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Habitat complexity of polychaete tube-caps: Influence of architecture on dynamics of a meioepibenthic assemblage

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ABSTRACT

A series of field experiments was conducted in a shallow sandflat in Tampa Bay, Florida, to examine the relationship between the abundance and diversity of meiofauna and the architectural complexity of tube-caps constructed by the polychaete, *Diopatra cuprea.* Two groups of azoic tube-caps were utilized: 1) tube-caps collected from the field and defaunated in the laboratory or 2) tube-caps created in laboratory aquaria with azoic sediment under controlled conditions. Tube-caps were designated "high" or "low" complexity based upon the amount of shell hash incorporated into tube-cap structure, replanted into sediments at 2 sites during February–April 1982 and collected 1, 3, or 4 days later. Meiofaunal-size organisms quickly recolonized experimental tube-caps. Harpacticoid copepods (adults, copepodites, nauplii) and juvenile amphipods displayed repeatedly higher abundance on tube-caps of high architectural complexity compared to those with low structural characteristics regardless of origin of tube-caps. This effect varied over space and time for some taxa. Examination of copepod species patterns revealed higher numbers of 72% of species on high complexity tube-caps over the experimental period; this relationship was modified occasionally by depth and day of retrieval. Correlation analysis of taxa abundance vs. quantitative measurements of architectural complexity reiterated the experimental trends, i.e. both copepod species richness and abundance of meiofaunal crustaceans were significantly positively correlated with the architectural complexity (amount of shell hash) of tube-caps.

Two additional experiments were conducted in November 1983 and March 1984 to further investigate one possible explanation for the abundance/complexity relationships of meiofauna taxa and tube-caps. To test whether large amounts of shell in tube-caps provide refuges from predators, recolonization experiments were conducted in both predator exculsion and open sites. Higher densities of harpacticoid copepods were recorded on tube-caps with greater amounts of shell hash regardless of predator activity. It is concluded that tube-cap complexity strongly influences abundance/species richness of meiofaunal crustaceans but a decrease of predator effectiveness on tube-caps with high complexity cannot explain the observed abundance/complexity relationship. The results from this study coupled with previous investigations on meioepibenthic assemblages provide a unique scenario of factors which, by controlling tube-cap turnover and architectural complexity, influence meiofaunal community structure.

1. Introduction

Relationships between the abundance and diversity of organisms and the structural complexity of habitats have been examined continually in both terrestrial (e.g.

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MacArthur and MacArthur, 1961) and aquatic (e.g. Abele, 1974) environs. A basic tenet which has emerged from many of these studies is that an increase in habitat complexity (changes in habitat physiognomy) or heterogeneity (changes in habitat form; see August, 1983) is accompanied by an increase in abundance and/or diversity of organisms. The positive association is suggested to be due to either: 1) increasing inhabitable physical space or opening of new niches for species exploitation or 2) providing refuge from predators. Much of the evidence to support the predicted relationship is correlative (e.g. Heck and Wetstone, 1977; Hicks, 1980; August, 1983) although some experimental evidence has also accumulated recently (e.g. Kohn and Leviten, 1976; Coull and Wells, 1983; McDonnell and Stiles, 1983; Gillinsky, 1984).

To a large extent, information on relationships between habitat complexity and heterogeneity and animal communities has come from studies focusing on density, arrangement, or physiognomy of vegetation. Vegetation structure has been correlated with, or experimentally studied in relation to, bird (MacArthur and MacArthur, 1961; Wiens, 1974), mammal (August, 1983), insect (Lawton, 1978; Gillinsky, 1984) and crustacean (e.g. Vince *et al.*, 1976; Crowder and Cooper, 1982; Nelson, 1979; Hicks, 1980; Heck and Thoman, 1981) communities in both temperate and tropical systems. Habitat complexity has also been used to refer to topographical complexity of nonliving structures (i.e. crevices in intertidal rock platforms) and species abundance and diversity of both benthic invertebrates and algae have been examined in areas where relief of geologically-provided microhabitats varies (e.g. Kohn and Leviten, 1976; Kohn, 1983; Lubchenco, 1983). Few studies have examined directly the relationship between faunal community structure and habitat complexity of structures provided by animals. Marine investigations on habitat complexity of corals and decapod crustacean (Abele, 1976) and gastropod (Kohn, 1983) community structure stand out as the only representative reports that address directly abundance and diversity relationships with structures provided by animals.

This study documents the relationship between faunal community structure and habitat complexity of a zoogenic structure in a marine system. I ask primarily whether there is any relationship between the abundance of small marine metazoans, i.e. meiofauna, and habitat architecture or physiognomy of tube-caps constructed by a polychaete, *Diopatra cuprea,* upon which meiofaunal-size organisms reside. Additionally, I compare species richness of harpacticoid copepods on tube-caps of varying architectural characteristics. A series of experiments designed to investigate complexity-abundance relationships and evaluate whether variation in predator effectiveness can account for predicted relationships is presented below.

2. Methods and materials

a. Background information. Meiofaunal organisms such as nematodes, copepods, and ostracods, and macrofauna such as amphipods and polychaetes are abundant infaunally. They also live associated on the tube-caps created by the polychaete, *Diopatra*

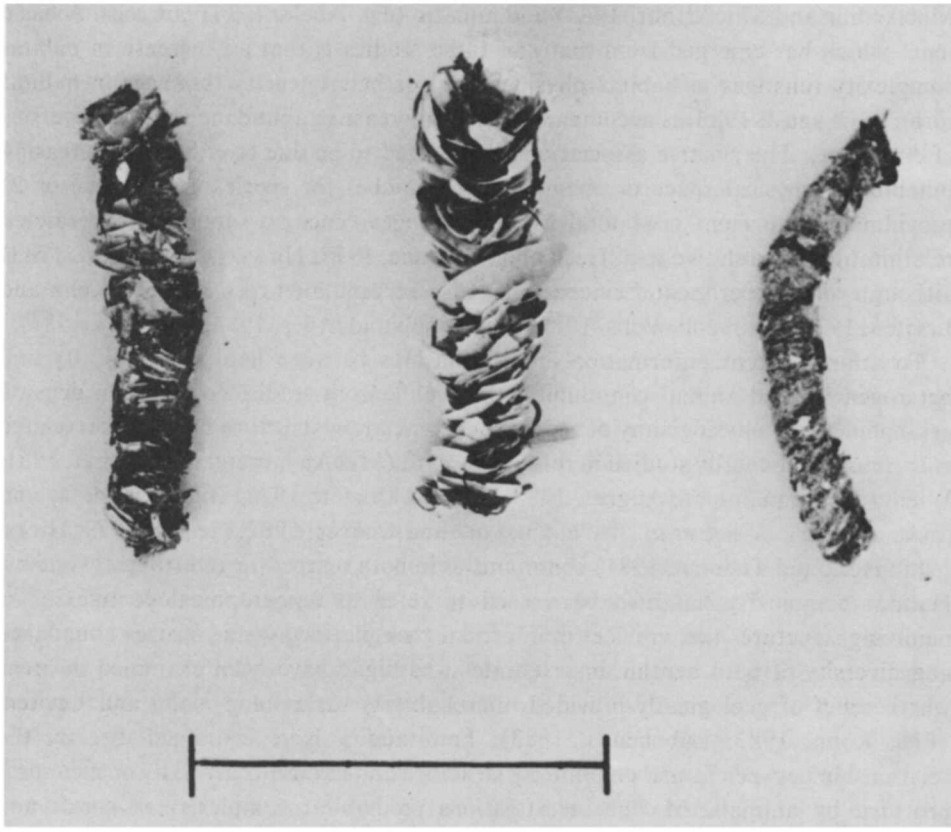

Figure 1. Tube-caps of *Diopatra cuprea* collected from shallow sandflat showing natural variation in architectural complexity or amount of shell incorporated into tube-cap. Scale line = 4 cm. *IC* values for tube-caps from left to right are .23, .37 and .10, respectively.

cuprea (Brenchley, 1975; Bell and Coen, 1982a). Tube-caps (defined as that part of the tube extending above the sediment surface) are composed of sand embedded in a mucopolysaccharide matrix which worms further decorate with shell, algae and assorted debris (Magnum *et al.*, 1968; Myers, 1970). The incorporated items reinforce the above-ground tube segment and may trap sand, detrital particles, or fecal pellets within the imbricate network (Fig. 1). Ornamentation of tube-caps may also facilitate predator detection and/or avoidance for *Diopatra* (Brenchley, 1976). Meiofaunal organisms associated with tube-caps inhabit and move among the sand or detrital particles sequestered by, or attached to, shell surfaces. Shell material does not serve as a "primary" substrate for meiofauna but may by its presence: 1) serve as refuges from physical stress or predator activity or 2) harbor detrital and microalgal food sources. Field collections of tube-caps from Tampa Bay, Florida for over two years revealed wide variation in the amount of bivalve shell material incorporated into tube-caps (see

Fig. 1, for example) and, thus, variation provides a natural spectrum of architectural characteristics. Here, the amount of decorative shell material or architecture can be considered equivalent to structural or habitat complexity (*sensu* Kohn and Leviten, 1976; Heck and Wetstone, 1977) and these terms are used interchangeably below.

In previous experiments, Bell and Coen (1982a) demonstrated how tube-caps of *Diopatra cuprea* can be defaunated and used to assess recolonization events of meiofaunal organisms. I used similar experimental methodology to test for the effects of habitat architecture on meiofaunal abundance and diversity (species richness) and conducted a series of short-term experiments offering tube-caps of varying architectural complexity to recolonizing meiofaunal assemblages.

The tube-cap system was utilized in this study for a number of reasons. First, a significant correlation between meiofaunal abundance and amount of shell material was noted from collections of tube-caps and associated fauna over a 2-year period (n = 110, R = .86, P = 0.001). Second, the tube-cap system is amenable to experimentation. Tube-caps are easily collected from the field and defaunated, or grown in laboratory aquaria. The amount of shell or architectural features also can be manipulated directly under laboratory conditions so that a range of biogenically created tube-caps with different architectural characteristics can be offered to meiofauna for recolonization. Thirdly, because worms are continually adding material to their tube-caps in response to sediment burial (Bell, unpubl.), virgin habitat constantly is being generated. Thus, the experimental methodology documented above mimics a natural phenomenon. Finally, architectural complexity can be directly compared because different amounts of the same compositional material (bivalve shell hash) can be manipulated. Thus, results of the recolonization experiments should not be confounded by comparing response of animals to substrata of different "quality" (i.e., different types of algae *vs.* shell *vs.* seagrass blades).

b. Experimental procedures. Two groups of experiments were conducted in 1982 to test the null hypothesis that habitat architecture of tube-caps does not affect the abundance or species richness of meiofaunal organisms. One group of experiments employed tube-caps which were collected from the field and classified visually as high or low architectural complexity based upon a high or low amount of shell, respectively, in tube-caps at the time of sampling (see Fig. 1). The other group of experiments utilized tube-caps created by *Diopatra cuprea* in laboratory aquaria. The latter set of tube-caps was created by worms placed into azoic sediments previously collected from the field and supplied with either large or small amounts of shell material also retrieved from the intertidal area. Thus, laboratory grown tube-caps resembled tube-caps collected from the field except that the amount of shell in laboratory tube-caps could be controlled directly and the age of laboratory tube-caps was known.

Field tube-caps were defaunated by repeated washings with $MgCl_2$ and autoclaving for 15 mins. at 120°C. Both types of azoic tube-caps offered habitats of distinct

Table 1. Outline of experimental design for field experiments using defaunated tube-caps. Numbers refer to the number of tube-caps retrieved from the field for each day—depth—architectural treatment combination of the original 8–10 tube-caps planted at the beginning of the experiment (Day 0). *L* = low architectural complexity; *H* = high architectural complexity; *S* = shallow; *D* = deep.

		Experiment 1 (February 1982)					Experiment 2 (March–April 1982)			
		LS	*LD*	*HS*	*HD*		*LS*	*LD*	*HS*	*HD*
Field-collected tube-caps	Day 1	5	7	5	7	Day 1	8	9	8	7
	Day 3	10	8	5	6	Day 3	8	8	8	8
						Day 4	8	6	7	5
Lab-generated tube-caps	Day 1	5	9	10	9	Day 1	8	9	7	8
	Day 3	3	0	3	0	Day 3	8	8	8	8
						Day 4	6	6	9	8

architectural characteristics (see Fig. 1) and meiofaunal immigration onto azoic tube-caps could be monitored.

Tube-caps grown in laboratory aquaria and field sites were clipped below the sediment-water interface and attached to applicator sticks by monofilament line. Worms were not included inside tube-caps. Defaunated laboratory-generated and field-collected tube-caps were replanted into a sandflat in Tampa Bay, Florida (Lat 27°58′N; Long 82°35′W) from which the worms were originally collected. A colored bead on a monofilament line was also attached to the applicator stick to identify experimental treatments in the field. Tube-caps were retrieved from the field 1–4 days after replanting. Longer trials are prohibitive because tube-caps without worms become flaccid after 5–7 days and are washed away. However, earlier investigations indicated that rapid (within days) recolonization of meiofaunal assemblages took place in Tampa Bay sandflats (Bell and Coen, 1982a; see also Reidenauer and Thistle, 1982). One to four days provided sufficient time for abundance of all taxa and species composition of harpacticoid copepods to recover to levels recorded for field assemblages from natural tube-caps collected during experimental trials.

Tube-caps of similar size (approximately 1.9–2.2 cm in length, Experiment 1; 2.8 cm in length, Experiment 2) were replanted into two designated sites ("deep" and "shallow") in the sandflat. Preliminary observations indicated that tube-caps of higher architectural complexity were usually found in shallow sites, while lower complexity tube-caps were more restricted to deeper areas located approximately 15 m beyond the shallow site with 15.0 cm more water cover. By transplanting tube-caps of both types of architectural complexity into shallow and deep sites simultaneously, any possible site effects could be assessed. Recolonization experiments were conducted 2 times—during February (Experiment 1) and March–April (Experiment 2) 1982 and Table 1 summarizes the number of experimental units and timetable for Experiments 1 and 2.

Manipulation of tube-caps necessitated the removal of worms. Although not critical to the interpretation of results, I examined whether the presence or absence of *Diopatra cuprea* inside tube-caps has any effect on meiofaunal abundance. A short-term field experiment was conducted in July 1982. Thirty *Diopatra* tube-caps with similar amounts of shell (this was later verified in the laboratory) were selected and worms removed from 15 tubes by inserting and securing a long probe down the tube. Tube-caps were identified by inserting markers next to them. The other 15 worms were similarly handled by investigators but no probe was inserted and worm activity was unaltered. After 2 days, the presence or absence of worms in tubes and collected tube-caps from both "prodded" and unaltered treatments was reconfirmed. Over a 2-day period, no significant difference in the number of meiofauna (nematodes or copepods) on tube-caps with or without worms was found (t-test, $P > 0.005$), and all copepod species on tube-caps with worms were also found on tube-caps without worms, suggesting that my utilization of "naked" tube-caps attached to applicator sticks may not seriously alter recruitment or maintenance of meiofaunal populations.

Tube-caps were retrieved from the field, preserved in 10% formalin-seawater and returned to the laboratory for extraction of fauna (see Bell and Coen, 1982a) and confirmation of architectural complexity. Tube-caps which were broken or damaged were excluded from analyses. All taxa (including some macrofaunal organisms) were enumerated and all adult and late stage harpacticoid copepods identified to species when possible. Nematode species from laboratory-generated tube-caps from the February experiments were also identified to lowest possible taxon.

Tube-cap architecture which was visually determined before replanting into the field, was quantified after faunal extraction in the laboratory. Tube-caps were measured for length and diameter, dried for 24 hr. at 60°C and weighed. An "architectural index" was derived based on a series of previous laboratory measurements and statistical relationships. Regression analyses indicated that the weight of shell removed from tube-caps was significantly related to total tube-weight ($R = .68$; $P < 0.0001$; $n = 56$) and the surface area of shells (weight of adsorbed detergent, Harrod and Hall, 1962) was also related to the weight of shells dissected from tube-caps ($R = .84$; $P < 0.0001$; $n = 62$). Thus, shell weight was related to the surface area of shells and this could be easily measured by weighing intact tube-caps after drying. I thus express an architectural index (IC) as weight of tube-cap (g) $\times$ [tube-cap length (cm)]$^{-1}$ (see Fig. 1). This architectural index (IC) is offered as a method to quantify "high" versus "low" experimental treatments in recolonization studies. Tube-cap IC values utilized in each experiment represented approximate upper and lower levels of complexity which existed in field or laboratory conditions at the time of study.

c. Statistical analyses. Although architectural effects were of primary concern in this study, I was interested in meiofaunal responses over space and time as well. Therefore,

I conducted a three-way ANOVA on numbers of major meiofaunal groups with architecture (high, low) day (1, 3, 4), and depth (shallow, deep) as main effects. If necessary, abundances were log $(Y + 1)$ transformed to meet assumptions of tests. Field-collected and laboratory-generated tube-caps were analyzed separately and considered not comparable directly because treatment of tube-caps prior to replanting differed. A three-way MANOVA with architecture, day and depth as main effects, was used to analyze the nine most abundant copepod species from each experimental set. If Bartlett's test was not significant for the nine copepod species, univariate analyses of variance were performed. Because so many laboratory grown tube-caps were lost on day 3 of the February experiment, I conducted a two-way MANOVA on copepod species and two-way ANOVA on major taxon abundance using depth (shallow or deep) and architecture (high or low) as main effects on day 1 only. A Spearman-rank correlation procedure was used to examine the relationship between the ratio of tube-cap weight and tube-cap length (*IC*) and abundance of major taxa and copepod species. The $\alpha = 0.05$ level of significance was used in analyses. Additional statistical procedures are outlined in the Results section.

d. Additional field experiments. Two sets of manipulative experiments were performed during November 1983 and March 1984 to evaluate the hypothesis that tube-caps with more shell provided refuges from predators (shrimps and juvenile fishes, see Bell *et al.*, 1984) thus maintaining higher abundances of meiofaunal taxa observed on tube-caps with greater architectural complexity (see Results below). Given the results from previous field experiments in 1982, I chose to conduct the experiment at the shallow site with laboratory-grown tube-caps of both high and low architectural complexity. Two subsites (0.25 m × 0.25 m) were arbitrarily marked out in November 1983 and March 1984. Two sets of 12 tube-caps, one set with the large amounts of shell, the other with little shell, were haphazardly planted into sediments, following earlier procedures (p. 651). One site was designated predator absent and a 0.25 m × 0.25 m cage of 0.62 cm mesh tops and sides, inserted 10 cm into sediment, surrounded the tube-caps of both architectural complexity treatments at this area. Tube-caps were placed at least 5 cm away from the sides of the cages. The predator present site also had a cage erected in the area, but the cage was removed prior to the planting of tube-caps of both high and low complexity treatments. All tube-caps were collected 2 days after replanting in November 1982 and 1 day after replanting in March 1984 and returned to the laboratory for processing. The experiment was internally controlled because only the abundances of recolonizing meiofauna on tube-cap treatments within cage areas or on tube-cap treatments from noncaged sites were compared. Abundances of recolonizing taxa on tube-caps of high *versus* low architecture within cages were compared with a *t*-test, as were numbers on tube-caps of high *versus* low architectural complexity in noncage areas. Thus, if abundances of meiofauna on high architectural complexity tube-caps were greater than those on low

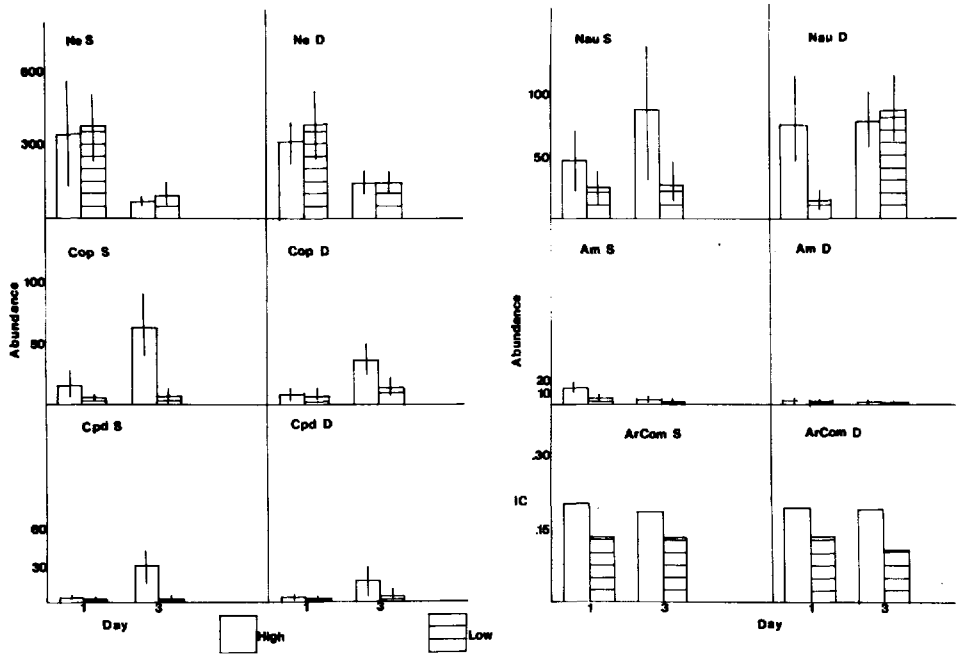

Figure 2. Mean abundance (± 1 s.d.) (y-axis) by treatment and day (x-axis) from Experiment 1 using field collected tube-caps. Densities are standardized to mean length (2.2 cm) of tube-caps (range of final length never exceeded ± 10% of mean in all experiments). Architectural complexity (= Arcom values (*IC*) in g shell × cm tube length^{-1}) for each treatment-day combination are provided for comparisons. High = high architectural complexity; Low = low architectural complexity; 1, 3, 4, = day of retrieval from field after replanting. Ne = nematodes; cop = copepods, stages IV–adult; cpd = copepodites; nau = nauplii; Am = juvenile amphipods; S = shallow; D = deep.

complexity tube-caps in the uncaged plot but the difference in abundances on tube-caps was not observed inside the predator exclusion plot particularly from low complexity tube-caps, then reduction of predator activities or provision of refugia could be implicated as an explanation for increased abundances on tube-caps of high architectural complexity. This experiment could not decipher whether, in the past, predation led to the selection of more complex tube-caps by meiofaunal prey. Rather, it was designed to test simply whether predator activity at the present time varied in high *versus* low complexity tube-caps as has been done in a variety of other systems (e.g., Coen *et al.*, 1981; Stoner, 1982).

3. Results

a. Major taxa. Nematodes and crustaceans (harpacticoid copepods and juvenile amphipods) were the most numerous taxa on experimental tube-caps. Other taxa such

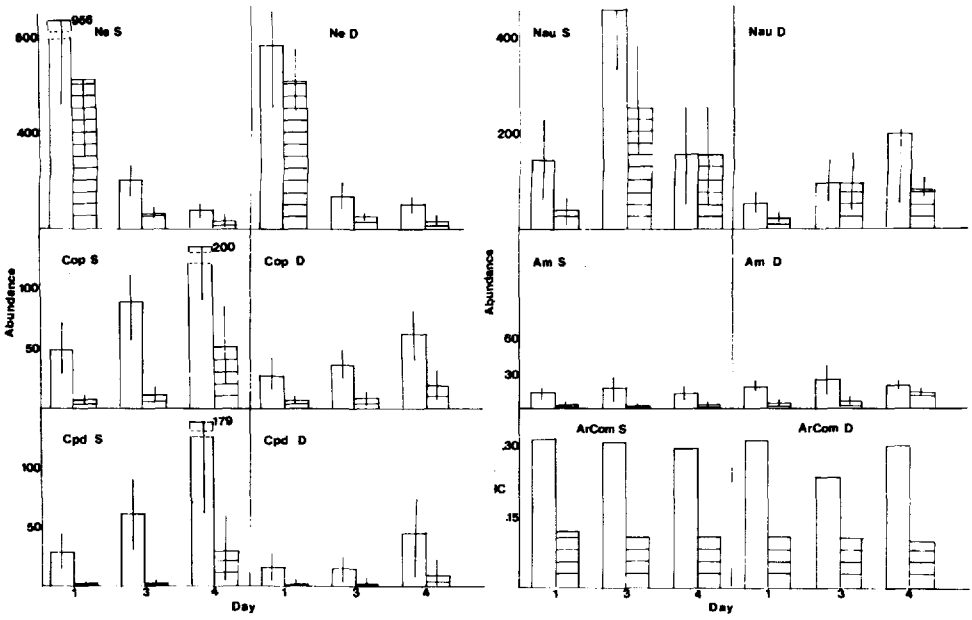

Figure 3. Mean abundance (± s.d.) (*y*-axis) by treatment and day (*x*-axis) from Experiment 2 using field collected tube-caps. Densities are standardized to mean length (2.1 cm) of tube-caps. Abbreviations as in Figure 2.

as juvenile polychaetes and bivalves, ostracods, and turbellarians also were recorded from tube-caps but only in low abundances and are excluded from the following discussions. Generally, taxa immigrated onto tube-caps quickly (see Figs. 2–5) and all species of copepods found on samples of natural tube-caps taken nearby were present within an interval of 2–4 days on experimental tube-caps. Nematode abundance showed inconsistent patterns of recolonization, i.e. sometimes increasing, sometimes decreasing. *IC* values calculated for experimental tube-caps were always within the range of those collected from field samplings (Bell, unpubl.) and differences between high and low complexity varied over dates and origin of tube-caps.

Analysis of variance of abundance of meiofaunal taxa on tube-caps from experimental groups utilizing field collected tube-caps (Figs. 2 and 3) indicated a variety of significant main effects or interactions. In Experiment 1 all crustacean taxa displayed a significant architectural effect with higher numbers on tube-caps of greater complexity. Significant time effects were also present with nematodes losing and crustaceans gaining numbers, respectively, as the experiment progressed from day 1 to 3. Significant time × architecture effects for nematodes were present with low complexity tube-caps losing more individuals than high complexity ones by day 3. However, adult copepods and copepodites (stages I–III) showed a different interaction with higher number of individuals recruiting to more structurally complex tube-caps

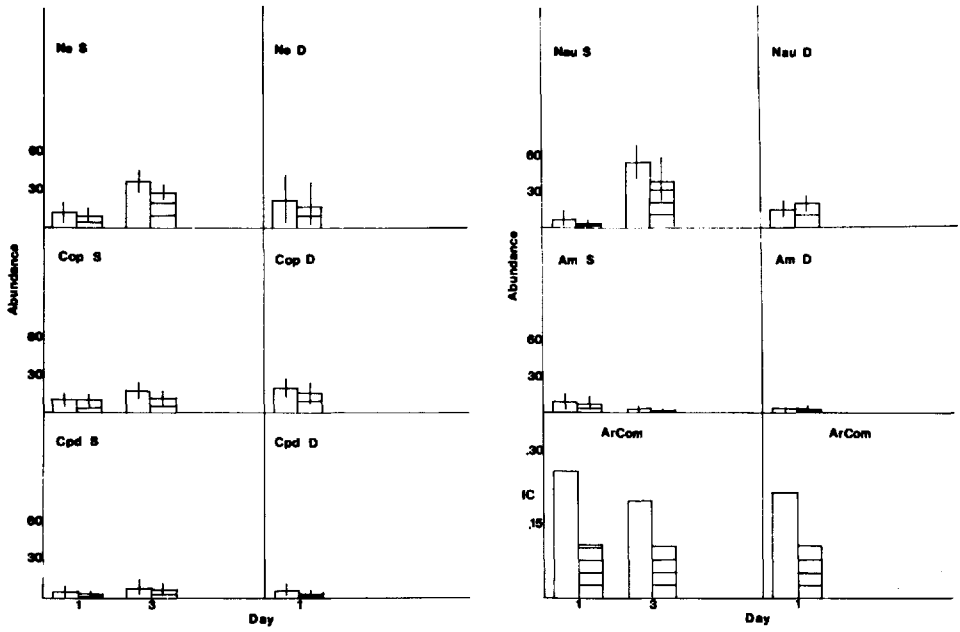

Figure 4. Mean abundance (± s.d.) (y-axis) by treatment and day (x-axis) from Experiment 1 using laboratory generated tube-caps. Densities are standardized to mean length (1.9 cm) of tube-caps. Abbreviations as in Figure 2. Values of meiofaunal abundance from Day 3 in the shallow site represent the mean of 3 tube-caps and these are not included in statistical analyses.

on day 3. Depth effects were noticed with numbers of copepods on high complexity tube-caps in shallow sites exceeding those from high complexity tube-caps in deep sites. A higher number of amphipods was found on tube-caps in shallow sites on day 1 but not on day 3 although amphipod abundances were generally low compared to copepod abundance.

Analysis of variance of Experiment 2 (field) (Fig. 3) generally agreed with those from Experiment 1. Nematode abundance again significantly decreased on tube-caps on days 3 and 4 compared to those on day 1 (Duncan's New Multiple Range Test $P < 0.05$). In contrast, adult copepods, copepodites, nauplii, and amphipods increased in number over time with abundances on day 4 significantly higher than densities on day 3 or 1 (Duncan's New Multiple Range Test, $P < 0.05$). Crustacean taxa had significantly higher densities on more complex tube-caps, but differences were *significant only on day 1. Some depth effects or interactions were also recorded with* significantly higher adult copepod abundance recorded in shallow sites. Higher *numbers of copepodites on tube-caps of increased architectural complexity were found* only in shallow sites while amphipods displayed a significantly higher number on tube-caps at deep sites.

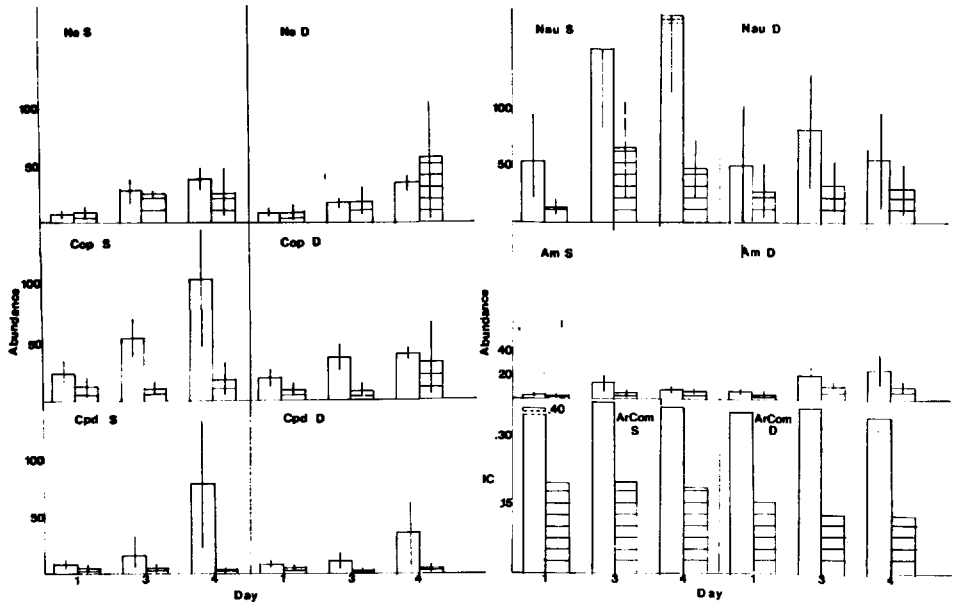

Figure 5. Mean densities (± 1 s.d.) (*y*-axis) by treatment and day (*x*-axis) of major taxa from Experiment 2 using laboratory-generated tube-caps. Densities are standardized to mean length (2.8 cm) of tube-caps. Abbreviations as in Figure 2.

Results from experiments utilizing laboratory-generated tube-caps conducted simultaneously with experiments utilizing field-collected tube-caps are summarized in Figures 4 and 5. A greater difference (as measured by *IC*) in architecture of high and low tube-caps existed in laboratory-generated tube-caps than those collected from the field. Statistical analyses of data in Figure 4 were reduced to a 2-way ANOVA (day 1 only) because tube-caps were badly damaged in the field by unidentified causes by day 3. Contrary to findings from experiments using field-collected tube-caps (Fig. 2), nematode abundance in shallow areas was lower on laboratory-generated tube-caps compared to that from field-generated tube-caps and generally increased over time. The reasons for these discrepancies in nematode accumulation patterns are unknown but may be related to the differences in defaunation methods of the tube-caps.

A significant architectural effect was recorded for copepodites with higher number of copepodites accompanying higher complexity, although numbers were low in both sites on laboratory-generated tube-caps. A variety of depth effects was also noted which were inconsistent among crustacean taxa (see Figs. 4–5).

I examined the nematode species composition from the February set of laboratory-generated tube-caps. The dominant nematode species were *Chromadorina* sp., *Siphophorella* sp., and *Monhystera* sp. which together made up approximately 70% of nematode species on both high and low complexity tube-caps. No species became disproportionately abundant on high complexity tube-caps compared to low complex-

ity tube-caps but rather a similar community composition was present on both types of tube-caps during the February experiment. Further information on nematode species composition is available upon request from the author.

Statistical analyses (3-way ANOVA) of the March–April series of experiments (Experiment 2, Fig. 5) for laboratory-generated tube-caps generally revealed similar main effects to that recorded for field-collected tube-caps (Fig. 3). Nematode abundance again showed no architectural effect but a significant day × depth interaction was present. Nematode abundance increased with time at the deep site only. Abundance of crustacean taxa was greater on day 4 than day 3 or 1 for adult copepods, copepod nauplii, and amphipods (Duncan's New Multiple Range Test, $P < 0.05$) and significantly greater on day 4 and 3 *versus* day 1 for copepodites. All crustacean taxa displayed a significant architectural effect with higher densities associated with more complex tube-caps. Adult copepod numbers were always higher on more structurally complex tube-caps but the numbers on day 4 in the shallow sites were higher than other time-depth combinations. Copepodite abundance was greater in tube-caps with increased architectural complexity but the difference between abundances on tube-caps of high and low complexity was greater in the shallow compared to deep sites. Likewise, naupliar densities were greater on more complex tube-caps but this difference was more noticeable in the shallow site. Also, nauplii were more abundant on days 3 and 4 compared to day 1 but only at the shallow site. Amphipod densities were generally significantly greater in deep sites regardless of day or architectural treatment in contrast to patterns from the first set of experiments.

b. Species patterns. Copepod species patterns of abundance were studied in detail. The suite of harpacticoid species represents a variety of morphological shapes including typical sediment dwellers and larger epiphytic forms. A large percentage of total copepods retrieved from tube-caps in Experiment 1 and 2 was composed of stage I–III copepodites. A high percentage of immigrating, early copepodite stages has not been previously reported from experimental studies on harpacticoid copepods. Of the older copepodites (stage IV–VI), nine species comprised 90% of recolonizing adult copepod fauna: *Halectinosoma* sp., *Paralaophonte* sp., Diosaccid sp. a, *Leptomesochra* sp., *Paramphiasella sirbonica, Harpacticus* sp., Diosaccid sp. b, *Mesochra* sp., and *Dactylopodia tisboides.* Other species found in low abundance on tube-caps included *Zausodes arenicolus,* Ectinosomatid sp. a, *Amphiascus* sp., and *Nitocra reducta fluvialis.* There was great variability in abundance of individual species on tube-caps, but, in general, all species found on high complexity tube-caps were also found on low complexity tube-caps. This information should be tempered by the realization that a large fraction of the copepod species community remains unidentified as early stage copepodites.

A 3-way MANOVA was performed on the densities of the nine most abundant copepod species from Experiments 1 and 2 for field-collected tube-caps and from Experiment 2 for laboratory-generated tube-caps to test whether there was a signifi-

cant effect of architecture on copepod abundance and whether this effect varied temporally and spatially. A two-way MANOVA was conducted on abundances of individual copepod species for laboratory-generated tube-caps from Experiment 1. The results of the MANOVA are presented in Table 2 which summarizes significant main effects or interactions. Abundances of adult copepod were generally greater on high complexity tube-caps with all species, except *Leptomesochra* sp. and *Paramphiasella sirbonica,* showing significantly higher numbers on more architecturally complex tube-caps (architectural effect) during Experiment 1 and/or 2. All species on high complexity tube-caps were also found on the low complexity tube-caps. A significantly higher number of individuals was found repeatedly on higher complexity tube-caps in shallow sites during the later days. As was true for the major taxa, interaction effects suggest that the observed differences between abundances of copepod species on tube-caps of different complexities are modified by depth and time.

c. Species richness and tube-cap complexity. Previous analyses were performed by categorizing tube-caps as either high or low complexity treatments. Using this approach, I have documented a consistent pattern of higher crustacean abundance with greater complexity of tube-caps. To investigate the relationships between structural complexity and abundance and copepod species richness over the entire range of complexity values, I performed a Spearman rank correlation procedure on abundance of crustacean taxa and copepod species richness (number of copepod species, stage IV-adult) and the architectural index (*IC*) for tube-caps from the field and laboratory (Table 3). In field experiments, abundance of all crustacean taxa, as well as copepod species richness were positively correlated with (*IC*) in Experiment 2 ($P < 0.05$) when all dates and sites were combined. On day 1 of Experiment 1 there were no marked differences in meiofaunal abundance over the range of tube-cap complexities (Fig. 2) and only amphipods showed a significant positive relationship to *IC* when all dates and sites were lumped. If only day 3 (Fig. 2) data are used, however, all taxa show a significant relationship to (*IC*). For laboratory generated tube-caps, all taxa and copepod species showed a significant positive relationship with (*IC*) in Experiment 2, while copepodites and amphipods displayed a similar pattern in Experiment 1. These data further support the positive relationship between tube-cap complexity and meiofaunal abundance and species richness demonstrated in experimental trials, although my qualitative surveys suggested that no species is exclusively limited to one type of tube-cap. After reviewing the data presented for Experiment 1 and 2 at both the major taxon and species level, the null hypothesis that the architecture of tube-caps has no relationship to meiofaunal abundance and species richness must be rejected for crustacean taxa, and meiofaunal copepods, specifically.

d. Additional experiments. Results from the November 1983 and March 1984 predator-manipulative experiments (Fig. 6) were statistically analyzed with a Student's *t*-test (Table 4). Because crustacean taxa showed a positive relationship with

Table 2. Summary of significant treatment or interaction effects for densities of nine most abundant copepod species from Experiments 1 and 2 utilizing field-collected and laboratory-generated tube-caps. Mean densities are presented below each main effect or interaction term and direction of inequalities is indicated. For interaction terms the order of means is given. H = high architectural complexity; L = low architectural complexity; S = shallow; D = deep; DMR = significant differences determined by Duncan's new multiple range test, underlined values not significantly different from one another; * = $P < 0.005$;** $P < 0.01$.

Field Collected—Experiment 1—February

Architecture					
Halectinosoma sp.	**	$H > L$			
		5.8	.64		
Paralaophonte sp.	**	$H > L$			
		5.3	1.44		
Harpacticus sp.	**	$H > L$			
		8.6	3.2		
Depth					
Halectinosoma sp.	**	$S > D$			
		8.2	.42		
Day					
Leptomesochra	**	Day 3 > Day 1			
		15.4	4.5		
Diosaccid sp. b	**	Day 3 > Day 1			
		2.27	.20		
Mesochra sp.	*	Day 3 > Day 1			
		2.17	0.0		
Day × Architecture					
Paralaophonte sp.	*	Day 3 (H)	Day 3 (L)	Day 1 (H)	Day 1 (L)
		4.5	.82	.82	.62
Leptomesochra sp.	**	Day 3 (H)	Day 3 (L)	Day 1 (L)	Day 1 (H)
		12	3.4	2.9	1.6
Architecture × Depth					
Halectinosoma sp.	**	S (H)	S (L)	D (L)	D (H)
		5.6	.50	.42	.28

Paralaophonte sp.	*	*S* (*H*)	*D* (*H*)	*S* (*L*)	*D* (*L*)		
		3.8	1.7	.40	.10		
Harpacticus sp.	*	*S* (*H*)	*D* (*H*)	*D* (*L*)	*L* (*S*)		
		7.4	3.4	2.5	1.3		
Diosaccid sp. b	**	*S* (*H*)	*D* (*L*)	*D* (*H*)	*S* (*L*)		
		1.2	.87	.33	.10		
Mesochra sp.	*	*D* (*H*)	*S* (*H*)	*D* (*L*)	*S* (*L*)		
		1.8	.2	0	.12		
Architecture × Day × Depth							
Diosaccid sp. a	*	Day 3 (*S*) (*H*)	Day 3 (*L*) (*D*)	Day 3 (*H*) (*D*)			
		1.0	.87	.33			
	*	Day 1 (*H*) (*S*)	Day 3 (*L*) (*S*)	Day 1 (*L*) (*S*)	Day 1 (*L*) (*L*)	Day 1 (*L*) (*H*)	
		.20	.10	0	0	0	
Leptomesochra sp.	*	Day 3 (*H*) (*S*)	Day 3 (*H*) (*D*)	Day 1 (*L*) (*S*)	Day 3 (*D*) (*L*)	Day 3 (*S*) (*L*)	
		9.2	2.8	2.4	2.1	1.3	
		Day 1 (*S*) (*H*)	Day 1 (*D*) (*L*)	Day 1 (*H*) (*D*)			
		1.2	.57	.42			
Diosaccid sp. b	*	Day 3 (*H*) (*S*)	Day 3 (*L*) (*D*)	Day 3 (*H*) (*D*)	Day 1 (*H*) (*S*)	Day 3 (*S*) (*L*)	Day 1 (*S*) (*L*)
		1.0	.87	.33	.20	.10	0
		Day 1 (*D*) (*L*)	Day 1 (*D*) (*H*)				
		0	0				

Field Collected—Experiment 2—March–April

Architecture			
Halectinosoma sp.	**	*H*	*L*
		15.3	1.01
Paralaophonte sp.	**	*H*	*L*
		10.5	3.4
Diosaccid sp. a	**	*H*	*L*
		3.12	.73
Diosaccid sp. b	**	*H*	*L*
		2.2	0
Mesochra sp.	**	*H*	*L*
		26.7	2.9
Dactylopodia tisboides	*	*H*	*L*
		15.0	8.9

Table 2. (Continued)

Depth							
Halectinosoma sp.	**	*D* > *S*					
		11.3 4.1					
Harpacticus	**	*S* > *D*					
		8.7 4.1					
Mesochra sp.	**	*S* > *D*					
		26.7 6.8					
Dactylopodia tisboides	**	*S* > *D*					
		12.1 5.2					
Day							
Halectinosoma sp.	**	Day 3	Day 4	Day 1	(*DMR*)		
		8.6	4.5	2.27			
Paralaophonte sp.	**	Day 4	Day 3	Day 1	(*DMR*)		
		7.3	4.8	1.87			
Paramphiasella sirbonica	*	Day 4	Day 3	Day 1	(*DMR*)		
		1.4	.39	0			
Harpacticus sp.	**	Day 1	Day 3	Day 4	(*DMR*)		
		7.5	3.6	1.7			
Dactylopodia tisboides	*	Day 4	Day 3	Day 1	(*DMR*)		
		11.7	6.4	5.8			
Mesochra sp.	**	Day 4	Day 3	Day 1	(*DMR*)		
		15.0	12.7	2.0			
Day × Depth							
Harpacticus sp.	*	Day 1 (*S*)	Day 3 (*S*)	Day 1 (*D*)	Day 4 (*S*)	Day 4 (*D*)	Day 3 (*D*)
		4.1	3.4	3.4	1.2	.50	.24
Halectinosoma sp.	**	Day 3 (*D*)	Day 4 (*D*)	Day 1 (*S*)	Day 3 (*S*)	Day 4 (*S*)	Day 1 (*D*)
		7.2	3.0	1.8	1.5	.75	.39

Laboratory-Generated—Experiment 1—February

Depth			
Harpacticus	*	*D* > *S*	
		4.5 1.6	

Laboratory-Generated—Experiment 2—March–April

Architecture				
Halectinosoma sp.	**	*H* > *L*		
		23.0 5.0		
Paralaophonte sp.	**	*H* > *L*		
		9.8 3.5		
Diosaccid sp. a	**	*H* > *L*		
		25.9 2.9		
Harpacticus sp.	*	*H* > *L*		
		7.8 5.6		
Mesochra sp.	**	*H* > *L*		
		6.2 1.8		
Dactylopodia tisboides	**	*H* > *L*		
		13.8 7.2		
Depth				
Diosaccid sp. a	**	*S* > *D*		
		25.2 3.4		
Mesochra sp.	**	*S* > *D*		
		7.2 2.0		
Dactylopodia tisboides	**	*S* > *D*		
		15.5 5.6		
Day				
Halectinosoma sp.	**	Day 3	Day 4	Day 1 (*DMR*)
		27.1	4.5	4.0
Paralaophonte sp.	**	Day 4	Day 3	Day 1 (*DMR*)
		6.7	3.9	2.7
Diosaccid sp. b	*	Day 3	Day 4	Day 1 (*DMR*)
		2.3	1.4	.5
Mesochra sp.	**	Day 4	Day 3	Day 1 (*DMR*)
		6.3	3.7	2.5

Table 2. (Continued)

Day × Architecture							
Halectinosoma sp.	**	Day 3 (*H*)	Day 1 (*H*)	Day 4 (*H*)	Day 4 (*L*)	Day 1 (*L*)	Day 3 (*L*)
		26.0	4.0	3.0	1.4	1.4	1.1
Paralaophonte sp.	*	Day 4 (*H*)	Day 3 (*H*)	Day 4 (*L*)	Day 1 (*H*)	Day 1 (*L*)	Day 3 (*L*)
		4.7	4.0	2.0	1.6	1.1	.4
Diosaccid sp. a	**	Day 4 (*H*)	Day 3 (*H*)	Day 1 (*H*)	Day 1 (*L*)	Day 3 (*L*)	Day 4 (*L*)
		11.3	10.8	3.6	1.5	.8	.6
Mesochra sp.	*	Day 4 (*H*)	Day 1 (*H*)	Day 4 (*L*)	Day 3 (*H*)	Day 1 (*L*)	Day 3 (*L*)
		4.7	2.3	1.6	.25	.16	.12
Day × Depth							
Halectinosoma sp.	**	Day 3 (*D*)	Day 3 (*S*)	Day 1 (*S*)	Day 4 (*S*)	Day 4 (*D*)	Day 1 (*D*)
		14.5	12.5	4.0	2.8	1.4	.14
Paralaophonte sp.	*	Day 4 (*S*)	Day 4 (*D*)	Day 1 (*D*)	Day 3 (*D*)	Day 3 (*S*)	Day 1 (*S*)
		3.6	3.1	2.4	2.1	1.7	.40
Mesochra sp.	*	Day 4 (*D*)	Day 1 (*D*)	Day 4 (*S*)	Day 3 (*S*)	Day 1 (*S*)	Day 3 (*D*)
		4.7	2.2	1.6	.25	.25	.12
Architecture × Day × Depth							
Mesochra sp.	**	Day 4 (*H*) (*D*)	Day 1 (*H*) (*D*)	Day 4 (*L*) (*S*)	Day 1 (*H*) (*S*)	Day 1 (*L*) (*D*)	
		4.7	2.1	1.6	.25	.16	
		Day 2 (*L*) (*D*)	Day 2 (*H*) (*S*)	Day 2 (*H*) (*D*)	Day 4 (*L*) (*S*)	Day 4 (*H*) (*S*)	
		.12	.12	.12	0	0	
		Day 1 (*L*) (*S*)	Day 2 (*L*) (*S*)				
		0	0				

Table 3. Spearman rank correlation coefficients for tube-cap complexity (*IC*) vs. abundance of major taxa and number of copepod species in Experiment 1 and Experiment 2. * = significant $P < 0.05$. All sites combined.

	Experiment 1		
	Field		Laboratory
	Day 1 and 3 $n = 53$	Day 3 only $n = 29$	Day 1 $n = 33$
Copepods	.17	.43*	.08
Copepodites	.12	.33*	.34*
Nauplii	.15	.43*	.10
Amphipods	.31*	.40*	.26*
# copepod species	.09	.31*	.37*

	Experiment 2	
	Field Day 1, 3 and 4 $n = 90$	Laboratory Day 1, 3, and 4 $n = 93$
Copepods	.58*	.64*
Copepodites	.48*	.61*
Nauplii	.44*	.32*
Amphipods	.26*	.66*
# copepod species	.56*	.72*

architecture in prior experiments (p. 655–658), I analyzed these organisms only in the predation experiments. Few amphipods were found on tube-caps during these experiments. Abundance of taxa on tube-caps was much lower than that recorded in earlier experiments following seasonal trends in density levels on natural tube-caps (Bell, unpubl.). The experimental trends from November 1983 and March 1984 mirrored those collected in 1982. Abundances of adult copepods, copepodites, and nauplii, however, were significantly greater on high complexity tube-caps regardless of the presence or absence of predators in both experiments (Table 4). In November, the increased abundances of copepods (adults and copepodites) on tube-caps with higher complexity was due mainly to a significantly higher number of *Harpacticus* sp. and Ectinosomatid sp. a as compared to tube-caps of lower complexity in both cage and noncage sites. The former copepod was a dominant species which showed a significant architectural effect in earlier experiments (Table 3). In March, an entirely different suite of species resided on tube-caps and a large increase in *Nitocra reducta fluvialis* was primarily responsible for the significantly higher numbers of copepods on tube-caps of high structural complexity inside and outside cages. It is apparent that some attribute of high complexity tube-caps with increased amount of shell other than reduced predator removal maintains higher densities of meiofaunal copepods.

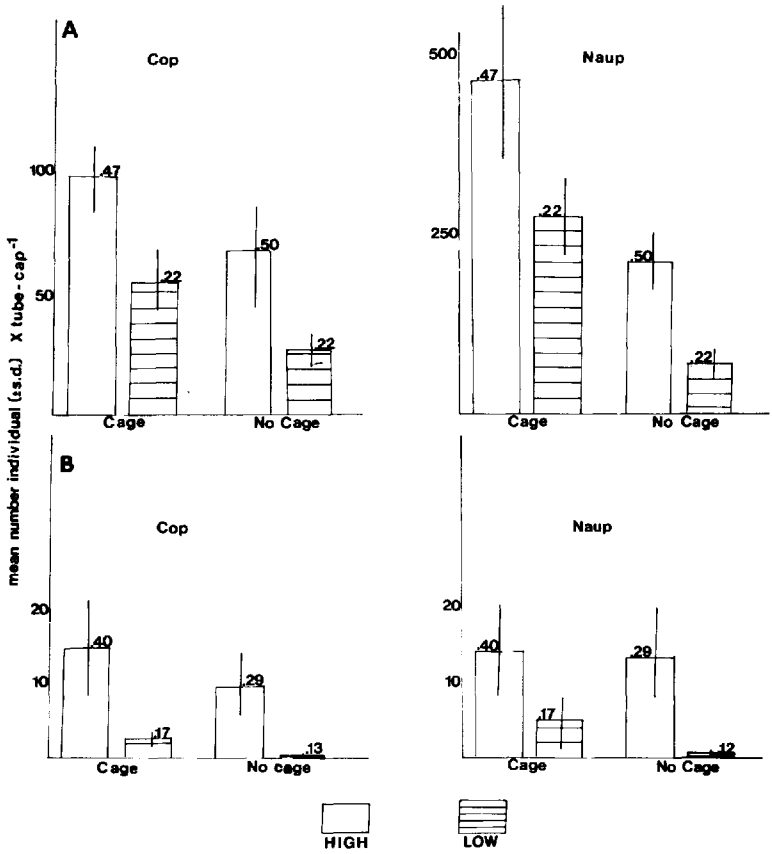

Figure 6. Mean abundances of copepods (Cop) (adults + copepodites) and Nauplii (naup) which recolonized tube-caps of different architecture (high *vs.* low) inside cages and in non-caged areas. Numbers above each bar represent mean (*IC*) for tube-caps from each experimental unit. A = November 1983; mean abundance standardized per 1.7 cm of tube-cap. B = March 1984; mean number standardized per 2.7 cm of tube-cap.

4. Discussion

The results from this series of experiments consistently demonstrate that the more shell material on the tube-caps of *Diopatra,* the greater the species richness and abundance of harpacticoid copepods. This effect was measured in different seasons and for copepod species from a variety of families and different developmental stages. In addition, there is a similar strong relationship between tube-cap complexity and juvenile amphipod abundance. Thus, in this subtropical shallow water system, meiofaunal crustaceans show the same association with zoogenic structures as has been experimentally demonstrated for larger fauna and plant- or geologically-generated structure from a variety of habitats (see Introduction).

Table 4. Summary of statistical analyses (*t*-tests) on abundances of major taxa on tube-caps of different habitat architecture inside and outside predator exclusion cages. Set A = November 1983 experiments; Set B = March 1984 experiments. For those taxa where significant differences were detected, the direction of the inequality is indicated. H = high architectural complexity; L = low architectural complexity. Data presented in Figure 6. * = significant $P < 0.05$.

	Inside cages	Outside cages
	Set A ($n = 12$)	
Copepods	$t = 3.06$*	$t = 5.2$*
	$H > L$	$H > L$
Nauplii	$t = 2.4$*	$t = 5.8$*
	$H > L$	$H > L$
Copepodites	$t = 3.06$*	$t = 9.3$*
	$H > L$	$H > L$
	Set B ($n = 8$)	
Copepods	$t = 5.4$*	$t = 5.4$*
	$H > L$	$H > L$
Nauplii	$t = 4.2$*	$t = 4.6$*
	$H > L$	$H > L$

My results agree with the findings of Kohn and Leviten (1976) who experimentally determined a direct link between physical topography of coral reef platforms and abundance and diversity of gastropods. They suggested that areas of high topographic relief may provide areas for recruitment of new individuals or settling sites for veligers. McDonnell and Stiles (1983) manipulated vegetative structures in terrestrial environments and recorded an analogous phenomenon: areas with high structural complexity served as recruitment foci for bird disseminated seeds. My results for nauplii and copepodites suggest that shell material in tube-caps may also play a similar role as recruitment sites.

Reduction in prey removal by predators from tube-caps with large amounts of shell could not explain the results of enclosure experiments. Rather, the best explanation alludes to some characteristic of tube-caps that attracts and/or supports higher densities and more species of copepods on a short timescale. As found here, Gillinsky (1984) noted a higher species richness of benthic invertebrates in freshwater ponds in areas with increased habitat heterogeneity (macrophytes) regardless of fish (predator) presence or absence (see Gillinsky, 1984, Fig. 1). In contrast, Lubchenco (1983) found no difference in settlement and/or survival of the algae *Fucus vesiculosus* on smooth rock *versus* rocks with crevices in the absence of predators; the quality of crevices as refuges was only apparent when herbivores were present (Lubchenco, 1983, Table 1).

The findings from tube-cap experiments contrast with the results of Coull and Wells (1983) who examined predator (fish) removal of harpacticoids and amphipods from

algae with varying surface to volume ratios. They demonstrated that reduced predation efficiency could account for the greater number of individuals found on highly foliose algae compared to algae of more simple physiognomy. Three of their dominant copepods (*Paralaophonte meinerti, Ectinosoma australe, Amphiascus lobatus*) are in the same family or genera as dominant tube-cap taxa (Table 2) although different trends are documented in the study reported here. My experiments on the contrary illustrate the importance of the micro-habitat offered by shell material incorporated into tube-caps as a determinant of meiofaunal species richness and abundance rather than acting as refuges from predation. Both predator protection and microhabitat provision for meiofauna may, however, operate simultaneously in shallow-water systems (see Hicks, 1980; Coull and Wells, 1983) but the relative importance of both remains unclear, since few investigators have simultaneously explored this possibility experimentally.

The qualities of tube-caps with high quantities of shell material or high architectural complexity which maintain high abundances or species richness of crustaceans may be related to: 1) the increased trapping of detrital material or attachment of food items or 2) provision of refuges from physical stress. Tube-caps at both sites are occasionally exposed by low tides and dessication may be reduced on tube-caps of high complexity if water films are maintained over the surface. In a related study, Bell and Coen (1982b) reported higher numbers of meiofauna on tube-caps which contained the macroalga *Ulva* in intertidal mudflats compared to tube-caps without algae suggesting that algae may prevent dessication of associated fauna. Such moderation of physical stress has been documented for other intertidal organisms residing in crevices in intertidal areas (e.g. Kohn and Leviten, 1976; Garrity, 1984) and may be important for meiofaunal organisms on tube-caps irregularly exposed during very low tides.

By using recolonization techniques, I documented the rapid immigration of meiofauna onto epibenthic structure with higher numbers and diversity of adult copepod species moving onto tube-caps with greater structural complexity. Whether or not these patterns of abundance and diversity on experimental tube-caps would be maintained longer was not tested. However, the consistent findings of greater abundance and species richness on more complex experimental tube-caps concur with the natural patterns recorded from tube-caps in the field (Bell, unpubl. and see p. 650). Furthermore, tube-caps are continually being constructed to avoid burial by sediment movement. In the Tampa Bay site, I estimated that 1.62 cm $\times$ d^{-1} of tube-cap length is added (Bell, unpubl.). Given that natural tube-caps can range from 2.1–3.5 cm in length, replacement of new caps and provision of new habitat could easily occur within 2–3 days. Thus, the experimental timetable approaches a natural temporal event and provides a logical explanation for patterns of abundance.

Site and day effects and interactions illustrate that spatial and temporal features of the environment may modify basic predictions on relationships between habitat complexity and associated faunal communities. Such variation in faunal-complexity

relationships has been poorly explored in earlier studies (see Introduction). The depth effects document that differences in recolonization abundance levels exist (Figs. 2–5). These may be due to differences between sites in the magnitude of the species pool immigrating onto caps. Sediment abundances of copepods are lower in deep compared to shallow sites and some recolonization onto tube-caps proceeds via this pathway (Bell and Coen, 1982a). Under natural conditions tube-caps in shallow sites have an increased probability of incorporating high levels of shell material into the tube-cap compared to deep sites as shell hash differentially accumulates in shallow areas in response to the local hydrodynamic regime (see also Brenchley, 1975). Therefore, an increased probability of having a large amount of shell incorporated into tube-caps as well as increased colonization levels by meiofauna may both combine to produce higher faunal abundance on epibenthic tube-caps in field collections from shallow sites.

The results from my study combined with previous investigations on tube-cap meiofaunal assemblages (Bell and Coen, 1982a) provide a unique scenario of interrelationships among processes influencing community structure in a subtropical sandflat. High numbers of meiofaunal taxa are found not only in sediments but also associated with tube-caps. Some copepod species in the sediments are also present on tube-caps but a separate suite of species generally exploits either tube-cap or sediments exclusively. Numbers of individuals and species composition on tube-caps seasonally varies but abundance and species richness of meiofauna on tube-caps are unaffected by the worm activities within a tube. As shown here, the direct relationship between high numbers of meiofauna and high structural complexity is best explained post-hoc by the provision of favorable microhabitats (food, recruitment sites, refuges from physical stress) by the incorporated shell items, rather than by a decrease in predator removal efficiency on tube-caps with large amounts of shell (c.f. Coull and Wells, 1983). Tube-cap complexity or surface area of shell material in tube-caps varies over depth, and tube-caps in both shallow and deep sites are continually being constructed in response to sediment burial. Meiofauna, especially early stage copepodites, invade virgin substrata quickly (days). The hydrodynamic regime too plays an important role in the shallow water system by controlling not only sediment movement and the rate of tube-cap regeneration but also the availability and distribution of shell hash for tube construction. Thus, the hydrodynamic regime, by modulating availability of construction material and turnover of macrofaunal biogenic structures controls abundance and diversity (species richness) of meiofaunal assemblages associated with such zoogenic features.

Because of the small size of meiofaunal organisms (i.e., $< 500\ \mu$), one might expect that these organisms may be especially adept at exploiting not only tube-caps but also products of a multitude of larger benthic organisms. Thus, the findings reported here for tube-caps and meioepibenthos may apply to a number of systems where epifauna are associated with biogenic structures. Habitat complexity as an important community structuring mechanism may operate in a similar fashion for meiofaunal assem-

blages on decorator crabs, decorating echinoderms (Bell and McClintock, 1981) or other biogenic sedimentary matrices that extend above sediments (e.g., Haines and Maurer, 1980).

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