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Development in an Estuarine Fouling Community: The Influence of Early Colonists on Later Arrivals

T.A. Dean[1] and L.E. Hurd

Section of Ecology and Organismic Biology, School of Life and Health Sciences, and
College of Marine Studies, University of Delaware, Newark, Delaware 19711, USA

Summary. Experiments were performed to determine if earlier colonists inhibited, enhanced, or were necessary for establishment of later colonists during development of an estuarine fouling community at Lewes, Delaware. We determined the significance of earlier stages on the successional process by functionally removing early colonizing species. Since settlement of sessile invertebrates onto our experimental test plates was seasonal, we were able to accomplish functional removal of early colonists by putting out clean test panels after these species had ceased settling. Comparisons between panels initially submerged at three different times in 1974 and 1975, and between panels put out at one-month intervals throughout the study (to describe seasonal settlement patterns) allowed us to determine interactions between adult populations of earlier colonists and colonizing individuals of later arriving species.

The dominant sessile species in our system and their times of settlement were: a barnacle (*Balanus improvisus*) – April through June, a polychaete (*Hydroides dianthus*) – July and August, a tunicate (*Molgula manhattensis*) – June through October, a hydroid (*Tubularia crocea*) – July through October, and a mussel (*Mytilus edulis*) – November through April. All successional series eventually came to be dominated by *M. edulis*, and it persisted as the dominant for over a year.

A variety of species interactions were observed. *M. edulis* inhibited colonization by all other dominants and *B. improvisus* partially inhibited settlement of *M. manhattensis*. The presence of adult *M. manhattensis* had no influence on summer settlement of *T. crocea*, but the hydroids enhanced settlement of tunicates in the fall. During both years of our study, larger settlements of mussels were noted on panels harboring tunicates and hydroids than on bare surfaces. *H. dianthus*, on the other hand, became established only on bare substrates, and colonization was almost totally inhibited by other dominants.

Development in our fouling community did not conform to any single model of community development presented to date. Instead, components of several models were observed within our relatively simple (in terms of number of species) system. For example, facilitation (enhancement of later colonists by earlier ones) and inhibition (resistance of earlier colonists to invasion by later colonists) were both observed. However, we found no evidence earlier colonists were essential for establishment of the next developmental stage. In fact, inhibitory interactions appeared to be much more prevalent than facilitative interactions. The former may also have more profound effects on community development since they more often determine eventual species compositions.

Introduction

Classical successional theory as popularized by Clements (1916) and later supported by Margalef (1968), Odum (1969) and others, suggests that early colonists of a newly disturbed site make modifications in the environment that are necessary for the establishment of later colonists. Once the later arrivals become established, they render conditions unsuitable for pioneer species. This view of community development has come under increasing attack in recent years as the universal or even the preeminent pattern of community development (e.g. McCormick, 1968; Connell, 1972; Drury and Nesbit, 1973; Horn, 1975, 1976; Connell and Slayter, 1977). Alternative models of succession have been presented, yet successional theory is still largely based on descriptive data. Theories have been based primarily on observation of communities of differing developmental age on similar sites or on observation of changes on a single newly disturbed site. Such studies have been informative, but have not determined the mechanisms by which changes in community structure occur. An experimental approach to community processes at the population level appears more promising in this respect (Connell, 1975; Connell and Slayter, 1977).

Although successional theory has historically been derived from studies of plant associations, experimental studies of other systems (especially marine epifaunal communities) have provided valuable information concerning factors which contribute to the structure of natural systems. Demonstration of the significance of competition and disturbance (Connell, 1961a, b; Paine, 1966; Dayton, 1971; Peterson, 1979) are notable examples. Epifaunal communities have proven amenable to experimentation since: (i) species turnover rates are high and changes in community structure occur over relatively short periods of time; (ii) many inhabitants are sessile and the limiting resource (usually space) is easily defined; and (iii) experimental manipulations are relatively easy to perform.

Our study deals with the development of a subtidal fouling community. We used experimental test panels initially submerged at different times to determine successional mechanisms. Since settlement of sessile fouling organisms was seasonal, we were able to functionally remove earlier seral stages from the successional sequence by putting out clean panels after the settlement period for earlier colonists had ended. By comparing colonization on

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[1] Present address: Marine Science Institute, University of California, Santa Barbara, California 93106, USA

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panels of varying stages of development, we were able to determine the types of interactions between species and their role in the developmental process. More specifically, we have determined the effect of earlier colonists on establishment of later colonists, i.e., whether early colonists facilitate or inhibit later colonization. We will also discuss how development of marine fouling communities relates to general successional models, and especially those recently reviewed by Connell and Slayter (1977) and Horn (1976).

We were primarily concerned with the five dominant sessile species within our system (those species which were ranked first in abundance during at least one month of the study). These species comprised over 90% of the total number of individuals in the system and were the primary occupants of space. Although we recognize that such an assemblage may also be defined as a guild (Root, 1967; Menge and Sutherland, 1976; Menge, 1976), patterns displayed by these species reflected patterns displayed by the community as a whole (Dean, 1977). Further, we will deal with succession as an idealized change in community structure over time in the absence of disturbance. Although disturbances are clearly significant structuring forces (e.g. Dayton 1971; Connell 1975), they are viewed here as extrinsic processes. The fouling community under study was in fact free of major predators and agents of physical disturbance during our study period (see Results). For the sake of simplicity, we will discuss succession at it applies to local, relatively homogeneous habitats, and disregard mosaic effects that may result from habitat heterogeneity over broader areas (e.g. Horn, 1974; Menge, 1976).

Study Area

The study described here was conducted in the Broadkill River estuary, Lewes, Delaware near the University of Delaware's marine station (38°40′N × 75°10′W). The Broadkill empties into Delaware Bay approximately 0.5 km from the study site via Roosevelt Inlet at a point approximately 7 km from the mouth of the Bay. Hydrography and water quality of the Broadkill have been previously described (de Witt, 1971). He classified the lower segment of the river in which our study site was located as a mesohaline-polyhaline estuary. Over the period of our study, temperature and salinity data were taken at the mouth of Canary Creek, a small tidal stream emptying into the Broadkill approximately 400 m upriver from our study site. Salinities ranged from 10 ‰ to 33 ‰, with mean fluctuations of 10 ‰ over a tidal cycle. Water temperatures varied seasonally from −1 to 28° C.

Methods

Fouling organisms were collected by allowing them to settle on 10 × 10 cm asbestos-cement panels attached to PVC racks. Racks were suspended from a floating dock with stainless steel cable to a depth of 0.5 m below the surface. Water depth at the study site was always greater than 1.5 m so that panels never came in contact with the river bottom. Racks were so positioned that panels were held vertically, parallel to river flow.

Panels were periodically removed and the side of the panel facing the dock was scraped clean. The panel and organisms attached to the fully exposed or river side of the panel were placed in plastic bags containing 70% ethyl alcohol. Panels were returned to the laboratory where taxa were identified and enumerated. Abundance of solitary species was determined by simply counting the number of individuals. Abundance of colonial species (e.g. hydroids) was estimated by determining percent panel surface area covered, as counting of individuals was not feasible for these species. We compared mean abundances of species on clean vs. previously colonized substrates and on substrates initially submerged at different times using a Mann-Whitney U statistic (Siegel, 1956).

Schedules for setting out and collecting panels were as follows:

(1) One-Month Panels. Five panels were submerged in May 1974. These were removed in June 1974, and replaced by five bare panels. Panels put down in June were removed in July and again replaced by bare panels. This procedure was repeated each month for the entire 20 months of the study, yielding twenty sets of one-month panels.

(2) May 1974 Series. Ninety-five panels were put down in May 1974. Five randomly chosen panels were removed in June 1974, another five were removed in July 1974 and so on. This generated nineteen sets of panels initially submerged in May 1974 and left in place for 1 to 19 months.

(3) March 1975 Series. Forty-five panels were put down in March 1975. Five panels were removed in April 1975, another five in May 1975, and so on through December 1975. This generated nine sets of panels that were all initially submerged in March 1975.

(4) September 1975 Series. Twenty panels were submerged in September 1975. Five of these panels were removed each month thereafter through January 1976. This produced four sets of panels, submerged from September 1975 through October 1975, September 1975 through November 1975, September 1975 through December 1975, and September 1975 through January 1976.

Results

Description of the Community

The subtidal fouling community in the Broadkill consisted of a variety of sessile and associated motile invertebrates. The dominant sessile species were the ivory barnacle, *Balanus improvisus;* the solitary tunicate, *Molgula manhattensis;* the hydroid, *Tubularia crocea;* the serpulid polychaete, *Hydroides dianthus;* and the blue mussel, *Mytilus edulis.* Other sessile species were present at different times but were never abundant. These included other hydroids and polychaetes, bryozoans, and anemones. Typical motile associates were gammarid and caprellid amphipods, isopods, and errant polychaetes. In all, a total of 24 sessile and 43 mobile species were identified. Most of these species (including the five dominants) were typical estuarine forms common to mesohaline-polyhaline waters in our region.

Predation of sessile forms by fish, blue crabs, starfish, or other large predators was never observed in our study area. Our own preliminary experiments using predator exclusion cages and recent work by Smedes (1978) indicated that there was no discernible effect of larger predators on the Broadkill fouling community. In addition, no physical disturbances such as ice damage or abnormally long durations of lowered salinities occurred during our study.

Variance in the number of individuals on replicate panels was generally high (Fig. 1). However, the species rank order of abun-

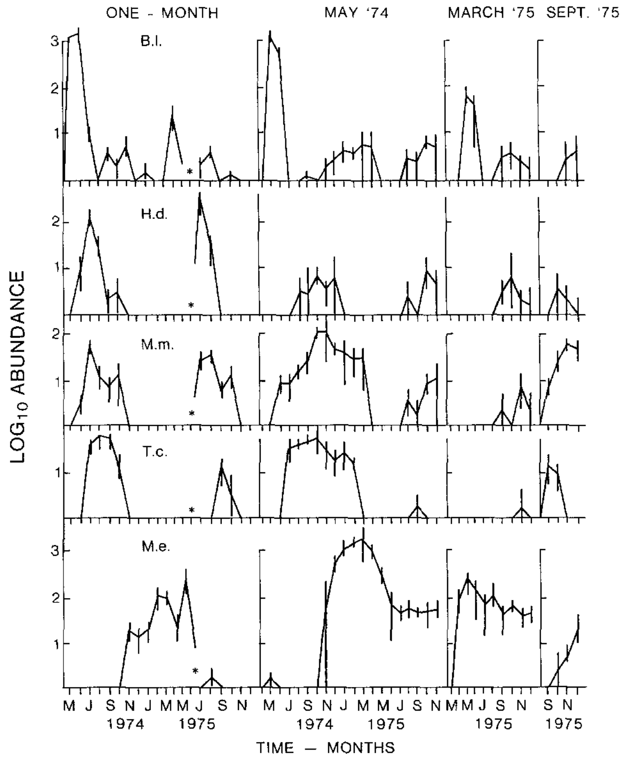

Fig. 1. Abundances of the five dominant sessile species as they occurred on one-month, May 1974, March 1975, and September 1975 panels. *B.i.* = *Balanus improvisus, H.d.* = *Hydroides dianthus, M.m.* = *Molgula manhattensis, T.c.* = *Tubularia crocea,* and *M.e.* = *Mytilus edulis*. Abundances for *T. crocea* are as percent cover. All others are numbers of individuals. Vertical bars are 95% confidence intervals. No data was available for the June 1975 one-month panels (*)

dance among replicates was consistent. The same species was the dominant on all five replicates in 47 of the 52 groups of replicates. Twice during months of almost equal abundances of *M. manhattensis* and *T. crocea*, the latter species was dominant on one of the five replicates while *M. manhattensis* was most abundant on the other four: once on one-month panels collected in December 1974 (when settlement of all species was light) *B. improvisus* dominated one of the five replicates while *M. edulis* dominated others; and twice (on May 1974 panels collected in September 1974 and on September 1975 panels collected in November 1975) when clusters of the small anemone *Haliplanella luciae* were dominant on only one of the five replicates.

Settlement Patterns

Seasonal patterns of settlement for the five dominant sessile species (observed on one-month panels) are shown in Fig. 1. *B. improvisus* settled in early spring, followed by summer and fall settlements of *H. dianthus, M. manhattensis,* and *T. crocea.* The time of peak abundance for these species was fairly consistent from year to year. *B. improvisus* settlement peaked in June 1974 and April 1975, *H. dianthus* in July of both 1974 and 1975, *M. manhattensis* in July 1974 and August 1975, and *T. crocea* in August 1974 and September 1975. Settlements of barnacles and hydroids were much lighter in the second year of the study. *M. edulis* was abundant on one-month panels in winter and early spring, with peak abundances of over 400 individuals per panel in March 1975.

Successional Sequences

Panels put out in May 1974 were first colonized by barnacles (Fig. 1). By July 1974, barnacles became covered by tunicates and hydroids and the number of barnacles was reduced from an initial cohort of > 1,200 to < 1 per panel. The *Molgula-Tubularia* assemblage persisted through March 1975, after which mussels became dominant. *M. edulis* began settling in November and by March had reached a mean abundance of > 1,800 per panel. From March through the end of the study, mussel abundance declined to a low of 32 per panel, but mean shell length increased from 3 to 37 mm and *M. edulis* continued to occupy almost all panel space.

March 1975 panels were initially colonized by mussels. Over 260 mussels per panel were observed in April. A small settlement of *B. improvisus* was also noted in April, prior to the time of complete substrate coverage by *M. edulis.* Barnacle abundance quickly declined ($\bar{X} < 1$ per panel in May 1975), and mussels completely dominated thereafter.

M. manhattensis and *T. crocea* were first to colonize September 1975 panels. By October, these substrates closely resembled panels put out in May 1974 and collected in the fall of 1974. Mussels began to settle near the end of the study, but did not reach large enough size and/or numbers to exert any notable influence on the community.

Species Interactions

As indicated previously *B. improvisus* settlement was heavy on bare panels initially submerged in May 1974 (Table 1). During the following year's peak barnacle settlement (April 1975), a mean of only 5.2 barnacles were found on mussel-covered May 1974 panels. A greater number of barnacles ($P < 0.05$, U-test) was observed on both bare one-month and on March 1975 panels collected in April 1975. The latter harbored small mussels but much bare space remained. Barnacle settlement was obviously inhibited by mussels.

H. dianthus settlement was never more than ten individuals per panel on any except bare one-month panels. During periods of peak attachment the polychaete was more abundant ($P < 0.05$, U-test) on one-month panels than on May 1974 or March 1975 series panels harboring barnacles and mussels, respectively (Table 1). Both barnacles and mussels appeared to inhibit *H. dianthus* settlement. Panels from another set of experiments (Dean 1977) that were initially submerged in July 1975 and removed in December 1975 harbored large numbers of both *H. dianthus* and *M. edulis.* Unlike barnacles, *H. dianthus* was able to survive for at least 6 months in the face of accumulating settlement by later colonists.

One-month panels collected in July 1974 (peak attachment period for tunicates) harbored more individuals of *M. manhattensis* than did May 1974 panels collected in July ($P < 0.05$, U-test). Tunicates on the latter were primarily found on barnacles which had occupied an estimated 60% of the panels' surface area (based on densities and mean test diameters) in the previous month. However, during fall 1974, tunicates were more abundant on the

Table 1. Mean abundances and net monthly increase in abundance of dominant sessile species during each species' peak settlement periods during 1974 and 1975. Dominant species from the previous month's sample are also given. Abundances for *T. crocea* are number cm^2 surface area covered/100 cm^2. All others are number of individuals/100 cm^2

Species	Series	Date sampled	Abundance	Net monthly increase	Dominant previous month
B. improvisus	One-month	May 1974	1,320	1,320	Bare
	One-month	April 1975	27	27	Bare
	March 1975	April 1975	65	65	Small *M. edulis* and Bare space
	May 1974	April 1975	5	5	Large *M. edulis*
H. dianthus	One-month	July 1974	169	169	Bare
	May 1974	July 1974	2	2	*B. improvisus*
	One-month	July 1975	338	338	Bare
	May 1974	July 1975	0	–	*M. edulis*
	March 1975	July 1975	0	0	*M. edulis*
M. manhattensis	One-month	July 1974	53	53	Bare
	May 1974	July 1974	8	–	*B. improvisus*
	One-month	October 1974	12	12	Bare
	May 1974	October 1974	90	80	*M. manhattensis* and *T. crocea*
	One-month	November 1975	1	1	Bare
	September 1975	November 1975	48	25	*M. manhattensis* and *T. crocea*
	One-month	August 1975	34	34	Bare
	May 1974	August 1975	2	1	*M. edulis*
	March 1975	August 1975	2	1	*M. edulis*
T. crocea	One-month	July 1974	42	42	Bare
	May 1974	July 1974	37	37	*B. improvisus* and *M. manhattensis*
	One-month	September 1975	13	13	Bare
	May 1974	September 1975	2	2	*M. edulis*
	March 1975	September 1975	1	1	*M. edulis*
M. edulis	One-month	December 1974	13	13	Bare
	May 1974	December 1974	566	502	*M. manhattensis* and *T. crocea*
	One-month	December 1975	1	1	Bare
	March 1975	December 1975	27	23	*M. manhattensis* and *T. crocea*

older panels than on one-month panels ($P < 0.05$, U-test). Over the month of October, a net increase of 80 tunicates per panel was noted on May 1974 panels, while only 12 tunicates settled on one-month panels submerged over the same period (Table 1). Most of the tunicates on older panels were found settling on hydroids. A similar trend was noted on September 1975 panels. Tunicates settled heavily on hydroid-covered September 1975 panels while none were observed settling on bare one-month panels submerged during the same period (Table 1). Once mussels became established, future tunicate settlement was inhibited. Fewer tunicates were noted on mussel-covered May 1974 and March 1975 panels collected in July and August 1975 than on bare one-month panels ($P < 0.05$, U-test).

Both barnacles and tunicates apparently had little effect on *T. crocea* settlement and/or growth. During periods of peak hydroid abundances (July 1974) similar abundances were noted on bare one-month panels and May 1974 panels previously colonized by barnacles and tunicates ($P < 0.05$, U-test, Table 1). Mussels, on the other hand, appeared to inhibit *T. crocea* settlement and growth. May 1974 and March 1975 panels collected in September 1975 were dominated by mussels and harbored fewer hydroids than one-month panels collected at that time ($P < 0.05$, U-test, Table 1).

Settlement of *M. edulis* was greater on substrates previously occupied by tunicates and hydroids than on bare surfaces. The net monthly increase in number of mussels on May 1974 panels over the period from December 1974 through March 1975 was greater than the number of mussels settling on bare one-month panels (Table 1). Similarly, at the beginning of the next year's mussel settlement, a mean of 23 individuals were added to March 1975 panels over December, while a mean of less than 1 mussel per panel was found on one-month panels (Table 1). Both May 1974 and March 1975 panels were previously occupied by tunicate-hydroid assemblages.

Thus, the effects of earlier colonists on later colonists ranged from facilitative (e.g., hydroids enhancing settlement of mussels) to almost totally inhibitory (e.g., mussels preventing settlement of the serpulid *H. dianthus*). However, in no case were earlier colonists found to be essential for development of later colonists. Mussels, for example, preferred settling on previously occupied substrates (e.g., the May 1974 panels, Fig. 1), but also settled on bare surfaces.

Discussion

Recent general reviews of successional theory by Connell and Slayter (1977) and Horn (1976) have outlined the contrasting models of community development and have provided available evidence in support of each. The specific models which are relevant to our study are briefly outlined below.

1. Facilitation Model. Each species in the successional sequence "paves the way" for later colonists, and later species make conditions unsuitable for their predecessors. This model was originally proposed by Clements (1916) and has until recently remained the most widely accepted. It has variously been termed the "Relay Floristics" model (Egler, 1954) and the "obligatory succession" model (Horn, 1976). The later appears the more appropriate, since it better reflects the underlying notion of this model that earlier colonists are necessary precursors of later colonists. Connell and Slayter (1977) indicated that in spite of its wide acceptance, there is little direct evidence in support of this model. They also suggested that it is most likely to be observed during primary successions. Horn (1976) stated that beech trees may have necessary precursors based on observations that beeches were seldom found in earlier seres of forest succession.

2. Tolerance Model. Earlier colonists have no effect on subsequent arrivals to the system (and/or all species are in the system from the outset) and the generally slower growing, more tolerant species that are better able to utilize resources come to dominate. Once established, these more tolerant species can inhibit reinvasion by others. This was proposed by Egler (1954) as the "Initial Floristic Composition" model and later termed the "Competitive hierarchy" by Horn (1976). Horn (1976) found that this may be the successional model most applicable to patterns observed in New Jersey beech forests. However, critical evidence showing that earlier colonists neither inhibit nor are necessary for invasion by later colonists has not been presented (Connell and Slayter, 1977).

3. Inhibition Model. Colonists resist future invasion and persist until disturbed. Even though this was coined as a successional model only recently (Connell and Slayter, 1977), evidence for inhibition is abundant. Examples come from terrestrial plant associations (e.g. Raynal and Bazzaz, 1975; Platt, 1975), marine algal associations (Dayton, 1973), and marine epifaunal communities (e.g. Osman, 1977; Sutherland and Karlson, 1977). This has even been cited as evidence against succession (Sutherland and Karlson, 1977), but the discrepancies appear to be rooted in semantics.

Each of the above models can be characterized by a single predominant interspecific interaction (Fig. 2). The facilitation model is based on interactions of the type $A \overset{+}{\underset{-}{\rightleftharpoons}} B$, where A is a necessary precursor of B, and B inhibits. A. In the tolerance model, A has no effect on B, but B inhibits A ($A \overset{0}{\underset{-}{\rightleftharpoons}} B$), and in the inhibition model A and B influence each other negatively ($A \overset{-}{\underset{-}{\rightleftharpoons}} B$).

A simplistic diagrammatic representation of the patterns of development observed in this study and the interactions which brought about those patterns are also shown in Fig. 2. On May 1974 panels, *B. improvisus* was first to colonize. Barnacles appeared to inhibit colonization by tunicates, but some tunicates were able to settle and out-survive the barnacles. *M. manhattensis* had no discernible effect on later hydroid settlement and the tunicate-hydroid assemblage persisted for several months. Fall settlement of tunicates was in fact enhanced by hydroids. Mussel settlement in winter was facilitated by this assemblage and the more tolerant mussels became dominant. Mussels persisted throughout the remainder of the study and inhibited future reinvasion by other species.

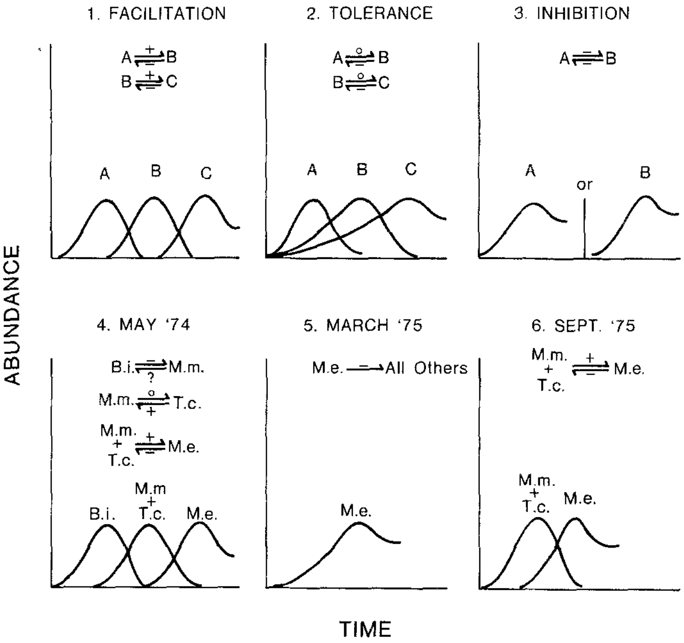

Fig. 2. A diagrammatic representation of abundance patterns resulting from interspecies interactions of both successional models (1, 2, and 3) and real world patterns as observed in this study (4, 5, and 6). Signs above the arrows indicate whether one species enhances (+), inhibits (−), or has no effect (0) on establishment of the other species. *B.i.* = *Balanus improvisus*, *M.m.* = *Molgula manhattensis*, *T.c.* = *Tubularia crocea*, and *M.e.* = *Mytilus edulis*. *Hydroides dianthus* was totally inhibited by other species and did not appear in the successional sequence. (All others $\overset{-}{\leftarrow}$ H.d.)

Panels initially submerged in March 1975 were immediately colonized by mussels, although at a somewhat slower rate than on substrates previously occupied by tunicates and hydroids. This pattern represents an almost "instant climax" and shows that early colonists enhanced, but were not necessary for, establishment of *M. edulis.*

T. crocea and *M. manhattensis* initially colonized September 1975 panels. Incipient invasion by mussels was evident by December 1975, and once again appeared to be facilitated by the tunicate-hydroid assemblage.

It is obvious when comparing patterns and interactions represented by successional models with those of the fouling community under study, that several discrepancies exist. First, more than one particular kind of interaction can be operating within a single community. Within our relatively simple (in terms of number of species) system, four distinct types of interactions were noted ($A \overset{+}{\underset{-}{\rightleftharpoons}} B$, $A \overset{0}{\underset{-}{\rightleftharpoons}} B$, $A \overset{-}{\underset{-}{\rightleftharpoons}} B$, $A \overset{-}{\underset{0}{\rightleftharpoons}} B$). This is in contrast to the single interaction models previously discussed. For example, the facilitation (or obligatory succession) model is composed entirely of interactions of the type $A \overset{+}{\underset{-}{\rightleftharpoons}} B$. Second, each interspecific interaction is not only represented by a sign, but has a magnitude. Negative or positive interactions are not all-or-none phenomena. While the $A \overset{+}{\leftrightarrows} B$ interactions of the facilitation (or obligatory succession) model suggest that A is a necessary precursor of B, this need not be the case. In our system, tunicates and hydroids enhanced settlement of mussels, but were not totally necessary. Although our data is less conclusive for negative interactions, it appears that barnacles inhibited settlement of tunicates without totally preempting them.

A large number of other works in marine epifaunal communities have also demonstrated that different types of interactions can occur within one system, and that these interactions can very in magnitude. Sutherland and Karlson (1977) have demonstrated that at Beaufort, North Carolina, the encrusting ectoproct *Schizoporella unicornis* almost totally inhibited settlement and growth of other species. Others (e.g. *Balanus*) were weaker resistors of invasion. In the same system, tunicates *(Botyrllus* and *Styela)* and sponges *(Haliclonia* and *Halichondria)* appeared to be facilitated by earlier colonists. Similarly, Boyd (1972) determined that in the Bodega Bay, California fouling community, most later arrivals were inhibited by earlier colonists. Yet in most cases total preemption did not occur. In the same community, the tunicate *Botrylloides* settled equally well on bare and previously occupied substrates.

A species' ability to invade mature assemblages and to resist invasion by others appears to be relatively constant over wide geographical areas. Various *Balanus* species are characteristically poor invaders (our study; Osman, 1977; Menge, 1976; Sutherland and Karlson, 1977; Dayton, 1971). *Hydroides* is a poor invader, but has little or no effect on colonizing ability of other species and is able to avoid being overgrown (Dean, 1977; Osman, 1977). *Schizoporella* colonies at both Beaufort (Sutherland, 1978; Sutherland, 1977; Sutherland and Karlson, 1977) and Woods Hole (Osman, 1977) were able to almost totally preempt other species, but were characteristically preempted by those same species (depending upon which became established first). *Mytilus edulis* settlement is facilitated by other species (our study; Bayne 1965; see Menge 1976 for other references) but earlier colonists are not essential (our study; Seed, 1969). Once established, mussels can gernally resist invasion by all others (our study; Paine, 1966; Dayton, 1971; Menge, 1976).

Conclusions

No one successional model presented to date has been shown to account for the changes in community structure observed in many systems. Community development is not necessarily mediated by a single type of interaction, but rather by a combination of different types of interactions among several dominant species. In spite of the persistence of the notion that earlier colonists "pave the way" for later colonists, earlier colonists appear to more often inhibit rather than enhance establishment of later arrivals.

In addition to the numerous citations of Connell and Slayter (1977) many other examples of inhibition have recently become evident. Woodin (1976) has suggested that inhibition is of paramount importance in dense marine infaunal assemblages. Experimental analysis of early stages in terrestrial plant succession (Platt, 1975; Platt and Weiss, 1977; Raynal and Bazzaz, 1975) and examination of historical information from forest-systems (Fox, 1977; Oliver and Stephens, 1977) reveal that inhibition is a major structuring force. Further, inhibition is widely occurring between sessile invertebrates (Dayton, 1971; Boyd, 1972; Sutherland, 1974, 1977, 1978; Sutherland and Karlson, 1977; Jackson and Buss, 1975; Menge, 1976; Osman, 1977), and between invertebrates and benthic algae (Dayton, 1971, 1973, 1975, Lubchenco and Menge, 1978) in marine hard substrate communities.

Negative interactions not only appear to be more frequently encountered, but also have a more profound effect on the outcome of community development. Facilitation influences only the rate of development while strong inhibitory interactions can determine species composition. In our system, *M. edulis* remained dominant (at least on a short-term basis) because of its ability to totally inhibit effective colonization of other sessile species. When negative-negative interactions exist, one of several species may dominate, dependent upon which arrives first. In both of these instances the prolonged dominance of a species is of course dependent upon self replacement (Horn, 1976) or vegetative growth (Jackson, 1977). If no clear preemptive (i.e., there is no species that can totally inhibit another) patterns are established, no dominant will emerge since continual recruitment by a less tolerant species will ensure its local existence. The eventual composition of a particular community is then largely dependent upon the ability of one or more species to inhibit other species' establishment.

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