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Marine Soft-Bottom Community Establishment Following Annual Defaunation: Larval or Adult Recruitment?*

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ABSTRACT: Recolonization, following annual summer defaunation of a large-areal soft-bottom community in Hillsborough Bay, Tampa, Florida, USA was investigated to determine whether adult or larval recruitment was primarily responsible for re-establishing the community. Two quantitative sampling designs were employed: (1) Samples of the natural bottom were collected one month after each defaunation during 1975, 1976 and 1977, and washed through a 500 μm sieve; (2) containers of azoic sediment were placed and collected weekly during a 10-week period immediately following the 1978 defaunation, and washed through a 250 μm sieve. The weekly samples contained almost all newly settled larvae, (99.7 %), while the monthly samples contained only 41 % newly settled larvae. Whether the community was established by adult or larval settlement appeared to be taxon specific. Polychaetes and molluscs were mostly present as newly metamorphosed larvae. Amphipods, cumaceans and flatworms were initially present as adults. The discrepancies in the results stem from differences in methodologies of the two designs. The conclusion follows that methodologies must be tailored to the specific question posed, and that in this study, the majority of the initial community was established by larval rather than adult settlement.

INTRODUCTION

The actual modes of establishment and maintenance of marine benthic communities have been of interest since Petersen (1913) first revealed patterns of occurrences of Danish North Sea fauna. Thorson (1946, 1950), observing that many organisms possessed a pelagic larval stage, believed that establishment and maintenance of the community was the result of an 'indiscriminant rain and random settlement' of pelagic larvae. As he investigated areas other than the North Sea, Thorson (1955, 1957) found repeatable patterns of community structure varying only slightly over a wide geographic range, which led him to postulate his theory of parallel level-bottom communities (Thorson 1958), and which altered his ideas of 'indiscriminant rain and random settlement'. Even though he later refuted the parallel level-bottom theory (Thorson, 1966), it nevertheless prompted him to consider alternatives to the 'indiscriminant rain and random settlement' hypothesis of community establishment and maintenance. He concluded that community composition in the benthos was dependent on larval settlement, but not in a random fashion. He felt that larvae were influenced by 3 major forces acting in concert: (1) selective forces acting directly on the larvae while in the water column; (2) ability of larvae to select the correct substratum and even delay metamorphosis until it is located; (3) larval predation at the time of settlement. Thus community composition would be influenced by the differential larval response to these forces.

Day (1977) and Rice (1978) demonstrated experimentally that environmental factors can influence metamorphosis of some polydorid polychaete larvae while the larvae are in the water column. Wilson (1953, 1954), Thorson (1966) and Scheltema (1974) showed that the ability to select the proper substratum and even to delay metamorphosis until it is found, is quite prevalent, at least for members of the Mollusca and Polychaeta. Larval predation at the time of settlement has been demonstrated to directly influence community composition (Ziegelmeier, 1970; Rees et al., 1977; Best, 1978).

Can marine benthic communities become established by means other than larval recruitment? Hard substratum communities, because of the sessile nature

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of most inhabitants, likely depend on larval settlement for establishment and maintenance. Whether soft-bottom communities conform to this pattern is in question. In Long Island Sound, New York, McCall (1977), using trays of laboratory defaunated sediments, demonstrated through recolonization experiments that the majority of the initial colonization (Group I species) was by larval settlement. Conversely, Dauer and Simon (1976), in a recolonization study of only the polychaete component of a soft-bottom community following a natural defaunation in Tampa Bay, Florida, implied that the initial colonization was not by larval settlement but by adult migration. Likewise, in a recent review, Pearson and Rosenberg (1978) opined that during the initial colonization of areas that have suffered total defaunation, adult migration might play a greater role than larval settlement. This view is partially based on the results of Brunswig et al. (1976) who found adult *Harmothoe sarsi* Kinberg (Polychaeta) and *Diastylis rathkei* Kroyer (Cumacea) colonizing defaunated sediments.

Infaunal benthos display two types of dispersal movement: (1) horizontal, crawling over or through the substratum; (2) vertical, leaving the sediment to swim or drift through the water column and subsequently settling. The most efficient movement from the point of view of recolonization is dictated by the size of the area to be repopulated. To illustrate this, we make the assumption that the most successful colonizers are those that arrive first. Consider 2 empty plots of substratum, one 1 cm^2, the other 1 km^2, and assume the area surrounding each plot is saturated with organisms. It is easy to conceive of the small area being repopulated by adults crawling in from the edges. As the size of the plot is relatively small, it is unlikely that an individual would settle from the water column before recolonization occurred from the edges. Similarly, for organisms to crawl to the center of a large plot and initially colonize would be unlikely as colonization from the water column would likely precede them.

The adults of certain taxa (most bivalves, gastropods, echinoderms, etc.) are incapable of vertical movement and, therefore, must rely on horizontal modes. Recolonization of large areas by these organisms would depend on vertical movement of larvae. Thomas and Jelly (1972), Dean (1978a, b) and Dauer (personal communication) have observed adults of certain polychaete species, which had previously been considered sedentary non-swimmers or were only thought to be in the water column during times of reproduction, swimming in the plankton. Dean (1978a, b) interprets this movement as migratory behavior. Several infaunal crustacean groups have also been reported to exhibit migratory swimming behavior (Calman 1912; Mills 1967).

In light of this evidence, the possibility exists that newly created large-areal spaces can be colonized initially from the water column by larvae and adults. The present study was initiated to test whether adult or larval settlement from the water column was responsible for the initial colonization of a large (> 3 km^2) soft-bottom area that undergoes an annual total defaunation.

MATERIALS AND METHODS

The study site is located approximately 50 m ESE from the Ballast Point pier on the western side of Hillsborough Bay, Tampa, Florida, at about 27° 53′ 15″ N and 82° 28′ 35″ W. This location was chosen as it is a site which undergoes an annual summer total defaunation, most likely attributable to anoxic conditions (Santos, 1979). Depth ranges from 4–5 m depending on tidal conditions, and sediments are mostly composed of fine particles (mean percent of silt/clay = 10.34). Tidal flow is slight, ≈ 0.5 knots.

As part of a larger study (Simon, unpublished report), during the period February 1975–July 1978, monthly benthic samples (with a single exception) were collected with SCUBA-diver-operated, hand-held PVC cores (inside diameter = 7.62 cm, surface area = 45.60 cm^2) to a depth of 15 cm. Ten cores were taken to insure an adequate sample size (Santos, 1979). Samples were sieved through a 500 μm screen. The portion retained was narcotized in a 0.15 ‰ solution of propylene phenoxetol (McKay and Hartzband, 1970) and fixed in 10 % formalin to which rose bengal (200 mg l^{-1}) had been added (Mason and Yevich, 1967). All benthic fauna were sorted from the sediment, identified to the lowest practical taxon and enumerated.

Qualitative determination of whether adults or larvae were present was made by the following method. Total length measurements were made monthly on 100 randomly chosen individuals of each species. In those instances where fewer than 100 individuals were present, all specimens were measured. The smallest organisms that were brooding young or carrying eggs were considered adults, as were individuals of comparable or larger size. As polychaetes fragment easily, total length measurements were difficult to obtain. For this taxon the width of the first setiger was used to indicate size, as Hobson (1971), Dauer (1974), and Buchanan and Warwick (1974) have shown this to be a reliable character highly correlated with total length. Organisms found at the first sampling periods following defaunations (by definition = the initial colonizers) were measured and the measurements compared to that of the smallest adult (as determined above);

those not satisfying the adult criteria were considered to have arrived as larvae.

Plankton tows, taken irregularly following the 1978 die-off, were used to determine whether larvae or adults were available for settlement from the water column. A fine-mesh net (144 µm) was towed at the study site either by hand (night) or behind a small boat (day) for varying periods of time (mean: 8 min). The plankton was returned to the laboratory and examined for the presence of infaunal organisms, which were identified to the lowest practical taxon and measured.

As the life histories of most species were unknown, an experiment was designed to ascertain whether the same conclusions could be supported if samples were taken at shorter intervals (weekly vs monthly). A 10-week recolonization experiment was initiated immediately following the 1978 die-off (Oct.--Dec. 1978). Sediment that had been collected from the study site 5–6 months earlier was rendered azoic by repeated (9–10 times) freezing and thawing. Random samples of the treated sediment contained no organisms. The sediment was placed in plastic cups (surface area = 26.66 cm^2) mounted in a Plexiglas frame which was attached to a stainless steel plate mounted 0.5 m from the natural bottom. To prevent loss of sediment and colonization from the upper levels of the water column during the lowering, covers were left on the cups. These were removed after the apparatus was secured

Table 1. Initial colonizing species following natural and experimental defaunations

Species	Natural 1975	1976	1977	Experimental 1978
Platyhelminthes				
Stylochus sp.	×			×
Rhynchocoela				×
Polychaeta				
Nereis succinea Frey & Leuckhart	×	×	×	×
Paraprionospio pinnata (Ehlers)	×		×	×
Gyptis vittata Webster & Benedict	×		×	×
Capitella capitata (Fabricius)	×		×	×
Eteone heteropoda Hartman	×		×	×
Glycinde solitaria (Webster)	×			×
Streblospio benedicti Webster	×	×		×
Parahesione luteola (Webster)	×	×		×
Pectinaria gouldii (Verrill)	×		×	
Minuspio cirrifera (Wiren)		×		×
Mediomastus californiensis Hartman		×		×
Melinna maculata Webster		×		
Diopatra cuprea (Bosc)			×	×
Polydora ligni Webster				×
Poecilochaetous johnstoni Hartman				×
Brania wellfleetensis Pettibone				×
Schistomeringos rudolphi (Delle Chiaje)				×
Onuphis sp.				×
Glycera americana Leidy				×
Phyllodoce arenae Webster				×
Syllis sp.				×
Oligochaeta	×	×	×	
Mollusca				
Acteon punctostriatus (C.B. Adams)	×			
Cochliolepis sp.	×			
Haminoea succinea (Conrad)				×
Nudibranchia				×
Mulinia lateralis (Say)	×		×	×
Mysella planulata (Stimpson)			×	
Amphipoda				
Ampelisca abdita Mills	×		×	×
Grandidierella bonnieroides Stephenson				×
Gitanopsis sp.				×
Cumacea				
Cyclaspis sp.				×
Copepoda				
Harpactacoida				×

and replaced just before each sample was collected. Four cups were collected every 7 d; these were replaced by new cups which were sampled 7 d later. All sampling was performed by SCUBA diving. Monthly samples taken as part of the larger study will be referred to as 'regular' samples to distinguish them from samples set out and collected weekly, which will be termed 'experimental' samples.

Cups were transported to the laboratory and the entire sample relaxed (0.15 % propylene phenoxetol) and fixed (10 % formalin with 200 mg l^{-1} of rose bengal stain). After 24–36 h, the sediments were sieved through a 250 μm screen. The portion remaining on the screen was examined for the presence of benthic organisms, which were identified to the lowest practical taxon, enumerated and measured as above.

At several times during the experimental recolonization study, core samples (surface area = 45.60 m^2) from the area immediately surrounding the apparatus were taken and treated similarly to determine if recolonization of the natural bottom was occurring.

RESULTS

Plankton tows revealed that larvae were present throughout the 10-week experimental study period. No adults were found in any tows. Several taxa were present in every tow: *Streblospio benedicti, Paraprionospio pinnata, Polydora ligni, Gyptis vittata,* unidentified polychaete larvae, *Mulinia lateralis* veligers, unidentified gastropod and bivalve veligers, barnacle cyprid larvae and decapod crustacean larvae.

Thirty-five species were found as initial colonizers during the first sampling period following defaunations (Table 1). Comparison of the initial colonization of the substratum following the natural defaunation (regular samples) with the initial colonization of the azoic substratum following the induced defaunation (experimental samples) revealed different patterns (Table 2). The most striking differences are the adult/juvenile (arrived as larvae) ratios. The regular samples, averaged over the 3 initial sampling periods, contained a mean of 59 % adults, while the experimental samples contained almost no adults (0.3 %). The experimental samples also demonstrated more initial species than the regular samples, 29 vs 20 (Table 1), even though the sample size for the regular samples was larger. In both types of samples, polychaetes were the dominant taxon (Tables 1, 2).

Taxonomic differences in whether adults or juveniles are the initial colonizers are presented in Table 3. Cumaceans, amphipods, harpactacoid copepods and the flatworm *Stylochus* sp. were initially present only as adults. The polychaetes were represented mostly by newly metamorphosed juveniles, except for 3 species. *Gyptis vittata, Parahesione luteola* and *Nereis succinea* were initially present as both adult and newly metamorphosed juveniles. Molluscs were always present as newly metamorphosed juveniles.

Table 2. Comparison of taxonomic and age structure of initial colonizers following natural and experimental defaunations. All numbers are percentages

Taxon	Natural 1975	Natural 1976	Natural 1977	Experimental 1978
Polychaeta	60.0	85.7	60.0	65.5
Oligochaeta	6.7	14.3	10.0	–
Amphipoda	6.7	–	10.0	10.3
Mollusca	20.0	–	20.0	10.3
Miscellaneous	6.7	–	–	13.8
Adult	65.0	57.0	55.0	0.3
Juvenile	35.0	43.0	45.0	99.7

Table 3. Occurrence of adult and juvenile stages of dominant macroinvertebrate species during the experimental study

Species	Adult	Juvenile
Streblospio benedicti	absent	present
Mediomastus californiensis	absent	present
Diopatra cuprea	absent	present
Mulinia lateralis	absent	present
Nereis succinea	present	present
Gyptis vittata	present	present
Parahesione luteola	present	present
Stylochus sp.	present	absent
Harpactacoid copepods	present	absent
Amphipoda	present	absent
Cumacea	present	absent

During 1975, 1976 and 1977, recolonization was initiated by the first month following the natural defaunation. The number of species and number of individuals accrued rapidly following the 1975 defaunation, and more slowly after the 1976 and 1977 defaunations (Fig 1, 2). However, following the 1978 defaunation (the time of experimental sampling), core samples taken from the sediment surrounding the experimental apparatus did not demonstrate any recolonization during the entire 10-week study. Yet, at the same time, the experimental samples that were 0.5 m from the bottom showed rapid initial colonization, both in number of species and number of individuals (Fig. 3).

DISCUSSION AND CONCLUSIONS

The constant presence of larvae in plankton samples demonstrated their availability for recruitment if suitable habitats were found. The larvae that were iden-

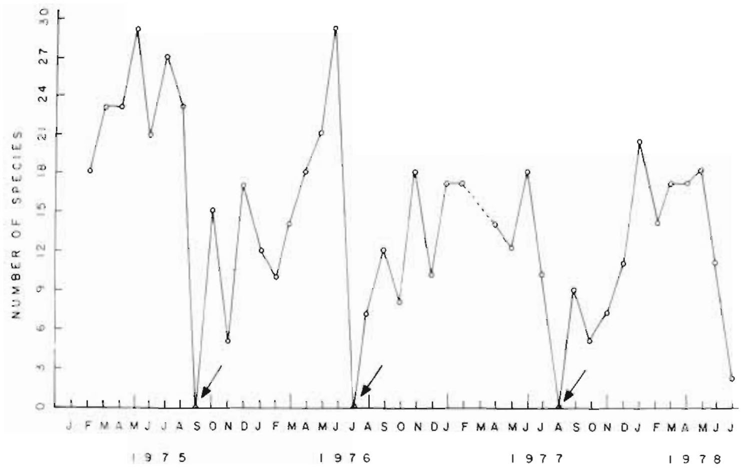

Fig. 1. Number of macroinvertebrate species present in Hillsborough Bay, Tampa, Florida (USA), at each regular sampling period, February 1975–July 1978. Broken line: interpolated values due to missing data

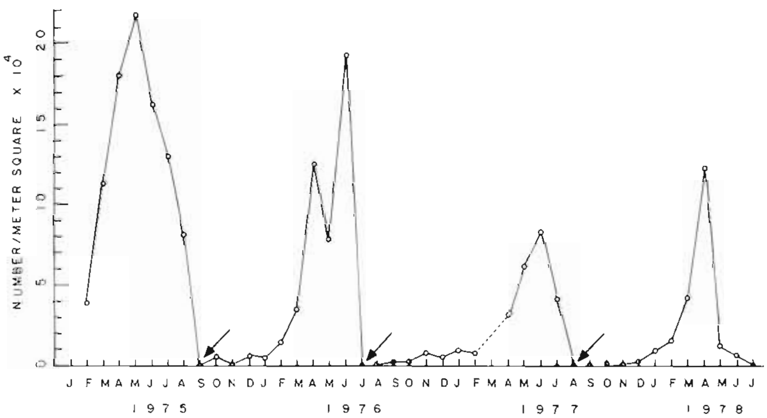

Fig. 2. Total density $m^{-2} \times 10^4$ of all macroinvertebrate organisms in Hillsborough Bay, Tampa, Florida, at each regular sampling period, February 1975–July 1978. Broken line: interpolated values due to missing data

tified from each plankton sample are a small portion of the total species from the study. Due to difficulties with larval identifications, it is not known whether most species found in the study were present in the plankton. It is reasonable to assume that not every species would be present as larvae at every sampling period. However, a sizable number of species must have been available so that the probability of recruitment consisting of more than 1 or 2 species was high. This is reinforced by the findings listed in Table 1, demonstrating that many species, rather than a select few, were able to initially colonize empty sediment. Only *Nereis succinea* was present at all recolonizations investigated.

The decision as to whether larvae or adults initially established the community varied depending on the taxon and samples examined. The experimental data revealed a picture contrary to the regular sampling data. Experimental samples showed an almost exclusive colonization by larvae (99.7 %, Table 2). Mollusca were present only as newly metamorphosed juveniles; polychaetes were almost all newly metamorphosed juveniles (> 99 %). The Platyhelminthes, Cumacea, Amphipoda and harpactacoid Copepoda were always initially present as adults. The regular samples, on the other hand, showed a majority of colonizers were adults rather than larvae. More than 50 % of the total polychaete fauna was composed of adults (Table 2).

Why does a discrepancy exist between the 2 groups of observations? We suspect the answer is related to 2 factors: (1) time interval between sampling, and (2) sieve size. Regular samples were taken at monthly intervals while the experimental samples were collected weekly. In South Florida, at least, the generation times of many small infaunal invertebrates are equal to or less than one month (personal observation). For example, 2 of the species dominant throughout both the last year of the regular study and the entire experimental study, *Streblospio benedicti* and *Mediomastus californiensis*, were initially present in the experimental study as juveniles. Within 2 weeks, cohorts of these individuals were bearing eggs. S. A.

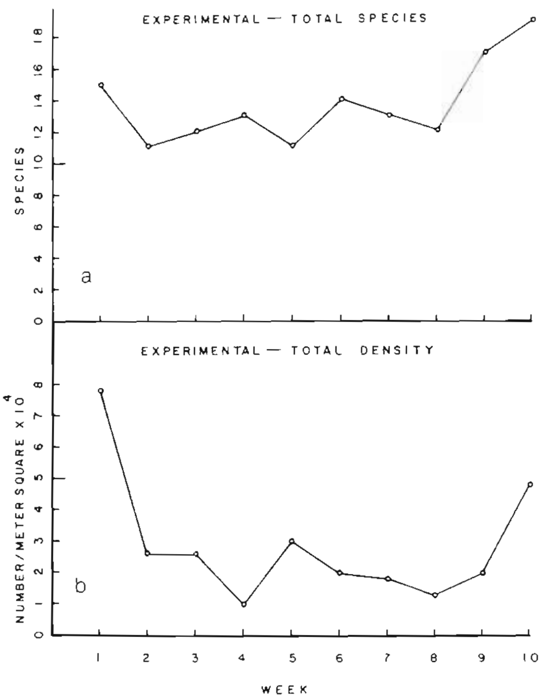

Fig. 3. Macroinvertebrate organisms in Hillsborough Bay, Tampa, Florida, present at each sampling period during the experimental study. (a) Total number of species; (b) total density $m^{-2} \times 10^4$

Rice (personal communication) determined that the egg to egg generation time of *Polydora ligni* from Tampa Bay could be as short as 21 d. Therefore, sampling performed less frequently than bi-weekly probably is not valid in determining whether adult or larval recruitment is primarily responsible for establishing the community. Reish (1959) has discussed the problems associated with sieve size. One of us (SLS, unpublished) has shown that although there is not much difference in species composition when comparing a 500 µm to a 250 µm screen, as many as 40 % of the number of juveniles can be lost through the larger sieve.

Once space becomes available, either through introduction of new habitat or abatement of conditions that originally caused the defaunation, recolonization proceeds rapidly. As the area surrounding the experimental apparatus was azoic, even after 10 weeks, we suspect that the anoxic conditions lasted longer than in the previous 3 years. However, because of the azoic nature of the sediments surrounding the apparatus, we are confident that all recruitment was from the water column and not the result of migration from the adjacent sediments.

The discrepancies in our findings which are allied to those of McCall (1977), and different from those of Brunswig et al. (1976) and Dauer and Simon (1976), may be attributed to differences in methodologies. The use of a sieve smaller than 500 µm and sampling more often than monthly, at least initially, (present study; McCall, 1977) give results more reflective of actual recruitment dynamics. This is an excellent illustration that methodologies should be tailored to the specific question under investigation. Utilizing one methodology to answer several questions may result in one or more questions being answered incorrectly.

In the present study we conclude that the majority of the initial colonization was performed by settling larvae rather than adults. Certain taxa, however, were found initially only as adults. Thus, a generalization concerning whether adult or larval recruitment is responsible for establishing the community is not possible without first defining the taxa in question.

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