indeed, at the Isles of Shoals localized extirpations of urchins are common (Harris 1997, P. S. Levin, J. A. Coyer, R. Petrik, and T. P. Good, *personal observations*), and we rarely observed urchins in our experimental plots. Presently, defoliation of kelp and gap formation in kelp beds are ostensibly due to encrustation with *Membranipora* because of the negative effects it has on kelp growth and survival. These negative effects are particularly pronounced after winter storms, as *Membranipora*-encrusted blades are less able to withstand water motion (Dixon et al. 1981, Lambert et al. 1992, Scheibling 2000). Additionally, our results showing decreased kelp survival in the presence of both *Membranipora* and *Codium* suggest that once *Codium* meadows are established, the negative impact on kelp—and thus opportunities for *Codium* colonization—are enhanced. Moreover, once kelp densities are reduced, it is possible that the lack of spore

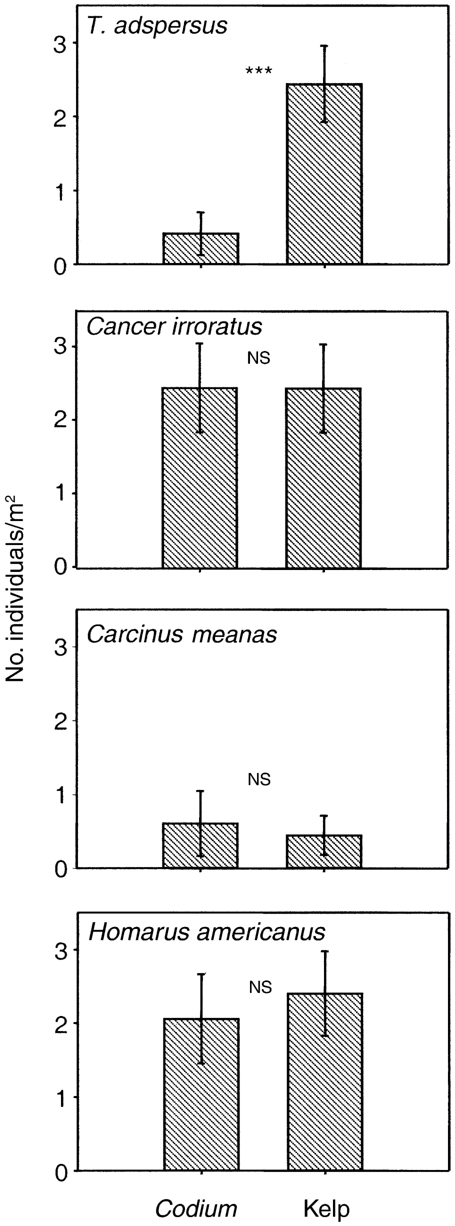

FIG. 6. The number of cunner (*Tautogolabrus adspersus*) and three common decapods colonizing experimental 1-m^2 *Codium* or kelp (*Laminaria saccharina*) plots. Data are means ± 1 SE.

$^{***}P < 0.001$; NS = nonsignificant at $P < 0.05$.

sources inhibits subsequent reestablishment of the population (Reed et al. 1988).

In the absence of *Codium,* however, kelp forests reestablish following even severe defoliation (Berman et al. 1992, Lambert et al. 1992, Scheibling 2000). Indeed, kelp forests still persist in wave-exposed sites at the Isles of Shoals, where *Codium* is probably unable to thrive (see also Trowbridge 1995). In sites where *Codium* and *Membranipora* co-occur, though, gaps are colonized by *Codium,* which in turn inhibits kelp recruitment.

By creating gaps in kelp forests, *Membranipora* facilitates the invasion of *Codium.* However, the relationship between *Codium* and *Membranipora* is indirect and likely both positive and negative in nature. *Membranipora* requires an algal substratum upon which to grow, and at our site occurred almost exclusively on kelps (Berman 1994). *Membranipora* does not occur on *Codium* because of its siphonous anatomy (Berman 1994). Through negative interactions with kelp, *Codium* has an indirect negative effect on *Membranipora.* By facilitating the rise of *Codium* and the demise of kelp, *Membranipora* may contribute to its own local reduction in abundance.

The ultimate impact of *Membranipora* on kelp forests also appears to depend on the presence of *Codium. Membranipora* ostensibly reduces growth and survival of kelp wherever it occurs; however, a reduction in the growth and survival of kelp does not necessarily lead to a shift from kelp to *Codium* dominance. Obviously, if *Codium* is not present or cannot grow successfully at a site then the community-level impact of *Membranipora* is reduced. Thus, *Membranipora* occurs on kelp blades on exposed shores at the Isles of Shoals and causes severe damage to kelp. However, kelp forests remain at such sites because gaps in kelp forests are recolonized by kelp rather than *Codium.* The physical stress associated with waves probably prevents *Codium* from establishing (Trowbridge 1995). Similarly, at a nearby site along the coast of southern Maine, winter storms resulted in the defoliation of *Membranipora*-encrusted kelp in a bed that had persisted for >25 yr (Lambert et al. 1992). However, *Codium* was absent from this site and the kelp forest reestablished in one year (Lambert et al. 1992).

While our data and the work of others support the hypothesis that the invasion of *Membranipora* led to the local rise of *Codium* and ultimately to the declining kelp populations, we cannot definitively rule out other causes for the decline of kelp. Changes in water temperature, for instance, may affect kelp populations (Ottersen et al. 2001). However, trends in climate indices such as the North Atlantic Oscillation do not correspond to changes in the algal assemblage at the Isles of Shoals (Hurrell 1995, Ottersen et al. 2001). Although our results suggest herbivory could cause the patterns we observed, overharvesting of urchins at our study sites suggests this mechanism is unlikely. Additionally, field notes from Arthur Borror (former Associate Director, Shoals Marine Laboratory) produced while he circumnavigated Appledore Island in a dory on an annual basis, show that kelp persisted at our study site for at least 20 yr, even when urchins were much more abundant.

The introductions of *Codium* and *Membranipora* are clearly associated with shifts in the algal assemblage of New England rocky reefs. Kelp and associated ma-

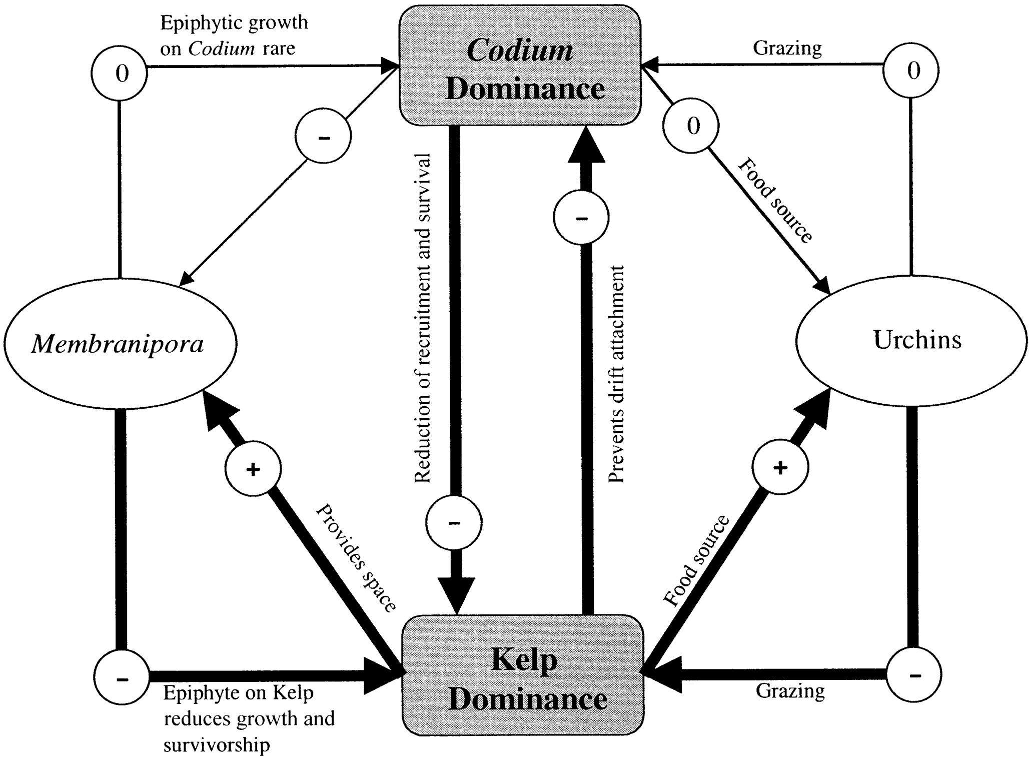

FIG. 7. A conceptual model of the kelp–*Codium–Membranipora* interaction. A "+" indicates a positive interaction, "−" indicates a negative interaction, and "0" indicates no interaction. When urchins are absent (because of overexploitation), *Membranipora* becomes a major agent of disturbance in kelp beds. This disturbance is required as an established kelp bed resists invasion by *Codium.*

croalgae are important nursery grounds for fish (Levin 1991, 1994*b*, Carr 1994, Tupper and Boutilier 1995*a*, Steneck 1997) and decapods (Bologna and Steneck 1993), and also provide important recruitment habitat for numerous other invertebrate species (Duggins et al. 1990). Settling post-larval cunner show a strong preference for understory kelp-bed habitats when settling from the water column (Levin 1991). As a result, the distribution of cunner recruits shows a positive correlation with the percent cover of these habitats, both within (Levin 1991) and among (Levin et al. 1997) sites. In our experiment in which we provided kelp or *Codium* habitat, cunner recruitment was six-fold higher on kelp than on *Codium*. Thus, our results suggest that the shift from kelp to *Codium* dominance may result in a reduction in the settlement of cunner at larger spatial scales.

Alternatively, cunner populations may not decline but may be concentrated into rarer kelp patches. In the absence of density dependence (e.g., Levin 1994*a*), small-scale changes in algal habitat may not be expressed as large-scale changes in cunner density. However, newly settled cunner can experience density-dependent mortality (Tupper and Boutilier 1995*a*), and a shift in the spatial structure of the habitat may amplify this density dependence (Levin et al. 2000). Moreover, after settlement, cunner prey upon animals that themselves depend on understory kelp forest habitat for food (e.g., amphipods, Levin 1994*b*). Such prey species are likely to be less abundant in *Codium* since it is largely unpalatable (Prince and LeBlanc 1992). The shift to *Codium* and corresponding reduction in the prey base for juvenile cunner may therefore result in reduced performance of fish that settle to *Codium* beds.

Although it has been nearly 50 yr since Elton (1958: 31) noted that we were "witnessing one of the great historical convulsions in the world's flora and fauna," we have only a rudimentary understanding of the mechanisms underlying most biological invasions (Ruiz et al. 1997). Several authors have suggested this lack of knowledge arises from the rarity of mechanistic experiments used to study invasions (e.g., Grosholz and Ruiz 1996, Kareiva 1996, Petren and Case 1996). Our experiments suggest that the invasion of one nonindigenous species facilitated the spread of a second introduced species with consequences for the entire community.

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