Journal of Marine Research, 42, 633–654, 1984

Influence of residents on the development of a marine soft-bottom community

by William G. Ambrose, Jr.[1,2]

ABSTRACT

Field experiments in a Maine estuary were designed to follow community development in newly exposed sediment to determine if resident infauna affect the settlement and survivorship of colonizing infauna and thereby effect changes in community structure. Sets of buckets consisting of control buckets (buckets with previously dried sediment) and two experimental treatments (*Nereis virens* or *Glycera dibranchiata* added to dried sediment) were exposed on three dates between June and October 1979 and sampled after 8, 16 and/or 24 weeks. At each sampling, new buckets were established. The index of proportionate similarity comparing the infaunal community of exposure periods with the same starting date was usually greater than the index comparing periods initiated on different dates indicating that assemblages of initial colonizers persisted for the length of the experiment despite the availability of potential colonizers. Large numbers of infauna colonized defaunated sediment, while over the same period of time infaunal density usually declined in sediment which originally contained infauna. Effects of disturbance, drying the sediment, on colonization were controlled by comparing densities in sediment exposed on different dates but after the sediment had been exposed 8 weeks. There was no significant difference in net changes in density between these conditioned sediments despite large differences in the density of their residents. Sediment with low initial density, however, always had a greater net change in density than sediment with high initial density, suggesting that residents had some effect on net changes in density. Highest densities of most infauna were recorded in the *Glycera* addition treatment and lowest in the *Nereis* addition treatment. *Nereis* abundance was reduced in the presence of *Glycera,* which may account for high densities in the *Glycera* addition treatment. It is important to know the species composition of resident assemblages before it is possible to make accurate predictions concerning effects of residents on colonization. The apparent response of colonists to disturbance, in this study drying the sediment, needs to be controlled in experiments designed to determine effects of residents on colonization.

1. Introduction

Colonization of new species and individuals of species already present can alter the structure of a community. Recently, Connell and Slatyer (1977) proposed three alternative models for the mechanisms of succession which emphasize the importance

1. University of North Carolina, Curriculum in Marine Sciences, Chapel Hill, North Carolina, 27514 and Institute of Marine Sciences, Morehead City, North Carolina, 28557, U.S.A.

2. Present address: Institute of Marine Biology and Limnology, Department of Marine Zoology and Marine Chemistry, University of Oslo, Oslo, Norway.

of residents in influencing the settlement and growth of colonizers. According to these models, residents can inhibit, enhance or have no effect upon settlement and growth of later colonizers. Changes in a community's structure, therefore, may be dependent on past events (e.g., predation and disturbance) which determined its present resident assemblage.

The importance of residents in influencing changes in community structure and determining successional sequences has been elegantly tested in marine benthic communities. Manipulative experiments have demonstrated that interactions between residents and invading species are important in structuring hard-substrate communities (e.g., Sutherland and Karlson, 1977; Sutherland, 1978, 1981; Sousa, 1979). In soft-bottom communities, the ability of established infaunal organisms to inhibit settlement by reducing the survivorship of invading larvae and newly settled juveniles is thought to be important in structuring such communities, particularly when infaunal densities are high (Rhoads and Young, 1970; Woodin, 1976; Peterson, 1979; Brenchley, 1981). Some infauna ingest larvae (Segerstråle, 1962; Mileikovsky, 1974; Breese and Phibbs, 1972; Wilson, 1980; Oliver *et al.,* 1982), but residents may also cause mortality of settlers by burial and ingestion of juveniles (Woodin, 1976; Wilson, 1981; Oliver, *et al.,* 1982). Several studies have tested the importance of "adult-larval" interactions (*sensu* Woodin, 1976) in influencing settlement patterns and structuring soft-bottom communities (Williams, 1980; Wilson, 1980, 1981; Hunt, 1981; Commito, 1982; Oliver *et al.,* 1982; Peterson, 1982). Based on this work, it would appear that in soft-bottom communities residents often have the ability to inhibit settlement and reduce the survivorship of colonizers. Recent work by Gallagher *et al.* (1983), however, has demonstrated that some infaunal species can facilitate recruitment. Colonization in soft-bottom communities, therefore, may not be independent of residents and established infauna may affect community development.

In this paper, I follow community development, changes in community structure, in newly exposed sediment. I test whether the presence of two predatory infaunal species, *Glycera dibranchiata* (hereafter *Glycera*) and *Nereis virens* (hereafter *Nereis*) influence densities of colonizing infauna and whether infauna which initially colonize unoccupied sediment modify subsequent colonization. Residents might affect community structure by affecting larval settlement and metamorphosis, and/or the survivorship and growth of colonists. I do not separate individual effects of adult-larval, adult-juvenile, and adult-adult interactions or even mortality of existing residents on changes in community structure. Instead, I test, in general, whether occupation by residents alters community development.

2. Materials and methods

a. Experimental design and sampling. Between June and December 1979, I conducted experiments on an intertidal mudflat 15 km up the Sheepscot River estuary at the town of Wiscasset, Maine (69° 40′ W long., 44° 00′ N lat.). Experiments were

located low in the intertidal zone (0.3 m above mean low water) in an area of poorly sorted mud. Physical and biological features of this site are described in further detail in Ambrose (1982).

Both *Glycera* and *Nereis* prey on infaunal organisms (Commito, 1982; Ambrose, 1982), although they may also be capable of deposit feeding (Klawe and Dickie, 1957; Adams and Angelovic, 1970; Fauchald and Jumars, 1979). Both species are easy to manipulate as adults because they are large (adult length over 10 cm and weight greater than 6 g) and robust. They also readily reburrow. *Glycera* and *Nereis* coexist in the experimental flat, as they do in many tidal flats in the area.

I used plastic buckets (36 cm high and 28 cm inside diameter, top area = 0.06 m^2) to hold azoic sediment. I defaunated buckets of sediment collected from the intertidal zone by drying them for one month. I tested the effectiveness of this procedure by sieving the contents of two haphazardly chosen buckets through a 0.5 mm mesh, staining the residue with rose bengal and sorting for animals. None were recovered. I collected sediment for drying one month prior to exposure.

The entire experiment occurred in the absence of predatory fishes, crabs and birds to: (1) prevent reduction of experimental densities of *Glycera* and *Nereis* by predation and (2) maintain high infaunal densities of colonizers and increase the likelihood that residents might affect colonization. I excluded epibenthic predators by attaching Dupont VEXAR mesh tops (6 mm mesh) to each bucket. I first drilled holes 1 cm below the rim of each bucket and using stainless steel wire attached a 5 cm high strip of VEXAR around the rim. Tops were attached to strips using nylon ties. Strips supported tops off the sediment surface and the holes also provided drainage for surface water. Cage fouling was not severe. Nevertheless, I cleaned fouling organisms and algae from the outside surface of cage tops and side strips with a wire brush every 3–5 weeks and all cages were cleaned at the start of an exposure period. This cage design was effective in excluding epibenthic predators for a similar period of time in other experiments (Ambrose, 1982).

I sequentially exposed sets of buckets with each set consisting of a control and 2 experimental treatments. Control buckets contained only azoic sediment. Experimental treatments were: (1) 9*X Nereis* (where *X* is average natural density, 50 *Nereis* with a first setiger width greater than 3 mm added to each bucket of sediment) and (2) 16*X Glycera* (one *Glycera* greater than 6 g added to each bucket). Each treatment and control were replicated 4 times within each set of buckets. In areas adjacent to the experimental site the average natural densities of *Nereis* (greater than 3 mm wide) and *Glycera* (greater than 6 g) were 90/m^2 and 1/m^2 respectively (Ambrose, 1982). I chose to manipulate large *Nereis* and *Glycera* because smaller individuals are more difficult to manipulate and may not be predators.

An experimental *Nereis* density of 9*X* was outside the range of densities (0*X* to 3*X*) recorded from thirty-one 0.02 m^2 cores taken from the experimental flat between 4 June and 10 June 1979 and used to determine natural *Nereis* density. A high experimental density was considered necessary to allow for mortality and emigration of

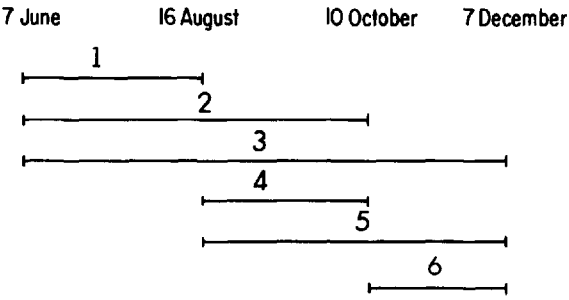

Figure 1. Initiation and termination date for each exposure period and number to identify periods are indicated. Four replicate buckets for the control, *Glycera* addition treatment, and *Nereis* addition treatment were established for each period.

worms during the experiment while still insuring a significant difference in the density of large *Nereis* between the *Nereis* addition treatment and control. Results of another experiment revealed that a 9*X Nereis* density is reduced to between 4*X* and 5*X* within 10 days (Ambrose, 1982). An adult *Glycera* density of 16*X* is greater than the highest density recorded from this area, 2*X*, during an extensive sampling program from 1970 to 1974 (Creaser, Maine Department Marine Resources, unpublished data).

Sediment was exposed for six different periods of time, which I refer to as exposure periods, each with a different duration and/or starting date. Sediment was exposed for 8, 16 and 24 weeks. Eight-week exposures began 17 June, 16 August and 10 October, 16-week exposures 17 June and 16 August and the 24-week exposure 17 June. As a result, sediment was exposed for overlapping periods of time (Fig. 1).

On 16 June I placed buckets of azoic sediment at the experimental site in a 6 by 6 matrix with buckets 1 m apart. I dug each bucket into the sediment until only 1 cm of the bucket wall remained exposed above the surrounding sediment. This made the level of sediment inside and outside the buckets equal. On the following low tide but while buckets were still covered by water, I mixed the sediment in each bucket by hand to increase the water content of the sediment. I randomly assigned treatments to buckets and added appropriate numbers of *Nereis* and *Glycera*.

At each sampling period, new buckets were placed into holes created by removal of sampled buckets. On 16 August more buckets were established than collected so I created two new rows of 6 buckets each. I used the same techniques for handling buckets and assigning treatments as described above.

I sampled buckets by removing them from the sediment and returning them to the laboratory where I sieved the entire contents through 0.5 mm mesh. This mesh will miss recently settled individuals of most species. I will discuss below effects of missing these individuals on the results of the statistical tests and the interpretation of these results. After sieving, the residue retained on the sieve was stained with rose bengal and stored in 12% formalin until sorting. I identified all polychaetes and bivalves to species,

Table 1. Feeding type and mobility/microhabitat of common taxa.

Taxon*	Feeding type**	Mobility/microhabitat***
(A) *Hobsonia florida*	DF	tube dweller, surface
(A) *Nephtys incisa*	DF, C	mobile, surface-subsurface
(A) *Nereis virens*	O	semipermanent burrows, surface to 35 cm
(A) *Notomastus latericeus*	DF	permanent burrows, subsurface
(A) Phyllodocids†	C	mobile, surface-subsurface
(A) *Polydora ligni*	DF, FF	tube dweller, surface
(A) *Scoloplos robustus*	DF	mobile, subsurface
(A) *Streblospio benedicti*	DF, FF	tube dweller, surface
(A) Oligochaetes	DF	mobile, surface-subsurface
(C) Copepods	DF	mobile, surface
(C) Cumaceans	DF	mobile, surface
(M) *Macoma balthica*	DF, FF	mobile, subsurface
(M) Other bivalves††	FF	mobile, subsurface

*(A)—annelida, (C)—crustacea, (M)—mollusca

**DF—deposit feeder, C—carnivore, O—omnivore, FF—filter feeder (Barnes, 1974; De Wilde, 1975; Fauchald and Jumars, 1979)

***Simon, 1965; Barnes, 1974; Fauchald and Jumars, 1979

†*Eteone longa, Phyllodoce arenae, P. maculata*

††*Ensis directus, Gemma gemma, Lyonsia hyalina*

but did not identify oligochaetes, copepods, and cumaceans further than class, subclass and order respectively.

Responses to the treatments were only analyzed for common taxa (density greater than 3.0 individuals per 0.06 m^2 bucket for control or either addition treatment for any exposure period). These taxa, their feeding habits, and microhabitats are listed in Table 1. I treated all bivalve species as a group because the densities of all bivalves other than *Macoma balthica* were low (less than 1.0 per 0.06 m^2). I also treated all phyllodocids as a group because densities of all species other than *Eteone longa* were low (less than 1.0 per 0.06 m^2). I arbitrarily defined three size classes of *Nereis,* small (less than 1.5 mm first setiger width), medium (1.5–3.0 mm) and large (greater than 3.0 mm) and treated each size class separately in the statistical analyses. I made these size separations for *Nereis* because different sized individuals might have different immigration and emigration rates and because it was important to determine if the manipulated *Nereis,* those in the large size class, were present in the *Nereis* addition treatment at the end of each exposure period.

b. Persistence of community structure. I used data from the control and addition treatments in all 6 exposure periods to determine if assemblages of initial colonizers (residents) persisted for the length of the experiment despite the availability of

potential colonizers. Persistence of a resident assemblage would suggest that residents were able to inhibit settlement and reduce survivorship of colonizers. If residents effectively excluded colonists, then sediment exposed the same date but sampled on different dates will have similar species and densities of residents. Sediment exposed on different dates may have different resident assemblages. I compared, pair by pair, the community composition of sediment from every exposure period with every other exposure period using the index of proportional similarity (Whittaker, 1975). I did this analysis separately for the control and addition treatments. In order to determine levels of significance, I randomly matched replicates from one exposure period with replicates from another period and derived mean similarity indices. I then determined significant differences between mean indices using the Tukey-Kramer procedure (Sokal and Rohlf, 1981). I also compared the density of total infauna which colonized during different exposure periods using one-way ANOVAs, with exposure period as the main effect, on the density of total infauna from the control and addition treatments. Because of the overlapping design (Fig. 1), exposure periods are not independent treatments. This should result in conservative ANOVAs, however, since factors affecting densities (larval availability, temperature, etc.) will be shared by different exposure periods. When an ANOVA was significant ($p < 0.05$), I used Duncan's Multiple Range Test to compare treatment means.

In all ANOVAs I tested for homogeneity of variances using the F-max test (Sokal and Rohlf, 1981). When the test indicated that sample variances were significantly different ($p < 0.05$) from each other, I transformed the data using a logarithmic transformation, $\log_{10}(x + 1)$, and retested. This transformation was sufficient to correct all heterogeneous variances. Unless otherwise indicated, untransformed data are presented in all figures and tables.

c. Effects of residents on changes in density. I made use of the overlapping design (Fig. 1) and results of ANOVAs comparing total infaunal density between exposure periods to determine whether changes in total density were independent of residents. All the ANOVAs comparing total density were significant ($p < 0.001$). I used the *a posteriori* Scheffe procedure to compare combinations of treatment means (Brownlee, 1965). I tested whether the mean number of organisms per bucket from an exposure period of 16 or 24 weeks equaled the sum of the mean number of organisms per bucket from two shorter, consecutive periods. In each comparison, the two shorter periods together spanned the same 16 or 24 weeks as the single long period. Four combinations of treatment means comprised the Scheffe contrasts: (treatment means are identified by number and refer to Figure 1): (1) $1 + 4 = 2$, (2) $4 + 6 = 5$, (3) $2 + 6 = 3$ and (4) $1 + 5 = 3$. Separate contrasts were made for the control and addition treatments.

In the above contrasts, buckets from the one long exposure period, 16 or 24 weeks, and the first of the two shorter periods had the same starting date. Therefore, the

history of change in infaunal density was assumably identical for both these sets of buckets until the first of the shorter periods ended. If the mean densities from the two shorter periods do not sum to the mean density from the corresponding long period then the net change in infaunal density during the second of the shorter periods and during the identical period of time for the long period must have been significantly different. This significant difference could be the result of differences in infaunal density at the start of the second period between buckets from the second short period (an initial density of zero) and buckets from the long period (containing resident infauna). Net change in density for the second short period is simply the mean density of infauna at the end of the period minus zero since the buckets began with azoic sediment. During this same time interval net change in density for the long period is the mean density at the end of the period minus the density at the beginning. Beginning density is estimated from the buckets of the first short period.

d. Effect of Glycera and Nereis on infaunal densities. I used ANOVA to determine individual effects of *Glycera* and *Nereis* on the colonization of other infauna. I also analyzed differences between treatments in the abundance of total infauna. I did separate one-way ANOVAs for each exposure period with polychaete predator density (control, *Nereis* addition and *Glycera* addition) as the main effect. When an ANOVA indicated a significant treatment effect ($p < 0.05$), I used Duncan's Multiple Range Test to compare individual treatment means. I excluded from the analyses any *Glycera* addition replicate from which a *Glycera* was not recovered because I had no way to determine how long the *Glycera* had been missing.

3. Results

a. Persistence of community structure. Assemblages of residents appeared to persist for the length of the experiment. Densities of the 8 most abundant taxa which settled into control buckets are displayed graphically in Figure 2. The pattern is very similar for addition treatments. The date an exposure period began appears to be more important in determining abundances of taxa than the length of the period. The similarity indices comparing exposure periods (Table 2) quantify the relationship between initiation date and community structure. This index varies between 0 (complete dissimilarity) and 1 (complete similarity). Similarity indices comparing periods with the same starting date were usually significantly greater than similarity indices comparing periods with different starting dates. For the *Nereis* addition treatment, all but one of the replicates for the 24 week period which began in June were lost so mean similarity indices could not be determined for comparisons involving this period. Significant differences in similarity indices between treatments from this period and others were determined using the *t*-test for comparisons of a single observation with a mean (Sokal and Rohlf, 1981).

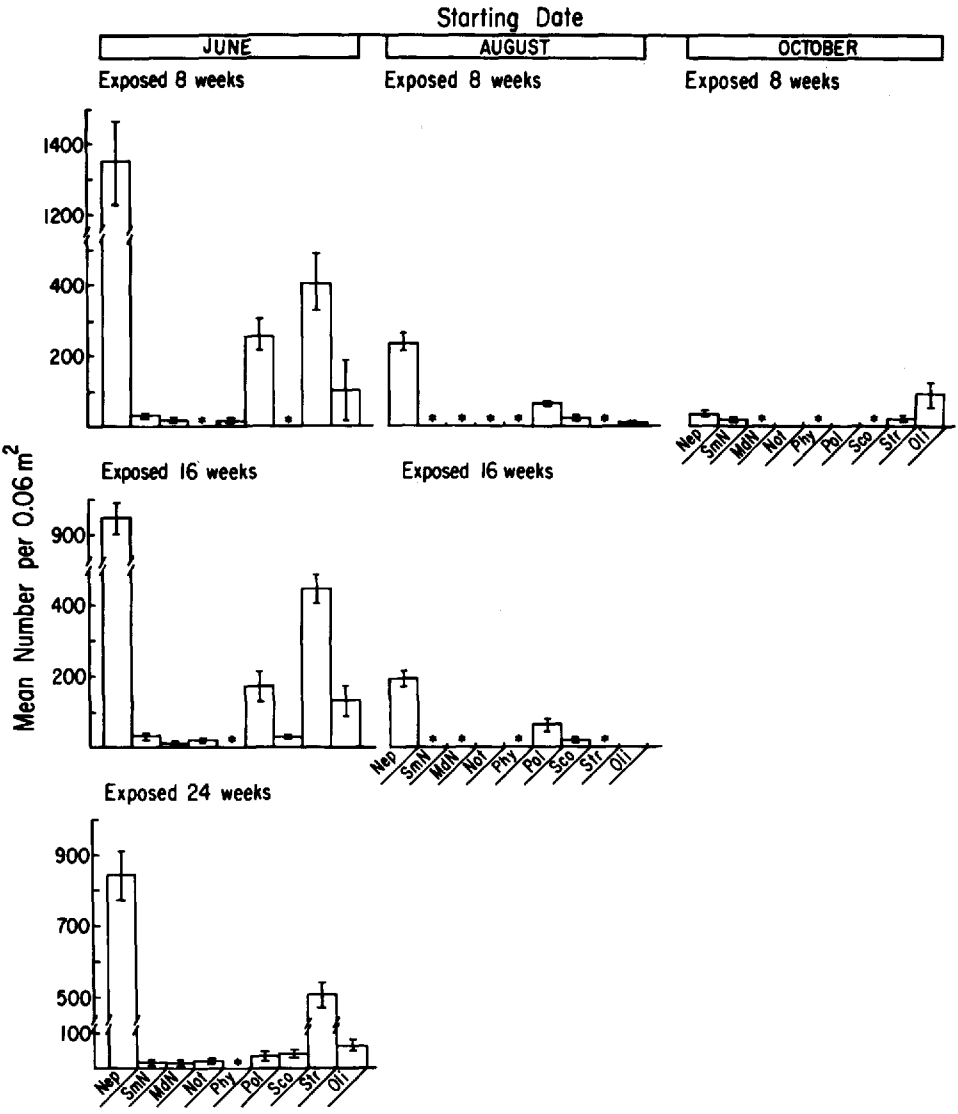

Figure 2. Mean number (±1 SE of the mean) per 0.06 m^2 replicate bucket of *Nephtys incisa* (Nep), small *Nereis* (SmN), medium *Nereis* (MdN), *Notomastus latericeus* (Not), *Polydora ligni* (Pol), *Scoloplos robustus* (Sco), *Streblospio benedicti* (Str), phyllodocids (Phy) and Oligochaetes (Olig) which settled into control buckets are presented. An asterisk indicates a mean abundance per 0.06 m^2 of less than 10 individuals. Starting date and length of exposure in weeks are indicated. Periods with the same starting date are aligned under one another.

Table 2. Mean proportionate similarity indices comparing treatments from every pair of exposure periods for control, *Glycera* addition and *Nereis* addition treatments. Starting date and duration of each period are indicated. The Tukey-Kramer procedure was used to determine significant differences between means. For contrasts involving the *Nereis* addition, June, 24-week exposure period for which only a single replicate was available indices were compared using the *t*-test for comparisons of a single observation with a mean. Means with common underline are not significantly different ($p > 0.05$).

Control

	June 8 wk.	June 16 wk.	June 24 wk.	August 8 wk.	August 16 wk.	October 8 wk.
June—8 wk.		.778	.778	.720	.726	.431
June—16 wk.			.833	.701	.673	.413
June—24 wk.				.645	.604	.431
August—8 wk.					.887	.342
August—16 wk.						.271

Glycera

	June 8 wk.	June 16 wk.	June 24 wk.	August 8 wk.	August 16 wk.	October 8 wk.
June—8 wk.		.840	.843	.727	.738	.327
June—16 wk.			.882	.655	.697	.350
June—24 wk.				.660	.723	.294
August—8 wk.					.880	.207
August—16 wk.						.183

Nereis

	June 8 wk.	June 16 wk.	June 24 wk.	August 8 wk.	August 16 wk.	October 8 wk.
June—8 wk.		.806	.815	.429	.543	.464
June—16 wk.			.842	.514	.639	.558
June—24 wk.*				.441	.469	.427
August—8 wk.					.881	.589
August—16 wk.						.596

*Indices were not compared.

The ANOVA comparing total infaunal density between exposure periods was significant ($p < 0.001$) for the control and addition treatments. The result of Duncan's Multiple Range Test for the control (Table 3) indicates that exposure periods initiated on the same date do not have significantly different densities of total infauna. Results for *Glycera* and *Nereis* addition treatments are slightly different from those for the control but in only one instance do exposure periods with different starting dates have infaunal densities which are not significantly different (Table 3).

Table 3. Comparisons of total infaunal densities between the six exposure periods for control and *Glycera* and *Nereis* addition treatments. Starting date and duration of each exposure period are indicated. Each value represents the mean number of individuals per 0.06 m^2 replicate bucket. A single replicate for the *Nereis* addition, June—24 week exposure period precluded its inclusion. The ANOVA's comparing densities between periods for the control and addition treatments were significant at $p < 0.001$. Duncan's Multiple Range Test was used to determine significant differences between means. Means with common underline are not significantly different ($p > 0.05$.)

Exposure Period					
June 8 wk.	June 16 wk.	June 24 wk.	August 8 wk.	August 16 wk.	October 8 wk.
Control					
2214.0	1837.3	1561.5	373.3	301.3	179.8
Glycera Addition					
2262.2	2032.8	2037.7	248.1	299.7	303.4
Nereis Addition					
1623.3	1712.4	—	734.0	352.9	176.3

b. Effects of residents on changes in density. The Scheffe contrasts which tested whether the mean number of organisms per bucket from an exposure period of 16 or 24 weeks equaled the sum of the mean number of organisms per bucket from two shorter, consecutive periods were all significant ($p < 0.001$). This indicates that the mean infaunal density per bucket from two consecutive exposure periods does not add up to equal the density in sediment exposed the same period of time. Therefore, the net change in infaunal density during the second of the two consecutive periods and during the same time interval of the single, long period were different. These net changes are compared in Figure 3 as a function of the difference in density between buckets from the second consecutive period and buckets from the single, long period at the beginning of the comparison period. I will discuss below comparisons in Figure 3 involving conditioned sediment. In Figure 3, buckets from the second consecutive period have the low initial density because they began with no infauna. These buckets always show a large increase in density of infauna. Net change in density for buckets which already contained infauna was frequently negative indicating that colonization was not always sufficient to replace lost residents (Fig. 3).

The large differences in net changes in density between buckets which initially contained azoic sediment (those from the second consecutive exposure period) and those which initially contained infauna (single, long period) (Fig. 3) might be unrelated to differences in the density of infauna between the two sets of buckets. Oliver (1979) showed that several species of larvae are attracted to recently disturbed (frozen, dried, moved) sediment. In my experiments it is possible that larvae might

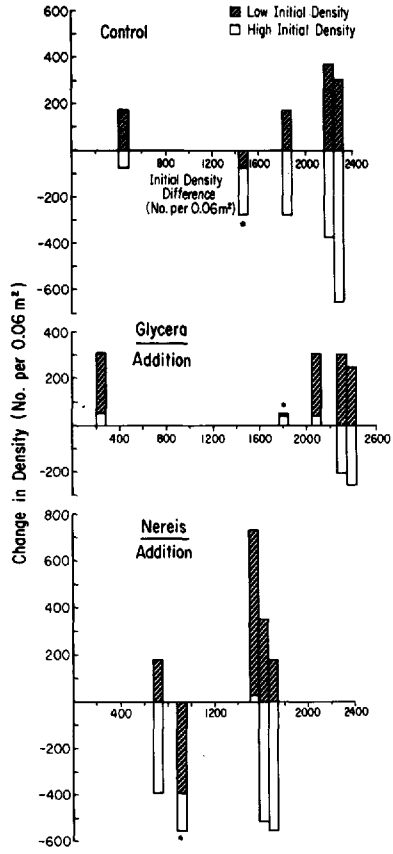

Figure 3. Comparisons of net changes in density (mean number of individuals per 0.06 m^2 bucket) between buckets containing different densities of residents as a function of the initial density difference between these buckets. Each comparison corresponds to one of the Scheffe contrasts. For control and *Glycera* addition, from left to right, periods being compared are (numbers refer to Fig. 1, low initial density listed first): 1) 6 vs. 5–4, 2) 5–4 vs. 3–2, 3) 6 vs. 3–2, 4) 4 vs. 2–1 and 5) 5 vs. 3–1. For *Nereis* addition: 1) 6 vs. 5–4, 2) 5–4 vs. 3–2, 3) 5 vs. 3–1, 4) 4 vs. 5–1 and 5) 6 vs. 3–2. An asterisk indicates that both sets of buckets contained conditioned sediment. In all other comparisons buckets with the low initial density began with azoic sediment (or azoic sediment and *Nereis* or *Glycera*).

have been more attracted to azoic sediment than to sediment which had been exposed 8 weeks or more. Differences in the attractive nature of sediment to settling larvae or immigrants would confound the tests I did to determine if residents affected net changes in infaunal density. I controlled for effects of disturbance, drying the sediment, on colonization by comparing net changes in density between two sets of buckets after each had been conditioned by at least 8 weeks of exposure. I accomplished this by using the Scheffe procedure to compare the following combina-

tion of treatment means (treatment means are identified by number and refer to Fig. 1): 5 − 4 = 3 − 2. This test compares the net change in density in the 24 week period which began in June, period 3, and the 16 week period which began in August, period 5, for the interval October to December (Fig. 1). The contrast was not significant ($p > 0.05$) for the control or the *Glycera* addition treatment. The contrast was not performed for the *Nereis* addition treatment because of the loss of replicates from period 3 but net changes in density were determined. The net change in density between October and December (identified by an asterisk in Fig. 3) for buckets from both periods was negative for the control and the *Nereis* addition treatment and positive for the *Glycera* addition treatment. Buckets with low initial density always had a greater net change in density than buckets with the high initial density.

The adult-larval hypothesis (Woodin, 1976) predicts that high densities of infauna will be more effective than low densities in preventing settlement and reducing survivorship of invading species. Therefore, initially greater differences in the density of residents between buckets from two exposure periods should result in greater differences in net changes in density. In Figure 4 I plot the difference in net change in density between buckets from two exposure periods (periods with buckets having a low initial density minus periods with high) as, in Figure 3, a function of the initial difference in their densitites. Each point in Figure 4 corresponds to one comparison in Figure 3. Only comparisons made over the same period of time can be compared because biological and physical factors were identical. For the control and *Glycera* addition treatment, the three comparisons with the lowest initial density differences represent the same period, October to December. For the *Nereis* addition treatment, the October to December time period was held in common by the two comparisons with the lowest and the comparison with the highest initial density differences. When the comparison involving only conditioned sediment is excluded, greater differences in the density of residents between buckets resulted in greater differences in net changes in density.

In Figure 4, the point representing the comparison which controlled for the effect of disturbance and compared only conditioned sediment always falls below the two points representing comparisons which utilized buckets containing azoic sediment and covered the same period. The distance between the point representing the comparison controlling for disturbance and the x-axis represents the degree to which residents alone determined differences in net changes in density between exposure periods at the indicated initial density difference. If residents had no effect on changes in density then this point would be on the x-axis, as it almost is for the *Glycera* addition treatment. Expressed as a percent of the total distance between the x-axis and a line between the two points representing comparisons with azoic sediment, the density of residents explains about 50% of the differences in changes in density for the control, 25% for the *Nereis* addition treatment and less than 10% for the *Glycera* addition treatment (Fig. 4). These estimates assume a linear relationship between differences in infaunal

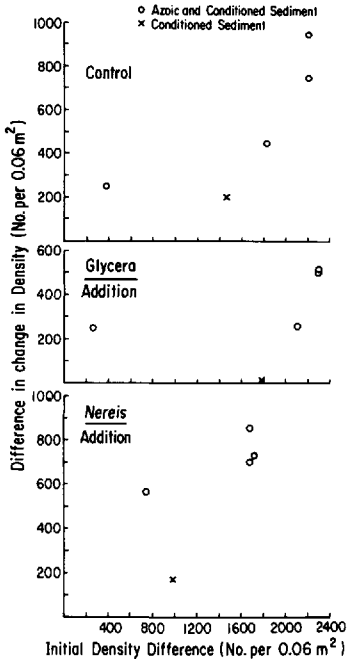

Figure 4. Difference in change in infaunal density between buckets containing different densities of residents (buckets with low initial density minus buckets with high) as a function of the initial density difference between these buckets. Comparisons in which one set of buckets contained azoic sediment (or azoic sediment and *Glycera* or *Nereis*) and comparisons in which both sets contained conditioned sediment are indicated with different symbols. The periods being compared are the same and occur in the same order along the *x*-axis as in Figure 3 (see Fig. 3 legend).

density and differences in net changes in density and will be lower if this relationship is not linear.

c. Effects of Glycera and Nereis on infaunal densities. Effects of predatory polychaete addition on the abundances of common taxa are indicated in Table 4. Of the 12 taxa whose response to the treatments was analyzed, only the abundances of *Nephtys incisa*, cumaceans and small *Nereis* were unaffected by the presence of *Glycera* or *Nereis*.

Large *Nereis* were always more abundant in the *Nereis* addition treatment than in the control (Table 4), indicating that elevated densities of *Nereis* were maintained for all exposure periods. An average of 61% of the *Nereis* added to the *Nereis* addition treatment remained until sampling. This corresponds to a density of approximately 5*X*.

The presence of *Nereis* at elevated densities significantly reduced the densities of

Table 4. The effects of predatory polychaete addition on the abundances of common taxa for all exposure periods. The untransformed mean density of common taxa and total infauna in control (C), and *Glycera* (G) and *Nereis* (N) addition treatments for each exposure period and the significance level of the ANOVA comparing these means are presented. Duncan's Multiple Range Test was used to determine significant differences between means when an ANOVA was significant ($p < 0.05$). Means with common underline are not significantly different ($p > 0.05$). Significance levels: *ns* = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

	June 8 weeks				June 16 weeks				June 24 weeks		
	G	C	N	Sig.	G	C	N	Sig.	G	C	Sig.
Hobsonia florida	3.5	3.5	0.3	*	4.8	5.7	1.8	*	4.9	1.3	*
Nephtys incisa	1156.3	1345.5	1030.3	ns	1103.3	946.0	889.0	ns	1292.0	844.0	ns
Small *Nereis*	31.8	28.8	31.3	ns	4.5	31.0	25.5	ns	5.5	16.5	ns
Medium *Nereis*	2.5	14.5	2.3	ns	4.5	11.3	4.8	ns	1.5	14.8	**
Large *Nereis*	0.3	0.8	28.3	***	0.0	3.3	31.0	***	0.0	2.8	***
Notomastus latericeus	5.3	5.3	16.3	ns	14.8	20.7	17.5	ns	20.0	18.0	ns
Phyllodocids	17.3	15.5	6.0	**	18.0	9.7	5.8	**	13.8	9.5	ns
Polydora ligni	362.8	257.5	93.3	*	199.5	178.3	97.8	*	73.0	37.5	ns
Scoloplos robustus	8.5	2.3	4.0	ns	46.3	31.7	33.5	ns	72.8	40.8	*
Streblospio benedicti	555.0	402.8	229.8	*	498.5	446.0	211.5	***	555.8	506.3	ns
Oligochaetes	122.5	100.8	148.0	ns	91.3	131.3	173.0	ns	45.3	63.0	ns
Copepods	0.0	0.3	79.5	*	0.3	3.7	213.3	***	0.3	0.3	ns
Cumaceans	8.8	8.5	2.3	ns	1.3	0.3	3.5	ns	1.3	0.5	ns
Bivalves	8.0	8.3	2.3	*	8.5	5.7	4.0	ns	8.0	5.0	ns
Total	2299.3	2213.8	1685.3	ns	2043.0	1837.3	1721.3	ns	2099.5	1561.5	ns

Table 4. (Continued)

	August 8 weeks				August 16 weeks				October 8 weeks			
	G	C	N	Sig.	G	C	N	Sig.	G	C	N	Sig.
Hobsonia florida	1.0	0.5	0.0	ns	2.5	0.7	0.0	ns	0.0	0.0	0.0	—
Nepthys incisa	143.3	237.5	241.0	ns	175.8	193.0	178.0	ns	33.3	37.0	46.7	ns
Small *Nereis*	0.0	1.3	1.8	ns	0.7	2.3	0.0	ns	17.0	15.8	6.0	ns
Medium *Nereis*	0.0	4.8	1.8	**	0.3	1.7	2.0	ns	2.7	4.3	1.7	ns
Large *Nereis*	0.0	0.5	29.8	***	0.0	0.3	34.0	***	0.0	0.5	34.3	***
Notomastus latericeus	4.3	1.5	1.0	*	3.4	0.0	0.0	ns	0.0	0.0	0.0	—
Phyllodocids	1.3	2.0	0.0	ns	7.5	8.0	0.0	***	3.7	4.0	2.0	ns
Polydora ligni	54.0	64.3	2.0	***	73.5	62.3	2.5	***	1.7	0.0	0.0	*
Scoloplos robustus	17.7	25.0	16.8	ns	27.3	23.0	19.5	ns	5.7	4.3	3.0	ns
Streblospio benedicti	5.0	3.5	2.8	ns	4.0	5.0	2.5	ns	37.7	21.0	6.7	ns
Oligochaetes	5.0	8.0	3.3	ns	1.3	0.0	1.5	ns	195.3	87.0	15.0	*
Copepods	1.8	7.8	420.8	***	0.3	0.3	106.5	***	0.0	0.0	59.7	***
Cumaceans	5.0	7.8	12.8	ns	2.0	2.0	2.5	ns	6.0	1.0	2.7	ns
Bivalves	0.7	1.5	1.0	ns	0.8	0.0	0.0	ns	0.0	0.0	0.0	—
Total	250.3	373.3	738.5	ns	304.5	301.3	353.0	ns	309.3	179.8	180.0	ns

Polydora ligni, Hobsonia florida, Streblospio benedicti, phyllodocids and bivalves. These taxa were significantly less abundant in the *Nereis* addition treatment than in the control during at least one exposure period (Table 4). Copepods were always 10 to 100 times more abundant in the *Nereis* addition treatment than in the control or *Glycera* addition treatment.

Glycera addition did not reduce the densities of most taxa but during at least one exposure period resulted in significantly greater abundances of *H. floridi, P. ligni, Scoloplos robustus, Notomastus latericeus* and phyllodocids compared to the control (Table 4). Abundances of medium and large *Nereis* were always lower in the presence of *Glycera* than in the control although differences were not always significant (Table 4).

Oligochaete abundance was significantly affected by the presence of the predatory polychaetes during the exposure period which began in October. There was no significant difference between addition treatments and control but oligochaetes were significantly more abundant in the presence of *Glycera* than in the presence of *Nereis.*

4. Discussion

Recently, Woodin (1976) and Peterson (1979) suggested that negative interactions between residents and invading larvae may be important in structuring soft-bottom communities. Persistence of an assemblage of residents may be interpreted to be the result of these interactions. The resident community can persist despite the availability of potential colonizers if residents inhibit the settlement and reduce the survivorship of colonists. In the experiments described here, sediment exposed on different dates had different assemblages of residents which persisted until the end of the experiment (Fig. 2, Tables 2, 3). The results suggest that interactions between residents and colonists might be important in structuring this community. Persistence of some species such as *H. floridi, P. ligni* and *S. benedicti* in the present study is aided by their rapid reproduction and direct development which enables these species to quickly replace lost individuals. The population dynamics of these species, which were often very abundant, undoubtedly contributed to the persistence of assemblages.

The effect of residents on community development was tested by comparing net changes in density between buckets which initially contained azoic sediment and buckets which contained established residents. These changes in density incorporated mortality of pre-existing residents as well as settlement and survivorship of new colonizers so do not strictly measure effects of residents on colonization. Densities usually declined or remained approximately the same in buckets containing residents while they increased, sometimes dramatically, in buckets which initially contained no infauna (Fig. 3). The same results were obtained by McCall (1977) and suggest that residents can have a large effect on a community's development.

There is no significant difference in net change in density between two sets of buckets despite large differences in their initial density of residents when I controlled for effects of disturbance, drying the sediment, on colonization and compared colonization of sediment conditioned by at least 8 weeks of exposure. This indicates that the differences in changes in density between newly exposed azoic sediment and sediment with infauna might have been the result of greater larval attraction to azoic sediment than to conditioned sediment. Previous studies which monitored colonization of disturbed or azoic sediment recorded initially high densities of certain species (Grassle and Grassle, 1974; McCall, 1977; Rhoads *et al.*, 1978; Zajac and Whitlatch, 1982 a, b) and it has been suggested that some species may be adapted to exploit disturbances (Thistle, 1981). To control for the effects of disturbance on colonization, I assumed that the attractiveness of azoic sediment disappeared after 8 weeks. This assumption is hard to assess because so little is known about larval site selection. If the attractive nature of disturbed sediment is due to a unique microbiota (Oliver, 1979), then 8 weeks of feeding and burrowing would likely alter the microbiota's original composition. Numerous studies have demonstrated that larvae use the presence of microorganisms attached to sediment as a settlement clue (see review by Gray, 1974). Larvae may be using differences in the microbiota of sediments to indicate differences in infaunal density between areas, making the apparent response of larvae to disturbed sediments an indirect adult-larval interaction.

Although there was no significant difference in net changes in density between conditioned treatments, the data indicate that residents still may have had some effect on changes in density. Even when only conditioned sediment is compared the greater net change in density still occurred in sediment with the low initial density (Fig. 3). The low contribution of residents to changes in density in the *Glycera* treatment may have been because the abundance of *Nereis*, which are capable of affecting densities, were reduced in the presence of *Glycera* (Table 4).

Failure of the 0.5 mm mesh to sample all juveniles will bias results of all Scheffe contrasts. In the Scheffe contrasts, the density of infauna at the end of the first of the two consecutive exposure periods was undoubtedly underestimated as a result of missed juveniles. Some of these individuals were certainly sampled at the end of the single, long period 8 or 16 weeks later. This sampling bias will result in a conservative test for the negative effects of residents on settlement and post-settlement survivorship because the density of organisms in buckets of the single, long exposure period (high initial density) at the start of the second consecutive period was actually greater than recorded. If all juveniles had been sampled initially, the result would have been a greater negative change in density. Initial densities were also undoubtedly underestimated from both exposure periods 3 and 5 in the comparison of net changes in density between buckets containing conditioned sediment. The starting density in buckets with the high initial density (period 3) was determined from buckets in place for 16 weeks while the starting density in buckets with the low initial density (period 5) was

determined from buckets in place 8 weeks. As in the previous contrasts, buckets with the high initial density (period 3) probably had a greater number of unrecorded juveniles to begin with unless all individuals grew fast enough to be sampled within 8 weeks.

Effects of *Glycera* and *Nereis* on densities confound effects of adult-larval, adult-juvenile and potentially even adult-adult interactions. Following the argument of Peterson (1982), if adult-larval and adult-juvenile interactions are important in structuring this community, then any effects of *Glycera* and *Nereis* on settlement should still be evident in the densities of adults 8, 16 or even 24 weeks later. There is, however, no way to separate adult-larval interactions and post-settlement mortality.

The presence of both *Glycera* and *Nereis* influenced abundances of infaunal taxa but the predators had opposite effects. While *Nereis* presence caused a substantial reduction in the abundance of several taxa, *Glycera* presence resulted in an increase in the abundances of many infaunal taxa (Table 4). I obtained similar results when *Glycera* and *Nereis* were added to undisturbed portions of the soft-bottom community (Ambrose, 1982). In those experiments, *Nereis* were nearly eliminated from *Glycera* treatments and I postulated that this caused the increase in infaunal abundances in *Glycera's* presence. In the experiments described here, medium and large sized *Nereis* were less abundant in the *Glycera* treatment than in the control during all exposure periods (Table 4). This interpretation assumes that *Glycera* activity did not enhance settlement. This seems reasonable because *Glycera* appear to have little effect on the physical environment and therefore are unlikely to affect larval site selection. *Glycera* maintain a semi-permanent burrow so do not disturb the sediment with continual burrowing activity, do not deposit large quantities of fecal material on the surface and are not active on the sediment surface (personal observation). Laboratory experiments have shown that *Glycera* prey on *Nereis* (Ambrose, 1982), although in the field low *Nereis* densities in the *Glycera* treatment could have been due to *Nereis* emigration.

Nereis may have reduced infaunal abundances by direct predation, disturbance and/or by influencing larval site selection. Remains of polychaetes, juvenile bivalves, *Corophium volutator* parts and oligochaetes have been recorded from *Nereis* fecal pellets (Ambrose, 1982). *Nereis,* however, disturb the sediment surface by extending large portions of their body onto the surface during feeding and by depositing fecal material there (personal observation). These activities could result in the burial of larvae, juveniles or adults or affect larval site selection. It is also possible that larvae have evolved the ability to detect and thereby avoid areas of high *Nereis* density.

Initial experimental densities of both *Nereis* and *Glycera* were unnaturally high. By 8 weeks, however, the experimental density of *Nereis* had declined to approximately $5X$ (Table 4). Other experiments indicate that this decline occurs within 10 days (Ambrose, 1982). An experimental density of $5X$ is much closer to the highest density, $3X$, recorded in the inital cores and makes the experiments a more realistic test of *Nereis*'s ability to influence colonization. Furthermore, although, confounded by

Glycera's presence the *Glycera* treatment acted as a *Nereis* removal treatment and provided a means of evaluating effects of continuous *Nereis* removal during colonization. A high experimental *Glycera* density could not be avoided without using larger buckets which were not logistically feasible. Nevertheless, laboratory experiments indicate (Ambrose, 1982) that even at lower densities the main effect of *Glycera* would still be a substantial reduction in *Nereis* density.

The settlement patterns I observed were almost certainly biased by the hydrodynamic effects of the bucket and VEXAR tops. Eckman (1983) has shown that even very small structures can modify sedimentation and recruitment patterns. While settlement patterns in the buckets and the surrounding unmanipulated flat were probably not identical this does not bias any of the statistical tests as all buckets were the same. As I mentioned above, one reason for using cage tops was to maintain high infaunal densities by reducing predation and increasing the likelihood that residents might affect colonization. The structure of the bucket and top alone probably enhanced recruitment and contributed to high infaunal densities.

Effects of residents on colonization have been shown to be important in structuring other soft-bottom communities (Williams, 1980; Wilson, 1980, 1981; Hunt, 1981; Commito, 1982; Oliver *et al.*, 1982; Peterson, 1982; Gallagher *et al.*, 1983; Watzin, 1983). In my experiments, adult-larval interactions, post-settlement mortality and mortality of residents were confounded. Nevertheless, it is apparent that residents are important determinants of successional events.

The size and mobility of the interacting species and the frequency and magnitude of their disturbance within the sediment need to be considered when attempting to model adult-larval interactions and the effect of residents on colonization (Brenchley, 1981; Wilson, 1981). In my experiments, *Nereis* caused substantial reductions in densities probably because the *Nereis* I manipulated were large, disturbed the sediment surface and were predators. I could detect no significant effect of smaller, early colonizing infauna on net changes in density once I controlled for the effect of disturbance due to defaunation. *Glycera,* although large and predatory, do not disturb the sediment surface and therefore do not reduce densities of most infauna. *Glycera* reduce *Nereis* abundance, so have an indirect effect on densities.

It appears unlikely that only one of the models proposed by Connel and Slatyer (1977) explains all the successional patterns observed in soft-bottom communities. Gallagher *et al.* (1983) provide evidence for the facilitation model while the results presented here and those of others (e.g., Wilson, 1980, 1981; Oliver *et al.*, 1982; Commito, 1982; Watzin, 1983) suggest that residents are also able to inhibit colonization to varying degrees. Some species, such as *Glycera* in the present study, may have an indirect effect on colonization by primarily affecting the density of one species. It is obviously important to know the species composition of resident assemblages before it is possible to make accurate predictions concerning effects of residents on colonization.

Acknowledgments. I would like to thank B. Beal, B. Duncan, S. Fegley, J. Hunt, M. Watzin, anonymous reviewers, and my committee members J. Carter, J. Commito, D. Frankenberg, C. Peterson, A. Stiven and J. Sutherland for critical review of this manuscript. I would particularly like to thank C. Peterson for insightful discussions and critical evaluation of all stages of this work. P. Bland, A. Eden, L. Geer, C. Hoss, M. McGinnis, D. Oakley and K. Sandøy spent many hours sorting samples. I thank the personnel at the Maine Department of Marine Resources, Boothbay Harbor, especially T. Creaser, for making laboratory space and equipment available. The University of North Carolina Institute of Marine Sciences provided laboratory and office space. MacDonalds' restaurants from Maine to North Carolina kindly provided the large number of buckets used in these experiments free of charge. This work was supported by a doctoral dissertation research grant from the Biological Oceanography Division of NSF (OCE 79-19916), an R. J. Reynolds Research Fellowship, a University of North Carolina Smith Fund grant, the University of North Carolina at Chapel Hill Curriculum in Marine Sciences, NSF grants OCE 77-07939 and OCE 79-09323 from the Biological Oceanography Program to C. Peterson and funds from my father W. G. Ambrose. Support during the preparation of this manuscript was also provided by a National Research Council Associateship with the Environmental Protection Agency and a Royal Norwegian Council for Scientific and Industrial Research postdoctoral fellowship.

REFERENCES

Adams, S. M. and J. W. Angelovic. 1970. Assimilation of detritus and its associated bacteria by three species of estuarine animals. Chesapeake Sci., *11,* 249–254.

Ambrose, W. G., Jr. 1982. The influence of the predatory polychaetes *Glycera dibranchiata* and *Nereis virens* on the structure of a soft-bottom community in a Maine estuary. Ph.D. thesis, Univ. of North Carolina, Chapel Hill, NC, 165 pp.

Barnes, R. D. 1974. Invertebrate Zoology, W. B. Saunders Co., Philadelphia, 870 pp.

Breese, W. P. and D. F. Phibbs. 1972. Ingestion of bivalve molluscan larvae by the polychaete annelid *Polydora ligni.* The Veliger, *14,* 274.

Brenchley, G. A. 1981. Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom communities. J. Mar. Res., *39,* 767–790.

Brownlee, K. A. 1965. Statistical Theory and Methodology in Science and Engineering, 2nd ed., John Wiley and Sons Inc., New York, 590 pp.

Commito, J. A. 1982. The importance of predation by infaunal polychaetes in controlling the structure of a soft-bottom community in Maine, USA. Mar. Biol., *68,* 77–81.

Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat., *111,* 1119–1144.

De Wilde, P. A. W. S. 1975. Influence of temperature on behavior, energy metabolism and growth of *Macoma balthica, in* The Biochemistry, Physiology and Behavior of Marine Organisms in Relation to Their Ecology, H. Barnes, ed., Aberdeen Univ. Press., Aberdeen, Scotland, 760 pp.

Eckman, J. E. 1983. Hydrodynamic processes affecting benthic recruitment. Limnol. Oceanogr., *28,* 241–257.

Fauchald, K. and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Ann. Rev., *17,* 193–284.

Gallagher, L. E. D., P. A. Jumars and D. D. Trueblood. 1983. Facilitation of soft-bottom succession by tube builders. Ecology, *64,* 1200–1216.

Grassle, J. F. and J. P. Grassle. 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. J. Mar. Res., *32,* 254–289.

Gray, J. S. 1974. Animal-sediment relationships. Oceanogr. Mar. Biol. Ann. Rev., *12,* 233–261.

Hunt, J. H. 1981. The importance of adult-larval interactions in determining abundance patterns of soft-sediment infauna. M. S. thesis, Univ. of North Carolina, Chapel Hill, NC, 59 pp.

Klawe, W. L. and L. M. Dickie. 1957. Biology of the blood worm *Glycera dibranchiata* Ehlers, and its relation to the blood worm fishers of the maritime provinces. Bull. Fish. Res. Can., *115,* 1–37.

McCall, P. L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. Mar. Res., *35,* 221–226.

Mileikovsky, S. A. 1974. On predation of pelagic larvae and early juveniles of marine bottom invertebrates by adult benthic invertebrates and their passing alive through their predators. Mar. Biol., *26,* 303–311.

Oliver, J. S. 1979. Physical and biological processes affecting the organization of marine soft-bottom communities in Monterey Bay, California and MucMurdo Sound, Antarctica. Ph.D. thesis, Univ. of California, San Diego, CA, 310 pp.

Oliver, J. S., J. M. Oakden and P. N. Slattery. 1982. Phoxocephalid amphipod crustaceans as predators on larvae and juveniles in marine soft-bottom communities. Mar. Ecol. Prog. Ser., *7,* 179–184.

Peterson, C. H. 1979. Predation, competitive exclusion and diversity in the soft-sediment communities of estuaries and lagoons, *in* Ecological Processes in Coastal and Marine Systems, R. J. Livingston, ed., Plenum Press, New York, 548 pp.

——1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension feeding bivalves, *Protothaca staminea* and *Chione undatella.* Ecol. Monogr., *52,* 437–475.

Rhoads, D. C., P. L. McCall and J. Y. Yingst. 1978. Disturbance and production of the estuarine seafloor. Am. Sci., *66,* 577–586.

Rhoads, D. C. and D. K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community structure. J. Mar. Res., *28,* 150–178.

Segerstråle, S. G. 1962. Investigations of Baltic populations of the bivalve *Macoma baltica* (L.). Part II. What are the reasons for the periodic failure of recruitment and scarcity of *Macoma* in the deeper water of the inner Baltic? Commentat. Biol., *24,* 1–26.

Simon, J. L. 1965. Feeding in the annelid *Eteone heteropoda.* U. S. Fla. Acad. Sci., *28,* 370–372.

Sokal, R. R. and F. J. Rohlf. 1981. Biomety, 2nd ed., W. H. Freeman and Co., San Francisco, CA, 859 pp.

Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology, *60,* 1225–1239.

Sutherland, J. P. 1978. Functional roles of *Schizoporella* and *Styela* in the fouling community at Beaufort, North Carolina. Ecology, *59,* 257–264.

——1981. The fouling community at Beaufort, North Carolina, a study in stability. Am. Nat., *118,* 499–519.

Sutherland, J. P. and R. H. Karlson. 1977. Development and stability of the fouling community of Beaufort, North Carolina. Ecol. Monogr., *47,* 425–446.

Thistle, D. 1981. Natural physical disturbance and communities of marine soft-bottoms. Mar. Ecol. Ser., *6,* 223–281.

Watzin, M. C. 1983. The effects of meiofauna on settling macrofauna: meiofauna may structure macrofaunal communities. Oecologia, *59,* 163–166.

Whittaker, R. H. 1975. Communities and Ecosystems, 2nd ed., MacMillan Publishing Co., New York, 387 pp.

Williams, J. G. 1980. The influence of adults on the settlement of spat of the clam, *Tapes japonica*. J. Mar. Res., *38*, 729–741.

Wilson, W. H. 1980. A laboratory investigation of the effect of a terebellid polychaete on the survivorship of nereid polychaete larvae. J. Exp. Mar. Biol. Ecol., *46*, 73–80.

—— 1981. Sediment-mediated interactions in a densely populated assemblage: the effects of the polychaete *Abarenicola pacifica*. J. Mar. Res., *39*, 737–748.

Woodin, S. A. 1976. Adult-larval interactions in dense infaunal assemblages: patterns of abundance. J. Mar. Res., *34*, 25–41.

Zajac, R. N. and R. B. Whitlatch. 1982a. Responses of estuarine infauna to disturbance I. Spatial and temporal variation of initial recolonization. Mar. Ecol. Prog. Ser., *10*, 1–14.

—— 1982b. Responses of estuarine infauna to disturbance II. Spatial and temporal variation of succession. Mar. Ecol. Prog. Ser., *10*, 15–27.

Received: *27 June, 1983;* revised: *21 March, 1984.*