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NOTE

Changes in the structure of a New England (USA) kelp bed: the effects of an introduced species?*

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ABSTRACT: Since its first observation in the Gulf of Maine (Northwest Atlantic) in 1987, the epiphytic bryozoan *Membranipora membranacea* has become the dominant epiphyte on laminarian kelps. This note describes changes in the structure of a kelp bed at Cape Neddick (Maine, USA) after the coincident increase of *M. membranacea*, evaluates the potential causes of the observed changes, and documents the short-term recovery of the kelp bed. Percent cover, length and density of kelps decreased significantly during 1989 through 1991 The dispersion of *Laminaria* spp. within the kelp bed was clumped on each sampling date at a large spatial scale (meters), while the distribution of *Laminaria* spp. changed from a random pattern to a clumped distribution on a smaller spatial scale (0.25 m^2). There were no consistent differences in storm intensity between years; densities of herbivores within the kelp bed were low and also have not changed between years. The coverage of *M. membranacea* on laminarian kelps increased 3-fold from 1989 to 1990, and the total coverage of other epiphytes decreased. It appears that the presence of *M. membranacea* on kelps has contributed to the defoliation of the kelp bed at Cape Neddick. This phenomenon may have important consequences to organisms that utilize kelps as habitat and shelter

In fall 1990 we noticed changes in kelp beds in the southern Gulf of Maine (Northwest Atlantic) at the Isles of Shoals, and off the coasts of New Hampshire and southern Maine, USA, that consisted of increased abundances of the epiphytic bryozoan *Membranipora membranacea* and the decrease in both density and size of kelp plants within these beds. The physical structure of these beds appeared to change dramatically from being dominated by large laminarian kelps to containing many broken stipes with few intact laminae. We decided to focus our studies on a previously persistent kelp bed at Cape Neddick, Maine, since this kelp bed had been under monthly observation since 1985. After a series of fall storms passed through the area, kelps within the kelp bed retaining intact laminae appeared to be smaller and relatively free of epiphytes, while the majority of drift kelps stranded on nearby beaches were covered by the introduced bryozoan *M. membranacea*. We hypothesized 3 potential causes to account for the changes observed within the kelp bed: (1) grazing by herbivores (*Strongylocentrotus droebachiensis* and *Lacuna vincta*), (2) differences in the severity of fall storms between 1989 and 1990, and (3) increased epiphyte abundances, particularly *M. membranacea* since 1989.

The bryozoan *Membranipora membranacea* was first observed in the Gulf of Maine in 1987 (Lambert 1990), and has since become the dominant epibiont on laminarian kelps (Berman et al. 1992). In the Gulf of Maine *M. membranacea* primarily recruits during the summer and once established on kelps, it often grows to cover entire surfaces of blades (Berman unpubl.).

This note documents the changes in the structure of a kelp bed after the invasion by *Membranipora membranacea*, presents an evaluation of the potential causes of the change, and documents the short-term recovery of the kelp bed. Our data indicate that the defoliation of the kelp bed was not consistent with differences in the intensity of storms between years, but did coincide with a dramatic increase in *M. membranacea*. Therefore, we suggest that the heavy encrustations of *M. membranacea* may have enhanced the susceptibility of kelp fronds to storm damage and infuenced the abundances and identities of organisms that utilize kelps as habitat and shelter.

Materials and methods. Field work was conducted from June to October, 1989 and 1990, and in May and July 1991 in a kelp bed at Cape Neddick, York, Maine, USA (43° 10′ N, 70° 36′ W). The site has large granitic outcrops covered with algae to a depth of 10 m MLW, and below 10 m the substratum is sand. Several age

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** Present address: School of Biological and Medical Sciences, Gatty Marine Lab, University of St. Andrews, St. Andrews KY16 8LB, Scotland, UK classes of laminarian kelps (*Laminaria saccharina* and *L. digitata*) dominate the kelp canopy and these species have been abundant and persistent at this site for at least 27 yr (Mathieson unpubl.).

Percent cover, length of intact lamina, and density of kelps were enumerated in randomly placed 0.25 m^2 quadrats. Randomization was accomplished by pairing random compass headings and distances from a haphazard starting point. Randomized quadrats only contained *Laminaria saccharina*. Percent cover of the kelp canopy was determined by recording the presence of kelps under each of 40 points within quadrats. Length was determined as the total distance between holdfast and tip of lamina, and length measurements were taken of all kelps within each quadrat.

The dispersion of kelps within the kelp bed was determined at 2 spatial scales. *T*-square sampling was used to test for random spatial patterns at a relatively large scale (meters) using Hines' test statistic for randomness (h_T) (Krebs 1989). Smaller scale spatial patterns were examined by enumerating the number of kelp plants in 0.25 m^2 quadrats, and then using the standardized Morisita index (I_d) to test for random distributions (Krebs 1989).

Weather data for the southern Gulf of Maine were obtained from the U.S. National Climatological Data Center. The site is moderately exposed to waves and wind from the Northwest to East, thus we examined variation in wind speed and number of days the wind blew from these directions between seasons and years to compare the intensity of storms in 1989 when the kelp bed persisted and in 1990 when it was defoliated.

The percent cover of epiphytes (the bryozoans *Membranipora membranacea, Electra pilosa* and the hydroid *Obelia geniculata*) on large kelps (> 800 cm^2) was quantified by randomly collecting 10 blades on 3 occasions during September and October 1989 and on 4 occasions during September to November 1990. We documented the coverage of all epiphytes on kelps to determine whether their abundances were affected by the invasion of *M. membranacea*. The outlines of each kelp blade and attached epifauna were traced onto paper and their areas were determined by digitizing them with a graphics tablet.

Analyses of variance were used to assess differences among seasons in percent cover, blade length and density of kelps, percent cover of epiphytes, and wind velocities. Quadrat counts were $\log(x+1)$ transformed and proportions were arcsine transformed to correct unequal variances (Bartlett's test, $p < 0.05$) (Zar 1984). Post-hoc multiple comparisons on percent cover of epiphytes were performed using Tukey's HSD test and unequal sample sizes were corrected with a Tukey-Kramer adjustment (Wilkinson 1990). Multiple Mann-Whitney *U*-tests with a Bonferonni adjustment to protect the experiment-wise alpha (Wilkinson 1990) were used to analyze data on epiphytes that did not conform to assumptions of least squares analysis.

Results. The structure of the kelp bed at Cape Neddick changed dramatically from 1989 to 1991. In summer 1990 the percent cover of kelps on the rocky substrata, and the length of kelps was greater than on other sampling dates (Fig. 1A, B). In addition, the density of intact kelps declined from summer 1990 to spring 1991. However, unlike the pattern exhibited for percent cover and length of kelps, the density of kelps in summer 1991 returned to a value similar to that observed in summer 1990 (Fig. 1C). The dominant organisms on primary substrata immediately after the observed changes were filamentous red algae and crustose coralline algae, which comprised the previous understory species within the kelp bed.

The dispersion of kelps did not change and was clumped at each sample date at the large spatial scale (summer 1990: $h_T = 1.72$, $p < 0.005$; fall 1990: $h_T = 1.98$, $p < 0.001$; spring 1991: $h_T = 1.62$, $p < 0.005$). However, at the smaller scale, the spatial pattern changed over time; kelp plants were randomly dispersed ($I_d = 0.417$) in summer 1990, but clumped in fall 1990 ($I_d = 0.518$) and spring 1991 ($I_d = 0.558$).

Grazers of kelps were scarce within the kelp bed during the study period. Sea urchins averaged 0.47 ind. m^{-2} shortly after the defoliation of the kelp bed and *Lacuna vincta* averaged 0.16 snails (SE = 0.08) per kelp blade (n = 25) during June to August 1989.

Weather patterns did not differ significantly in summer and fall between 1989 and 1990. Wind speed was significantly greater in the fall than in the summer of each year, and this difference was greater in 1990 than in 1989 (Table 1). There was no significant difference in the number of days the wind blew from the NW to E in the summer and fall of 1989 and 1990 ($\chi^2 = 0.092$, $p = 0.762$).

The abundance of *Membranipora membranacea* on kelps increased 3-fold from 1989 to 1990. In September 1990 a significantly greater amount of *M. membranacea* (52.5 % ± 8.5) covered the surfaces of kelps at Cape Neddick than at any other time (Tukey's p = 0.002). In October and November 1990 after a series of fall storms passed through the area, only 22.7 % ± 6.5 of surfaces of kelps were covered by *M. membranacea*; this was not significantly different than the amount of *M. membranacea* (21.2 % ± 3.9) on kelps in fall 1989 (Tukey's p = 0.973) (Fig. 2). The combined coverage of *Electra pilosa* and *Obelia geniculata* decreased (Fig. 3), but only the abundance of *O. geniculata* showed a significant decline between years (p = 0.013).

Discussion. Since its first observation in the Gulf of Maine in 1987 the epiphytic bryozoan *Membranipora membranipora* has become the dominant epiphyte on

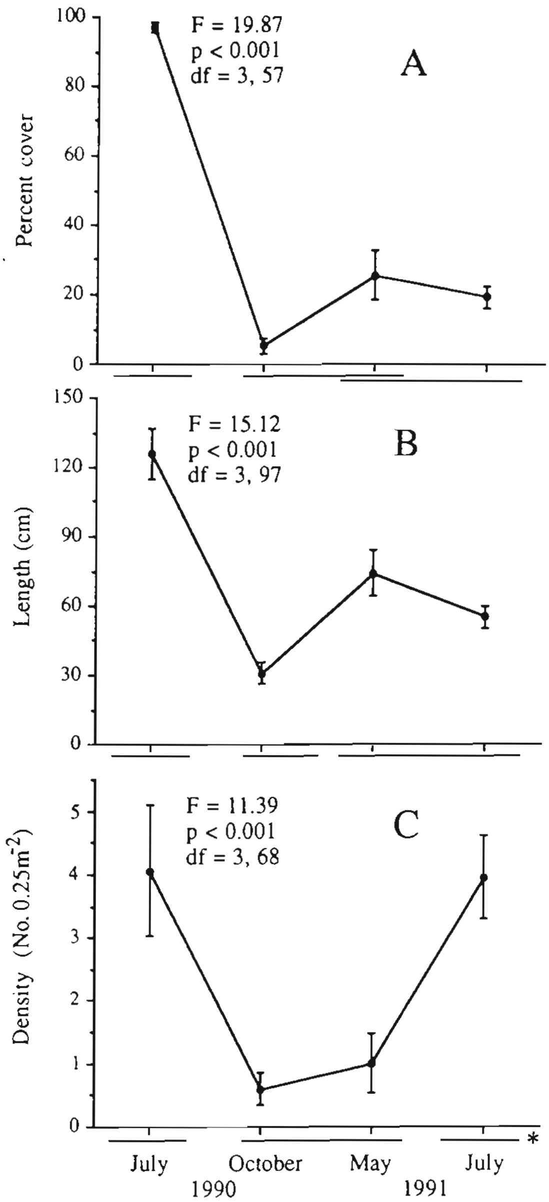

Fig. 1. *Laminaria* spp. Mean percent cover (± SE), length (± SE) and density (± SE) of kelp on rocky substrata in randomly sampled 0.25 m^2 quadrats in 1990 and 1991. Significant differences between seasons by Tukey-Kramer HSD multiple comparison test are indicated by horizontal lines ($p < 0.04$). *Density of kelps in summer 1990 and summer 1991 is not significantly different

laminarian kelps (Berman et al. 1992). Numerous observations from researchers report dramatic increases in the abundance of *M. membranacea* on kelps in 1990 at Damoriscotta Estuary, Maine (S. Craig pers. comm.), Cashes Ledge, Maine (L. Kintzing pers. comm.), the Isles of Shoals and coastal New Hampshire (P.S.L. pers. obs.), and Cape Cod Canal, Massachusetts, USA (E. Enos pers. comm.). In particular, at Cape Cod Canal, kelps became essentially absent on

Table 1. Mean velocities (±SE) of wind from the NW and E at Cape Neddick in summer and fall 1989 and 1990. (Between years: $F_{1,596}$ = 1.797, p = 0.181; between seasons: $F_{1,596}$ = 6.606, p = 0.010)

Year	Wind velocity (naut. miles h^{-1}) Summer	Fall
1989	7.61 (0.31)	8.11 (0.28)
1990	6.54 (0.22)	8.69 (0.29)

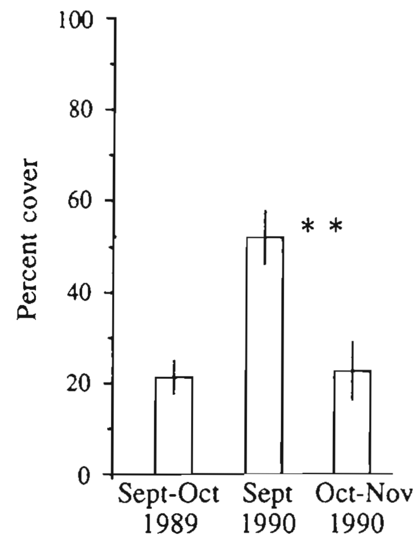

Fig. 2. Mean percent cover (± SE) of *Membranipora membranacea* on large *Laminaria saccharina* blades sampled in September–October 1989 and September–November 1990. Sample sizes: September–October 1989, n = 27; September 1990, n = 20; October–November 1990, n = 20. **$F_{2,57}$ = 6.763, p = 0.002

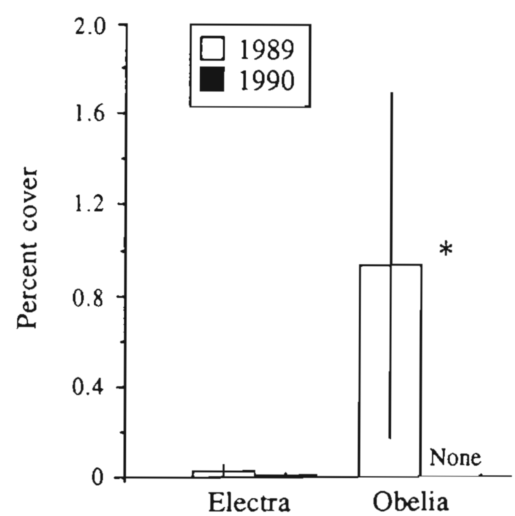

Fig. 3. Mean percent cover (± SE) of *Electra pilosa* and *Obelia geniculata* on large *Laminaria saccharina* blades sampled in September–October 1989 and September–October 1990. Sample sizes: 1989, n = 24; 1990, n = 13. *p = 0.013

hard substrata which had previously harbored lush beds of *Laminaria* spp. before the appearance of *M. membranacea*. These observations along with our data indicate that the invasion of *M. membranacea* is not strictly a local phenomenon and has had at least an important short-term impact on New England kelp beds.

Substantial seasonal, as well as interannual changes in the structure of the kelp bed at Cape Neddick were documented during 1990 and 1991. Seasonal changes in the percent cover of kelps are well known. Witman (1987) documented a 33 % reduction in percent cover of kelps from July to November 1983 in a site near our Cape Neddick location. He attributed the loss of kelps to dislodgement caused by fall storms, which included a major storm from the northeast during October 1983. In fact, he found entire kelp plants, complete with holdfasts, on nearby beaches after storms. In contrast, we found a much greater (90 %) reduction in canopy cover than Witman (1987). Furthermore, the loss of canopy at Cape Neddick occurred by blade loss only; the stipes and holdfasts were left intact. Seasonal variation in the length and density of kelps has also been reported (Parke 1948, Kain 1979, Chapman 1984). As expected, we found kelps to be longest in summer after a period of rapid growth, but the shortest lengths observed in fall 1990 are inconsistent with patterns elsewhere (Lüning 1979, Johnson & Mann 1988). Additionally, fall and winter storms normally reduce the number of kelps (Witman 1987, Johnson & Mann 1988), but not to the extent we report here. The return of the density of kelps in spring 1991 to initial levels observed in 1990 suggests a recovery of the kelp bed. However, the shorter lengths and low percent cover indicate that the kelp bed is composed primarily of new recruits.

Herbivore densities are low at this site. In June 1983 Witman (1987) found 20 to 280 urchins m^{-2} at a nearby offshore site and in 1985 Child et al. (1985) found 98 and 50 urchins m^{-2} at 2 areas around Cape Neddick compared to an average of 0.47 urchins m^{-2} in our study. Broken stipes dominated the substratum at Cape Neddick, thus the damage was inconsistent with urchin grazing (Lawrence 1975, Schiel & Foster 1986). The damage was more similar to that found on plants heavily grazed by *Lacuna vincta* (Fralick et al. 1974), except the remaining fronds and stipes were not riddled with small holes and *L. vincta* was much less abundant than reported by Fralick et al. (1974). Thus, grazing by herbivores does not appear to be an important agent contributing to the changes we observed in the kelp bed.

The association between *Membranipora membranacea* and kelps in other locations has been well documented (Woollacott & North 1971, Bernstein & Jung 1979) and studies have demonstrated that encrustations increase the effects of wave surge and storm disturbance on their hosts (Woollacott & North 1971, Lobban 1978, Dixon et al. 1981). Calcareous encrustations make the laminae brittle and inflexible, which can cause plants to fracture when exposed to wave surge. Dixon et al. (1981) showed in a transplant experiment that large encrustations of *M. membranacea* increase blade loss in *Macrocystis pyrifera*. They attributed intensified blade loss to physical damage from waves and surge, and to foraging activities of fish tearing the kelps when feeding upon the bryozoan (Yoshioka 1973, Bernstein & Jung 1979). At Cape Neddick, storms in early fall 1990 impacted the kelp bed and caused a 50 % reduction in coverage of *M. membranacea* on kelps (Fig. 2).

Why might *Membranipora membranacea* be more deleterious to New England kelp beds than to populations of kelps in other locations? In other areas where *M. membranacea* is well established dorid nudibranchs are abundant and feed upon the bryozoan (Seed 1976, Todd 1981, Harvell 1984, Yoshioka 1986). Predation pressure by nudibranchs may keep bryozoans from covering entire fronds and the majority of kelps within a stand. In the Gulf of Maine *M. membranacea* does not yet appear to have any predators. Nudibranchs have not been found on any colonies as yet, and fish predation has not been observed. Thus, at present the growth of colonies of *M. membranacea* appears to be unrestricted by predation and competition (Berman et al. 1992).

We suggest that the invasion of *Membranipora membranacea* has had at least a severe short-term impact on the kelp population at Cape Neddick. *M. membranacea* and its subsequent increase in abundance coincided with changes in the kelp bed and apparently have increased the importance of storms to the dynamics of this kelp population. We believe that the possibility of disease contributing to these changes within the kelp bed is unlikely because the damage was not a slow deterioration over an extended time, but rather a dramatic removal of kelps over a few weeks. Although this kelp bed recovered in terms of density during the spring 1991 recruitment period, the presence of *M. membranacea* may become an important factor to the persistence of kelp beds in future years when strong storms and high coverage of *M. membranacea* co-occur.

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