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Recent Invasions of the Gulf of Maine: Three Contrasting Ecological Histories

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Abstract: *Introduced species are common members of estuarine communities where their role as competitors and predators is of concern. This paper examines the invasion of Gulf of Maine benthic habitats by the ecologically similar alien invertebrates Styela clava, Botrylloides diegensis, and Membranipora membranacea.*

Styela clava increased slowly in abundance at study sites in Beverly, Massachusetts and Portsmouth, New Hampshire. We found no evidence of competitive dominance by S. clava, even though it is the competitive dominant in similar habitats elsewhere. Botrylloides diegensis rapidly became a dominant species after its arrival in the Great Bay Estuary, but this dominance was short-lived. B. diegensis persists in the estuary as an early colonist of primary space and as an epibiont on secondary substrates in established communities. Membranipora membranacea became the dominant epiphyte on laminarian kelps within two years. Although M. membranacea overgrew the native epiphytes Obelia geniculata and Electra pilosa in the overwhelming majority of encounters, these native species are more common on other algal hosts. Therefore, competitive dominance is not likely a factor in the successful invasion of the Gulf of Maine by M. membranacea.

These species provide evidence for opposing views of the role of competition in mediating community invasion. We show that ecological similarity among species is not an accurate criterion to predict either the mechanism of invasion or the means of persistence. In addition, these data indicate that biological invasions must be examined on broad spatial and temporal scales; short-term or narrowly focused studies can lead to incorrect conclusions.

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Resumen: *Las especies introducidas son miembros comunes de las comunidades estuariales donde su rol como competidores y consumidores es preocupante. Este trabajo examina la invasión de los hábitats bénticos del Golfo de Maine por los invertebrados introducidos y ecológicamente similares Styela clava, Botrylloides diegensis y Membranipora membranacea. Styela clava aumentó en abundancia en los sitios de estudio localizados en Beverly (Massachusetts) y Portsmouth (New Hampshire). No encontramos evidencias que indicaran una dominancia competitiva por parte de S. clava, a pesar de que es una especie que domina competitivamente hábitats similares en otras regiones. Botrylloides diegensis se transformo rápidamente en una especie dominante después de su arribo al Estuario de la Bahía Grande, pero su dominancia fue de corta duración. B. diegensis persiste en el estuario como colonizador temprano de espacios primarios y como epibionte sobre sustratos secundarios en comunidades establecidas. Membranipora membranacea se transformó, en un período de dos años, en la epífita dominante sobre kelps Laminariales. Si bien M. membranacea creció sobre las epífitas nativas Obelia geniculata y Electra pilosa, en la gran mayoría de las veces que entraron en contacto, estas especies nativas son más comunes sobre otros hospedantes algales. Es probable, por lo tanto, que la dominancia competitiva no sea un factor en la invasión exitosa del Golfo de Maine por parte de M. membranacea. Estas especies proveen evidencia a favor de puntos de vista opuestos sobre el rol de la competencia en la mediación de la invasión de comunidades. Nosotros demostramos que la semejanza ecológica entre especies no es un criterio apropiado para predecir ni los mecanismos de invasión ni los medios de persistencia. En forma adicional, estos datos indican que las invasiones biológicas deben ser examinadas en escalas temporales y espaciales amplias; estudios a corto plazo o estrechamente enfocados pueden llevar a conclusiones erróneas.*

Introduction

Studies of introduced species have provided a range of results with respect to the effects of invading species on the native community (Elton 1958). Some studies found that invaders have had a measurable, often devastating, impact on the native community. Effects range from shifts in resource utilization patterns by indigenous species (Mortgan et al. 1978; Race 1982; Brenchley & Carlton 1983), to alteration of food webs (Zaret & Paine 1973; Herbold & Moyle 1986), to local or regional extinction of native species (Clarke et al. 1984). Invading species succeed at the expense of native species by out-competing native species for resources or by preying upon them. In contrast, other investigations documented few changes in the native community as a result of species invasions (Simberloff 1981; Roughgarden 1986; Berman & Carlton 1991). In these cases, invasive species succeeded by colonizing habitats with resources (such as food or space) unused by native species.

In recent years a number of species have been introduced into the Gulf of Maine. These species include the European nudibranch *Tritonia plebeia* (Allmon & Sebens 1988), the Asian green alga *Codium fragile tomentosoides* (Carlton & Scanlon 1985), the Asian and Californian tunicates *Styela clava* and *Botrylloides diegensis*, respectively (Carlton 1989), and the European ectoproct *Membranipora membranacea* (Lambert 1990). This study focuses on the invasion of the southern Gulf of Maine by the sessile invertebrates *Styela clava*, *Botrylloides diegensis*, and *Membranipora membranacea*. The goals of this study were to document the arrival and subsequent changes in abundance of these three species, and to examine the implications of the mechanisms of successful invasion represented by these three species in the context of marine benthic community structure.

Study Species

Styela clava is believed to have come to the Atlantic coast of North America from Japan via Europe sometime in the late 1960s (Carlton, personal communication). Carlton states that the first observation of *S. clava* was on Long Island, New York, in 1973, and that by 1988 its range expanded to include the North American coast from Connecticut to Maine. Carlton also reports that *S. clava* is a competitive dominant, occurring in dense stands in regions previously dominated by *Mytilus edulis*.

Botrylloides diegensis was released by a biologist into Eel Pond, Woods Hole, Massachusetts, in the summer of 1972 (Carlton 1989). It spread rapidly, both north and south, and now occurs from Long Island Sound to Casco

Bay, Maine. Carlton stated that *B. diegensis* is a space dominant on hard substrates throughout southern New England.

Membranipora membranacea occurs both in Europe (Ryland 1970; Eggleston 1972) and on the Pacific coast of North America (Osburn 1953; Yoshioka 1982a,b). Scattered reports of the occurrence of *M. membranacea* on the Atlantic coast of North America have been published prior to this report. Osburn (1944) stated that an ectoproct identified as *M. membranacea* occurred on the marsh plant *Ruppia maritima* in Chesapeake Bay at salinities of 6–13‰. Dudley (1973) concluded that this report was in error, however, and that Osburn's *M. membranacea* was probably an undescribed species of *Membranipora*. More recently, Walters & Wetthey (1986) reported collecting an ectoproct they called *M. membranacea* in intertidal habitats: on *Fucus* spp. at Harpswell, Maine and Durham, New Hampshire, and on *Chondrus crispus* in Long Island Sound. Based on examination of historical herbarium specimens and personal observations, we found that the common Membraniporine species on fucoid algae at Durham, New Hampshire is *Electra pilosa*; we found no specimens which resemble *M. membranacea*. Based on this and communications with the authors, this latest report is believed to be in error. Therefore, we feel that the species we call *Membranipora membranacea* is not the same as that identified above, and that the species we are describing is in fact a new arrival in the Gulf of Maine.

Materials and Methods

Species arrivals in the New Hampshire and southern Maine coastal zones were documented primarily by personal observations. The observations, beginning in 1969, include extensive collections from a variety of habitats, dive logs, photographs, and videotapes taken within the southern Gulf of Maine study area. Patterns of abundance were documented using the methods outlined below.

Styela clava was gathered as part of collecting trips to marinas in Beverly, Massachusetts (1–3 per year) and Portsmouth Harbor, New Hampshire (5–20 per year), since the spring of 1970. These data form the basis for documenting changes in this species' abundance. Regular monitoring of a panel experiment established at Newcastle, New Hampshire, in the winter of 1979 (see description below for *Botrylloides diegensis*) has provided additional data on the population of this tunicate at the mouth of Portsmouth Harbor, New Hampshire.

The appearance and pattern of abundance of *Botrylloides diegensis* was documented using two panel studies conducted in Portsmouth Harbor, New Hamp-

shire. A long-term study was initiated in 1979 (Harris & Irons 1982). Ninety-six 0.1 m² plexiglass panels were established at the Coast Guard Station at Newcastle, New Hampshire. They were photographed seasonally for four years, and are now photographed annually. Winter photographs were selected from the overall data pool because they had the highest abundance of compound ascidians. From these, a stratified subsample of yearly photographs was selected on the basis of photographic clarity. Percent cover of *B. diegensis* was determined by projecting the image onto a grid of 1 m² boxes and tallying all boxes that were one-quarter covered by *B. diegensis*. Differences between percent cover in both substrate angle and time were compared using a two-way ANOVA (on arc-sine transformed data) and A matrices to test hypotheses of interest.

The second panel study was conducted at the Commercial Fishing Pier, Portsmouth, New Hampshire. This short-term study documented the effect of micro-predators on the sequence of species appearances in early successional fouling communities (Lambert 1985). Percent cover of all sessile organisms was determined by point analysis on a grid of 400 dots and analyzed by a two-way ANOVA on arc-sine transformed data (Zar 1984).

The timing and pattern of the early invasion history of the ectoproct *Membranipora membranacea* was documented as part of a study conducted at Cape Neddick, York, Maine, from June 1987 through May 1989 (Lambert 1990). *Laminaria* spp. blades ($n = 5$), covered with the hydroid *Obelia geniculata*, were collected twice monthly with no reference to ectoproct colonies present on the blade. Ectoproct colony areas (both *M. membranacea* and *Electra pilosa*) were quantified by tracing them onto paper and measuring them (in square centimeters) with a microcomputer and digitizing pad. Data were standardized to 100 cm² of kelp surface area to adjust for different sampling units (Seed et al. 1981). Differences in ectoproct abundance between the first (June 1987–May 1988) and second (June 1988–May 1989) years were determined using a *t*-test on the standardized data.

The frequency of occurrence of *Membranipora membranacea*, *Obelia geniculata*, and *Electra pilosa* on subtidal algae was compared at Cape Neddick from Fall 1988 through Spring 1989. Samples of *Laminaria saccharina* and *Agarum cribrosum* were haphazardly collected by SCUBA divers. *Chondrus crispus* samples were obtained by collecting all *C. crispus* plants from within ten replicate (0.1 m² quadrants). The relative abundance of these epiphyte species on the three algal substrates was compared using Chi-Square statistics.

In order to compare the abundance of *Membranipora membranacea* on large (more than 60 cm total length) and small (less than 50 cm total length) *Lami-*

naria saccharina, five replicate samples of fifty sporophytes of each size class were collected from Cape Neddick in October 1988. Chi-Square statistics were used to determine whether a significant difference in percent occurrence of *M. membranacea* existed between the two algal substrates.

A comparison was made between the relative size of *M. membranacea* colonies on sporophytes of *Laminaria saccharina* and *Agarum cribrosum*. Samples of these two algae were collected in December 1988 at Cape Neddick. These blades were brought to the lab, where *M. membranacea* colonies were sorted into size classes: less than 100 cm², 101–1000 cm², 1001–10,000 cm², and more than 10,000 cm². The frequency of colonies in each category was compared among algal substrates using Chi-Square statistics.

Seasonal and exposure differences in the percent occurrence of *Membranipora membranacea* were examined by collecting samples of *Laminaria* spp. at exposed and protected locations at Cape Neddick and at the Isles of Shoals during Fall 1988 and Spring 1989. The protected site at Cape Neddick is a shallow kelp bed at the back of the cove formed by Nubble Island and Cape Neddick; the exposed site is in the zone of overlap of distribution of *Laminaria* spp. and *Agarum cribrosum* at the semi-exposed northwest corner of Nubble Island. Samples from the exposed site at the Isles of Shoals were collected at the base of a rock ledge extending downward from the southeast side of Star Island. The samples from the protected site at the Isles of Shoals were made in Gosport Harbor at a site off Smuttynose Island.

The relative competitive abilities of *Membranipora membranacea*, *Electra pilosa*, and *Obelia geniculata* were documented using kelp blades collected bi-monthly at Cape Neddick from June through October 1989. Blades were scanned under a dissecting microscope, and the outcome of each encounter between each *M. membranacea* colony and any other colony of *M. membranacea*, *O. geniculata*, and *E. pilosa* was recorded. A win was recorded when one *M. membranacea* colony overgrew the growing edge of another colony by more than 3 millimeters. This distance was used to determine a victory because it is greater than the length of a cystid of both *M. membranacea* and *E. pilosa*, and we felt overgrowth of more than one cystid was necessary to identify a win situation. A loss was recorded when the growing edge of a *M. membranacea* colony was overgrown by any other colony by more than 3 mm. A standoff was recorded when no overgrowth had occurred. Encounters with overgrowth less than 3 mm were not included in the analysis.

In all cases, algal blades were maintained in a closed sea water system at the University of New Hampshire (12° C and 34‰). Counts were made and measurements taken within 24 hours of collection.

Results

In the spring of 1970, *Styela clava* was rare on floats in marinas in Beverly, Massachusetts. At that time, a one-hour search by ten students resulted in the location of 1–3 individuals. By the late 1970s, *S. clava* had become common, and it is now abundant on primary space.

The first specimen of *Styela clava* we located in New Hampshire was found on a float in Portsmouth Harbor in 1985. As of November 1990, *S. clava* had not been found on the panels located at the Coast Guard Station at Newcastle, New Hampshire. The size of the northern population of *S. clava* is, therefore, not increasing as rapidly as the population in Beverly, Massachusetts.

The first specimens of *Botrylloides diegensis* were collected in the Great Bay Estuary at Fox Point and in *Zostera marina* beds in the summer of 1981. *B. diegensis* colonies first appeared on the long-term panels in 1982; it became a major space occupant in 1985 (Fig. 1). A significant ($p < 0.05$) interaction was found between surface angle and year. Significant differences ($p < 0.05$) were found between all three surface angles in 1985 and between lower, vertical, and upper surfaces in 1986. *B. diegensis* is currently present on the panels in low numbers of small colonies, primarily as an epiphyte on mussels.

Further evidence of the dominance of space by *Botrylloides diegensis* was shown by the short-term panel study in 1984. *B. diegensis* overwhelmingly dominated lower surfaces (mean 68.6, SE = 3.9) when compared to upper surfaces (mean 3.8, SE = 2.8). Levels decreased in 1985; *B. diegensis* covered 30.6% (SE = 4.9) on lower surfaces and 9.6% (SE = 3.2) on upper surfaces.

Membranipora membranacea was first observed on

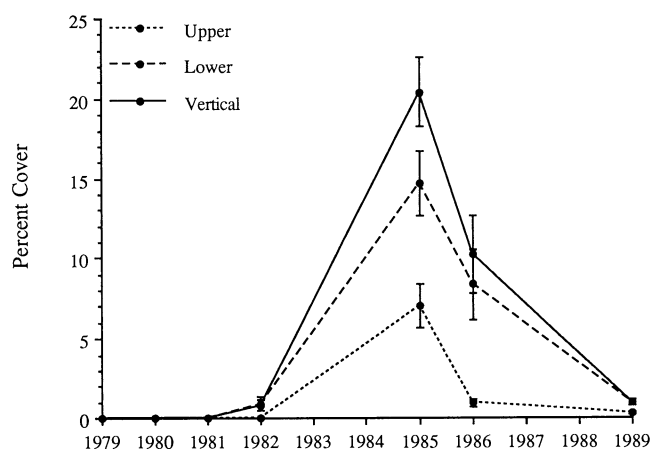


Figure 1. Mean percent cover (\pm SE) by *Botrylloides diegensis* on plexiglass panels located under the Coast Guard Pier at Newcastle, New Hampshire, from 1979 through 1989.

Laminaria saccharina blades at the Isles of Shoals in August 1987. Although this ectoproct could be seen at Cape Neddick later that same year (W. Lambert, personal observation), the first colonies collected in the samples taken at Cape Neddick were found in July 1988 (Fig. 2). During the study period, the ectoproct abundance on *Laminaria* spp. blades increased by an order of magnitude. There was no change in the abundance of *Electra pilosa* on kelp blades between years (t -test, $p = 0.118$), and the increase in ectoproct cover was due solely to the invasion by *M. membranacea* (t -test, $p < 0.05$).

Significant differences in percent occurrence of *Obeilia geniculata*, *Electra pilosa*, and *Membranipora membranacea* were found among the three algal substrates ($p < 0.05$). *O. geniculata* was most common on *Agarum cribrosum*, and *E. pilosa* was the dominant epiphyte on *Chondrus crispus*. *M. membranacea* showed its greatest abundance on *Laminaria* spp. blades (Fig. 3), occurring on 1 per 1790 *C. crispus*, 25 per 176 *A. cribrosum*, and 350 per 685 *Laminaria saccharina*.

M. membranacea had a significantly ($p < 0.05$) higher percent occurrence on large *Laminaria saccharina* blades (mean 84.46, SE = 0.06) than on small blades (mean 15.89, SE = 0.048). In addition, *M. membranacea* colony size was significantly larger on *L. saccharina* than on *A. cribrosum* ($p < 0.05$) (Fig. 4); this pattern of larger colonies on *Laminaria* spp. was observed in all samples collected during the study period. In addition, it was rare to find a blade of *A. cribrosum* completely covered by *M. membranacea*, while co-occurring *Laminaria* spp. blades were often over 90% covered by this ectoproct.

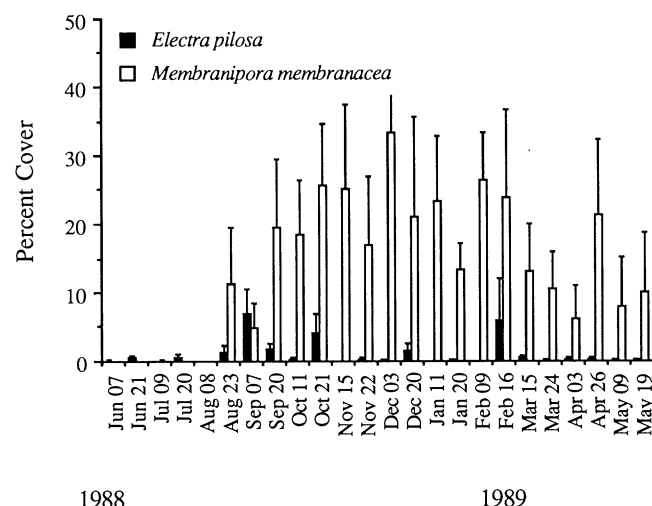


Figure 2. Mean percent cover (\pm SE) of ectoprocts on *Laminaria* spp. blades collected at Cape Neddick, York, Maine (after Lambert 1990).

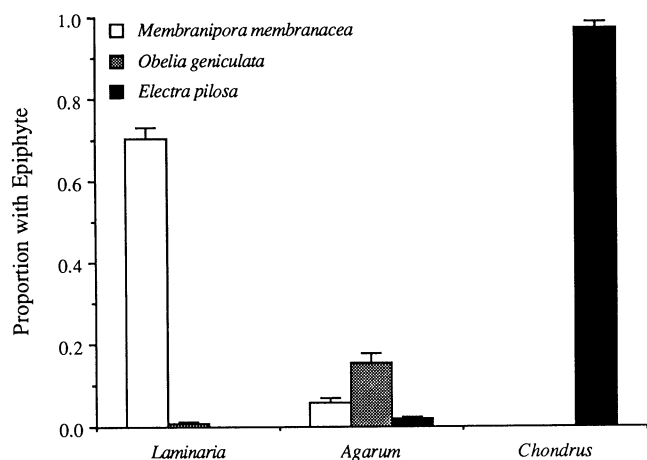


Figure 3. Percent total occupancy (\pm SE) by the epiphytes *Membranipora membranacea*, *Obelia geniculata*, and *Electra pilosa* on *Laminaria saccharina* (n = 685), *Agarum cribrosum* (n = 176) and *Chondrus crispus* (n = 1,790).

The relative abundance of *Membranipora membranacea* varies among sites and between seasons (Fig. 5). At both locations, *M. membranacea* was more common at exposed sites than at protected sites. At Cape Neddick, *M. membranacea* showed greater abundance in the fall than in the spring, while the pattern was reversed at the Isles of Shoals.

The competitive ability of *Membranipora membranacea* compared to *Electra pilosa* and *Obelia geniculata* was found to be high (Fig. 6). Encounters between two *M. membranacea* colonies rarely resulted in over-

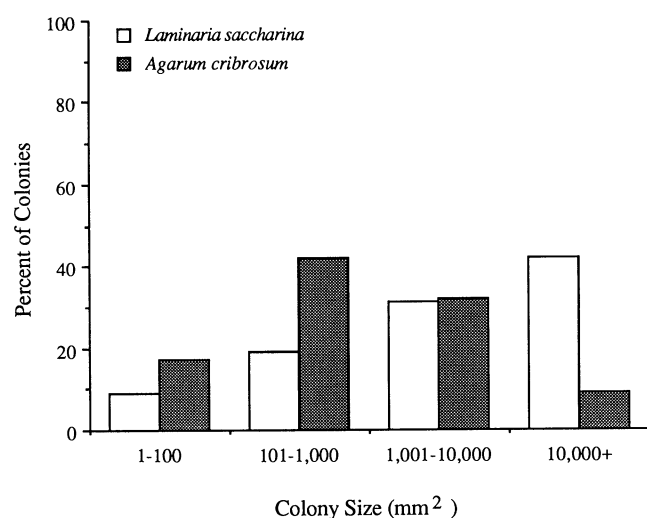


Figure 4. Size distribution of *Membranipora membranacea* colonies on *Laminaria saccharina* (n = 365) and *Agarum cribrosum* (n = 169) collected at Cape Neddick, York, Maine.

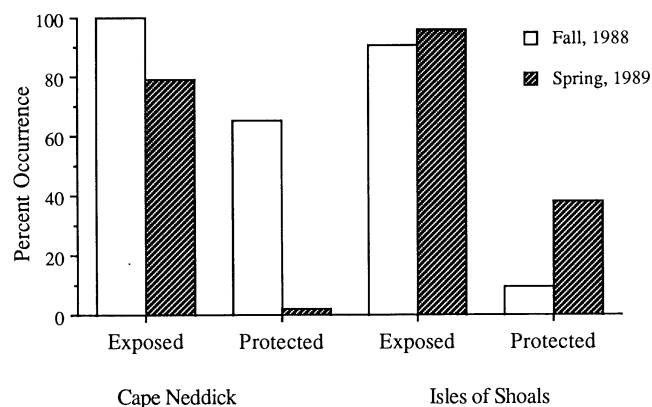


Figure 5. Percent occurrence of *Membranipora membranacea* on *Laminaria* spp. blades collected at the exposed and protected sites at Cape Neddick, York, Maine, and at the Isles of Shoals, Maine.

growth. In contrast, *M. membranacea* overgrew *E. pilosa* and *O. geniculata* in the majority of all encounters with these organisms (67% and 97%, respectively).

Discussion

During the last twenty years, three sessile invertebrates have become conspicuous members of benthic and fouling communities in the southern Gulf of Maine. The solitary tunicate *Styela clava* was first found at Beverly,

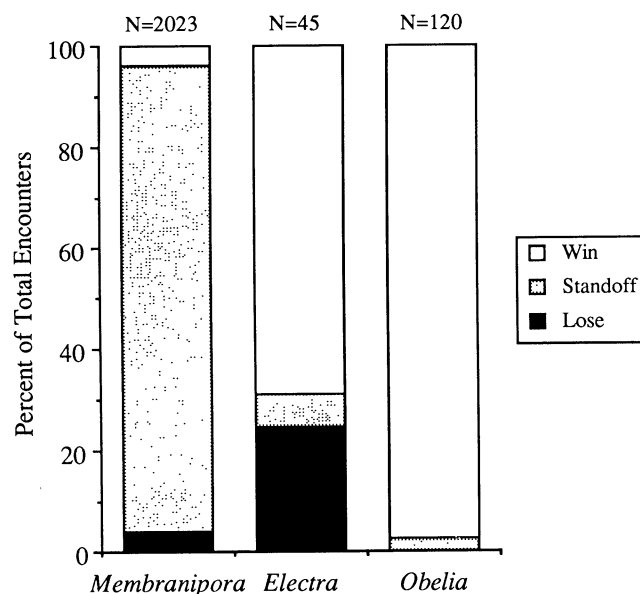


Figure 6. Percent of total encounters between *Membranipora membranacea* and other kelp epiphyte species that resulted in overgrowth by *Membranipora* (Win), overgrowth by the other epiphyte (Lose), or no overgrowth (Standoff).

Massachusetts in 1970. This record predates Carlton (1989) by three years. Populations of *S. clava* slowly increased in fouling communities at Beverly, Massachusetts and Portsmouth, New Hampshire, to present abundances. *Botrylloides diegensis* arrived in the Great Bay Estuary in 1981, and by 1985 it had become one of the dominant encrusting species in fouling communities. *B. diegensis* then decreased slowly in abundance; it is now a common early colonizer of hard substrates and occupier of secondary substrates in established communities. Colonies of *Membranipora membranacea* were first observed at the Isles of Shoals in 1987. In three years *M. membranacea* has become the dominant kelp epiphyte off the coast of New Hampshire and southern Maine. It appears to be spreading both north (L. Kintzing & S. Craig, personal communication) and south (J. Witman & J. Winston, personal communication).

Two views exist regarding competitive mechanisms used by nonindigenous species for successful invasion. One view considers the success of invaders to arise from the competitive dominance of the invader over ecologically-similar native species. This invasion mechanism produces dramatic effects on the native community (Elton 1958). The other view considers the success of introduced species to arise from low faunal diversity in the invaded community, where the invader can enter and find unused or underused resources. Species invading these habitats are added to the community without necessarily altering it (Birch 1979; Carlton 1979; Berman & Carlton 1991).

We find evidence for both of the above mechanisms among the three species studied. South of New Hampshire, *Styela clava* represents the competitive dominance view (Carlton 1989). In more northern locations, however, populations of *S. clava* have not reached the same high densities. Perhaps physical conditions within the Great Bay Estuary inhibit successful establishment of *S. clava*. The long-term effects of *S. clava* on northern fouling communities are unknown. If it remains rare, its impact is expected to be minimal; *S. clava* will be one of the many short-lived species that coexist in fouling communities. However, if the northern populations increase as they did in Beverly, Massachusetts and further south, we predict that *S. clava* will competitively exclude *Mytilus edulis* and *Metridium senile* from many subtidal surfaces.

When *Botrylloides diegensis* arrived it filled the role of competitive dominant (Lambert 1985); in 1984 it overgrew both encrusting and erect ectoproct, *Obelia* spp., *Tubularia* spp., *Semibalanus balanoides*, and *Botryllus schlosseri*. By 1985, the pattern changed; while it remained a competitive dominant, cover by *B. diegensis* decreased by 50%. *B. diegensis* is now persisting by colonizing primary space in early successional communities (J. Berman & L. Harris, unpublished data) and secondary space in established communities (herein).

Two distinct possibilities exist with respect to the long-term effects of *B. diegensis* on benthic and fouling communities in the Great Bay Estuary. *B. diegensis* could repeat the cycle of abundance it demonstrated during the 1980s or maintain its current role within the community.

Although *Membranipora membranacea* overgrows all other kelp epiphytes, the habitat it invaded was largely unused by native species. This pattern contrasts with the mechanisms used by *Styela clava* and *Botrylloides diegensis* because it did not involve competitive dominance over native species. Even though the importance of competition with native species may be minimal, recent research indicates that *M. membranacea* has had a dramatic impact on the kelp habitat at Cape Neddick, Maine (Lambert et al., in review). Kelps encrusted with *M. membranacea* are apparently more susceptible to fracturing during storm surge. The long-range effects of the invasion by *M. membranacea* will likely depend upon the distribution and severity of damage to kelp bed habitats and to the reactions of native species to changes in habitat structure.

These three comparable species entered similar habitats, yet the mechanism of their invasions differed. Further, the means used to enter a community were not necessarily those used to persist. *Styela clava* achieved competitive dominance in habitats where it is abundant. *Botrylloides diegensis* entered the system as a competitive dominant; it has persisted in a manner similar to *Botryllus schlosseri*, as an occupant of primary space in early successional communities and secondary space in established fouling communities. *Membranipora membranacea* entered an underused habitat and apparently has had a severe impact on kelp beds. Therefore, ecological similarity among species may not be an accurate criterion to predict either the mechanism of a species' invasion or the means of its persistence.

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