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The structure and organization of a kelp forest ecotone: The
Diopatra ornata community

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San Jose State University, 1989

THE STRUCTURE AND ORGANIZATION OF A KELP FOREST ECOTONE:

THE *DIOPATRA ORNATA* COMMUNITY.

A Thesis

Presented to

The Faculty of Moss Landing Marine Labs

San Jose State University
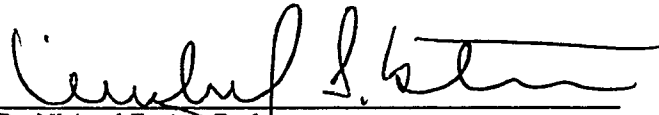
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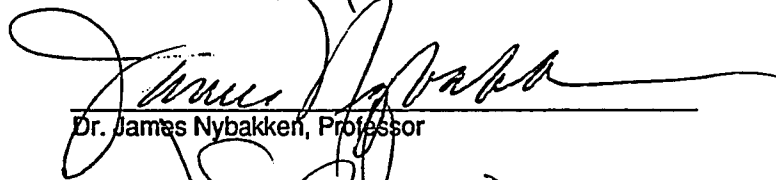of the Requirements for the Degree

Master of Science

By Stacy L. Kim

December 1989

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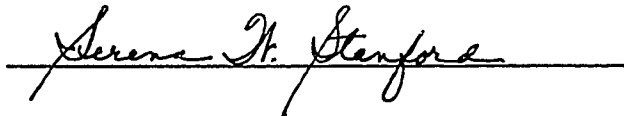
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ABSTRACT

THE STRUCTURE AND ORGANIZATION OF A KELP FOREST ECOTONE: THE *DIOPATRA ORNATA* COMMUNITY.

by Stacy L. Kim

Food availability and disturbance were important factors in establishment and existence of *Diopatra ornata* dominated ecotones between kelp forest and sand. *D. ornata* were larger at the rock edge of the mat in protected sites and larger at exposed sites than at protected sites. This correlated with greater abundance of food. Increased food availability resulted in greater worm growth in six months. Common species, including *D. ornata,* were more abundant at protected sites. 50% of the common species were densest at the rock edge of the community. These were mostly motile organisms concentrated where detrital food was plentiful. Infaunal species were distributed evenly throughout the community, but all species densities dropped precipitously at the sand edge of the mat. Community structure was consistent during one year of sampling. Time needed to establish a *D. ornata* mat and slow worm growth indicate the ecotone would be slow to recover from disturbance.

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INTRODUCTION

Many dense infaunal communities in shallow subtidal sand habitats are dominated by one species, generally a tube building polychaete or amphipod (Ecological Services Program 1981, Jones 1969). The extensive mats produced by these "anchor species" have many effects on the community, both physical and biological. Along the coast of California, the interface between rock reef/kelp forest and areas of unstable sand bottom is generally dominated by *Diopatra ornata* tube mats. An ecotone community whose most prevalent species forms a sediment stabilizing tube mat is a unique system to test for structuring ecological factors.

Natural history

Diopatra is an onuphid polychaete that builds a strong parchment tube that extends nearly a meter into the sediment. The hook shaped tube projects a few centimeters above the sediment surface and is extensively decorated with bits of shell and debris (Hartman 1968). The tube caps' primary function appears to be trapping food (Fauchald and Jumars 1979, Rhoads *et al.* 1978), although Brenchley (1976) found that tube decoration with large debris facilitated predator detection and avoidance by making the worm more sensitive to water motion.

Fauchald and Jumars (1979) described onuphid polychaetes such as *Diopatra ornata* as omnivorous scavengers that can become functional specialists when one food type is prevalent (see also Lipps and Ronan 1974, Magnum and Cox 1971). Congenerics *Diopatra cuprea* and *Diopatra leuckarti* feed primarily on drift algae (Bailey-Brock 1984, Fry and Parker 1979, Magnum *et al.* 1968).

Tube mats

Tube mats become habitat for a whole new suite of organisms that do not utilize sandy

bottoms without such mats (Fager 1964). Abundances of many species are greatly increased within a mat when compared to shifting sand habitat nearby (Bailey-Brock 1984, Bell and Coen 1982a, Luckenbach 1984b, Woodin 1976, 1978, 1981). This may be due to changes in the physical environment created by the structure the tubes provide, such as refuge from water flow (Woodin 1978) or from predation (Ban and Nelson 1987, Luckenbach 1984b, 1982, Orth 1977, Woodin 1976, 1981). Substrate availability for attachment of plants and animals (Pillsbury 1950), increased spatial heterogeneity (Bell 1984, 1985, Bell and Coen 1982a & b) and increased oxygenation of the sediments (Meyers et al. 1987) are other physical changes that are due to the presence of tubes. Tubes and macrofauna appear to actually have a destabilizing effect on sediments (Eckman et al. 1981, Luckenbach 1986) but the organic sediment binding from mucous and associated meiofauna overwhelm this effect to create a more stable substrate than sand without tube dwellers (Dingler et al. 1981, Fager 1964, Featherstone and Risk 1977, Orth 1977, Rhoads et al. 1978). The worm tubes may bind the sediment to the extent that motile organisms which move through sand or use it as a hiding place are excluded, further changing community structure (Rhoads et al. 1978).

Biotic factors in tube mats may also change the density of associated organisms. Preferential larval settlement within mats (Eckman 1983, Fauchald and Emerson 1975, Luckenbach 1982, Peckol and Baxter 1986) can change the eventual species composition of the community. Food items that are more abundant in the vicinity of a dense tube mat include trapped detritus and drift algae (Magnum et al. 1968, Rhodes et al. 1968), recently settled larvae (Luckenbach 1982, 1984a, 1987), and the tube mat organisms and associated species as prey (Emerson 1975, Fager 1964, Rosenthal et al. 1974, Webster 1968). Fishes from the adjacent reef or sand bottom may move into the mat community to feed (Davis et al. 1982, Edwards et al. 1971, Turner et al. 1969). Densities of up to 3000 worms/m^2 have been found in central California (ABA Consultants 1985). With biomass this high, the tube mat may be an exploitable food source for the grey whale,

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Eschrichtius robustus. These whales are known to feed on tube mats in British Columbia and the Bering Sea (Oliver and Slattery 1985, Oliver *et al.* 1984), and have recently been observed from the surface feeding near kelp forests in central California (Alan Baldridge pers. comm.). Diving observations in the same areas revealed an extensive *Diopatra ornata* tube mat with pits similar to those made by feeding whales in the Bering Sea (John Oliver pers. comm.). The mat community can thus be affected by selective larval settlement, increased food availability, or increased predation by animals on foraging expeditions.

Artificial reefs

Artificial reefs provide ideal settings to study the development of sand bottom communities associated with areas of hard substrata. While often very complete information is collected on the hard bottom epifauna, flora and fish populations, very little monitoring has been done on the changes occurring in the sediments surrounding the reef (Carlisle *et al.* 1964, Carter *et al.* 1985, Turner *et al.* 1969).

Diopatra ornata is one of many organisms whose distribution may be affected by artificial reefs. While reefs change both the physical and biological environment of the surrounding sediments, it is likely that the biological changes have more of an effect on *D. ornata.* Development of a consistent and abundant drift algal food source (Magnum *et al.* 1968) may increase the densities of the worms, which may in turn become prey items for predatory fishes from the reef (Ed DiMartini pers. comm.). Changes in the sandy bottom and development of an ecotone community may be just as dramatic (Davis *et al.* 1982) and important to the reef community as the succession on the new hard substrate.

The questions

The ecotone between rocky reefs and sandy bottoms harbors a distinct community which

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interacts with both the adjacent habitats. This study examined the development, composition, and areal extent of this ecotone community, and the factors which influence its structure.

Research began with descriptive studies of the areal and seasonal abundance and distribution of dominant species in the *Diopatra ornata* community. In *Diopatra cuprea* dominated communities, the factor structuring the system appears to be predation (Luckenbach 1982, 1984a, 1987, Woodin 1976, 1981). Is this factor also important in *D. ornata* tube mat communities? Peckol and Baxter (1986) examined *D. cuprea* population dynamics and concluded that tidal exposure controlled worm densities, while field studies done by Magnum *et al.* (1968) suggest that a greater abundance of drifting food results in higher worm densities. Do these factors control *D. ornata* densities as well?

As a pattern in the sizes of the worms became evident, observations and experiments were performed to determine causal factors: correlations with the amount of available food and degree of exposure, worm transplants, and food availability manipulations to observe worm growth under different conditions. The development of *Diopatra ornata* mats around artificial reefs built on soft sediments was also examined. Is a *D. ornata* ecotone community a weedy opportunistic community or a long term stable one?

The specific questions this study addressed were:

1. What ecological factors are the structuring forces in the *Diopatra ornata* dominated ecotone community?

2. Which factors are most important in determining *Diopatra ornata* distribution, size, and density?

3. Which factors have effects on all ecotone species densities and distributions?

4. How long does it take an ecotone community to develop around rocky reefs?

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MATERIALS AND METHODS

Study sites

Most of the field work was conducted in the Hopkins Marine Reserve at the southern end of Monterey Bay, California (Figure 1). A kelp forest extended from inside a protected cove in front of the reserve to the more exposed coast at Otter Point. Five permanent sampling sites in *Diopatra ornata* dominated tube mat communities along this kelp forest were established and relocated by lineups on shore and subsurface buoys attached to fence anchors in the bottom. Two sites on the southern end were protected from prevailing swell by rock reef and kelp (Sites 1 and 2). Sites 3 and 4 were more exposed to swell and adjacent to the kelp forest. Site 5 was fully exposed to swell from all directions. Though all the sites were more protected than the coast outside the bay, they still encompass a distinct exposure gradient.

Additional sampling was conducted at four artificial reefs along the southern California coast. The reefs were:

Hermosa Beach Artificial Reef (33°51'18"N, 118°24'36"W), in 72 ft of water, constructed of quarry rock and concrete shelters in 1960,

Old Marina del Rey Artificial Reef (33°57'50"N, 118°29'05"W), at 65 ft, made of 2000 tons of quarry rock in 1965,

Camp Pendleton Artificial Reef (33°19'30"N, 117°31'42"W) at 43 ft, built of 10,000 tons of quarry rock arranged in six modules in 1980, and

New Marina del Rey Artificial Reef (33°57'50"N, 118°29'05"W), at 65 ft, constructed of 11,000 tons of quarry rock in 16 modules in 1985 (Carlisle 1977).

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Qualitative observations

Natural reefs

At each of these sites, the ecotone habitat was sampled in four areas. These were:

Inner - at the most protected edge of the mat, closest to the kelp forest and rock reef,

Middle - in the middle of the mat, away from kelp forest, rock reef and sand bottom,

Outer - on the most exposed edge of the community, closest to the sand bottom, and

Away - in the sand bottom away from the obvious *Diopatra ornata* dominated

community.

At each of the five sites densities of conspicuous organisms were determined by field counts in each area (inner, middle, outer, and away). Sampling was done once a month for a year, from March 1987 to March 1988. Counts of large infrequent organisms were taken in 10 m^2 areas (1 x 10 m band transects, n = 2). Abundant large organisms were counted in 1 m^2 quadrats (n = 3), and small organisms were counted in 0.175 m^2 quadrats (23.5 cm radius circular quadrats, n = 5). Quadrats for the count and infaunal samples were located haphazardly (*sensu* Fager 1968). Only the four most abundant and regular members of the community from each sampling regime were analyzed in detail.

To determine size distributions of *Diopatra ornata* and to check the accuracy of field counts of smaller organisms infaunal collections were made quarterly in June 1987, September 1987, December 1987 and March 1988. Three haphazardly located replicates of 0.0075 m^3 diver held can cores (15 cm deep x 11.5 cm radius, see Oliver *et al.* 1980 for detailed description) were taken in each area at each site. They were immediately sieved over a 0.5 mm mesh screen, fixed in 10% formalin, and after two weeks or more, transferred to 70% ethanol. Large infaunal organisms were sorted from the residue, separated by species and counted. *D. ornata* inside tube diameters were measured to the nearest mm with a conical brass device similar to a ring sizing tool. For selected samples, the *D. ornata* tubes were dissected and the diameter, length and weight of the worms

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were measured to calculate correlations between size parameters.

The amount of available food in the form of drift *Macrocystis pyrifera* was recorded in February and August 1988. Collections of drift from within haphazardly located 1 m^2 quadrats (n = 3) were made at all sites, in the inner, middle and outer areas.

Artificial reefs

The time frame for development of an ecotone around rocky structures was examined at four artificial reefs in southern California. In November 1986, 0.175 m^2 quadrat counts (n = 3) and can core samples (n = 1) were taken along transects perpendicular to the reef edges. Samples were taken between 0 and 5 m from the rock edge. The reefs were constructed of similar materials and had been in place for different lengths of time. Although there was little replication, these samples suggest recognizable changes with time in the establishment of a *Diopatra ornata* mat.

Experiments

Algal consumption

To determine if the amount of food consumed by *Diopatra ornata* correlated with the size or location of the worms, weighed blades of *Macrocystis pyrifera* were set out at all five sites in February and August 1988. The blades were attached with clothespins to the *D. ornata* tubes, collected after one week, and reweighed. Five replicates each were haphazardly set out in the inner and middle areas, with controls out of the worms' reach just off the bottom.

Food availability and worm growth

To determine the effects of food availability on worm size, experiments manipulating the abundance and accessibility of food were conducted. At the two protected sites (1 and 2) permanent 10 x 10 m experimental stations were set up in August 1987. Fence anchors screwed

into the bottom marked the four corners, and rope baselines marked at every meter were stretched between them along the N/S direction. The E/W line, also marked at every meter, could be moved along the N/S baselines to precisely relocate coordinates. These lines were removed between maintenance dives to reduce effects of fouling, trapping and scour on the surrounding *Diopatra ornata* mat.

For experimental manipulations within these 100 m^2 stations, Cartesian coordinates for 25 plots were collected using a random numbers table. The plots were 0.25 m^2 and marked with 40 cm long 1.25 cm diameter PVC stakes, pounded flush with the sediment surface in opposite corners and connected by parachute cord strung tightly between them. The plots were randomly divided into three experimental and two control groups of five each. The experimental manipulations were:

+K - added food in the form of fresh *Macrocystis pyrifera* blades tied to the parachute cord,

-E - removal of epifaunal algae by gently clipping it off the tubes by hand, and

+K -E - both added food and removed epifauna.

Control groups were:

EC - experimental controls, unmanipulated but still disturbed by the stakes and strings, and

C - completely undisturbed.

The plots were maintained by clipping and/or feeding once a month for a year, and sampled by coring at six (February 1988) and twelve (August 1988) months. Samples were treated the same as quarterly infaunal core samples.

Worm transplants and growth

Worms were transplanted between areas to test the hypothesis that worm sizes were related

to area differences, especially variations in the amount of drift algae. At each protected site (1 and 2) worms were transplanted from the middle of the bed to the inner edge and visa versa. Six can cores from each area were moved to the other area and placed in 12 x 20 cm PVC tubes sunk flush with the sediment surface, and six cores were replaced in PVC tubes in the same area. These tubes were closed and collected after six months, in August 1988, and processed like the other can core samples.

Statistical analyses

Statistical calculations were performed using Statview II on a Macintosh II, with further manipulations by hand per Underwood (1981) when necessary. For all species count and kelp weight data, Scheffe's Box test for each of the factors (date, site, and area) was performed between replicates. When there were no significant differences, data were pooled and the appropriate ANOVA or t test done. Assumptions were not tested because the ANOVA is fairly robust to deviations from the normal distribution and to heterogeneity of variances (Underwood 1981, Zar 1984). Occasionally, when the number of data points exceeded computer capacity, the data were split along appropriate lines (*i.e.*, separated into two six month periods) and the required test performed. When the ANOVA found significant differences but no interactive effects, a Student-Neuman-Keuls test was performed to determine which means were significantly different.

Worm size data from qualitative sampling were treated similarly to density data, using mean size rather than mean density. Sizes were ranked data in 1 mm increments. Non parametric tests were used for comparisons of experimental manipulations because the assumptions of normality and equal variances did not hold. Mean sizes were compared between replicates by a Kruskal-Wallis test. If there were no significant differences the data were pooled and a Mann-Whitney U or Kruskal-Wallis performed between the different treatments.

Measurements of worm size and weight and tube size were compared by simple correlation.

RESULTS

Worm size correlations

Diopatra ornata size patterns were deduced from tube sizes which were significantly correlated with worm sizes ($p<0.001$, Zar 1984). Since *D. ornata* is capable of withdrawing very deep into the sediments (over 30 cm), some individuals were not captured in can cores, but cores collected all the tube tops of *D. ornata*. Because every tube in a sample was measurable, tube diameters were the most consistent and unbiased measure of worm size obtainable. The correlation between worm size and tube size (Table 1) allows tube size measurements to be validly extended to real differences in worm sizes. The low (but significant) correlation coefficients indicate wide variability between worms in all dimensions.

Qualitative results

Of the larger epifaunal organisms, all the species except *Pisaster giganteus* showed significant differences between sites along the exposure gradient (Table 2). All species except *Loxorhynchus crispatus* and Laminariales showed a significant difference between inner, middle, and outer areas. The densities of *Tegula* spp., *Pachycerianthus fimbriatus*, *L. crispatus* and Laminariales were significantly different at different times. *Tegula* spp., *P. fimbriatus*, *Pycnopodia helianthoides*, *Cryptochiton stelleri*, *Asterina miniata*. *L. crispatus*, and Laminariales, and *P. giganteus* all showed significant interactive effects between date and site, but none of the species showed interactive date and area effects.

Among infaunal organisms, significant differences between sites were found for *Diopatra*

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ornata and *Thelepus crispus.* There were significantly more of both species at the protected

sites. Differences between areas were significant for *T. crispus,Chaetopterus variopedatus* and

Phyllochaetopterus prolifica, and for *D. ornata* during the second six months of sampling. *T.*

crispus and *P. prolifica* were densest in the middle of the bed, *C. variopedatus* at the outer edge

of the bed, and *D. ornata* at the inner edge. *D. ornata* showed a significant date effect, and in *T.*

crispus the date effect was limited to the second six months of sampling. Interaction effects

between date and area were significant during the first six months, and between date and site

during the second six months for both *D. ornata* and *T. crispus.* Both of these species' field

densities had minimums in January/February and maximums in June.

Because field counts of the smaller organisms might not be as reliable during times of higher

swell, and small recruits might be missed, laboratory counts of infaunal organisms were also

compared. All four worm species showed a significant difference with site, but only *Diopatra*

ornata showed significant differences with area. *Thelepus crispus* and *Chaetopterus*

variopedatus densities were significantly different with date. *Phyllochaetopterus prolifica* and *C.*

variopedatus density varied with interactions between time and site, and *D. ornata* density with

interactions between time and area. *T. crispus* means showed a gradient but not definite clusters

when analyzed by SNK.

Counts from infaunal can cores also show the abrupt drop off in numbers at the edge of the

mat (Figure 2). The edge of the community is a very clean, distinct line.

Lab counts of infauna may be more accurate than the field counts, especially during the winter

when surge and low visibility often obscured the smaller organisms. However, field data were

taken every month instead of every quarter and may add detail, especially for changes with date.

Emerson's (1975) finding that >95% of the *Diopatra ornata* tubes in the field were occupied, and

the rapid decomposition of unoccupied tubes in seven days (Bell and Coen 1982a) are support

for the accuracy of field counts under good conditions. *Chaetopterus variopedatus* densities

were significantly different in the lab counts only, and the greater number of field samples may be more accurate. But *D. ornata* densities only showed significant seasonal differences in the field counts, the minimum observed during the winter may actually be due to field conditions. Unless both field and lab data show significant differences, treat the results with caution.

To summarize briefly, all abundant species in the *Diopatra ornata* community showed significant differences between sites along an exposure gradient except *Pisaster giganteus*. An area effect was significant for half the species; *Pycnopodia helianthoides, Cryptochiton stelleri, Asterina miniata, Pachycerianthus fimbriatus, D. ornata,* and *Tegula* spp.. Significant seasonal differences were found for Laminariales, *P. fimbriatus, Tegula* spp., and *Loxorhynchus crispatus.*

Diopatra ornata were the same average size at all sites along the exposure gradient. However, the pattern of size distribution within inner, middle and outer areas of the mat was different between sites (Figure 3). At the protected sites (1 and 2), there was a trend of smaller worms in the middle of the bed than on the inner and outer edges. At the exposed sites (3, 4 and 5), the differences between worms from different areas were smaller, and the pattern was inconsistent between sites.

Kelp availability

The observed pattern of larger worms at the edges, against the rock reef in protected areas, correlated strongly with the amount of drift *Macrocystis pyrifera* available as food. The amount of kelp available at the protected sites was significantly greater at the edges of the bed than in the middle in both summer and winter. Differences in the weight of drift kelp found in the middle compared to the inner edge of the bed were not significant at the three exposed sites. The pattern was more pronounced during the summer (Figure 4) and significant only at the protected sites (1 and 2), where the size pattern in the worm population was also most distinct.

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Kelp consumed

Offered an abundance of kelp, the larger worms at the inner edges of the protected sites ate more than the small worms in the middle of the bed. The equally sized (large) worms throughout the bed at the exposed sites ate equivalent amounts of drift kelp throughout the bed. Though statistical tests showed no significant differences between the amount of *Macrocystis pyrifera* eaten at the inner edge and in the middle of the *Diopatra ornata* bed, the pattern was consistent (Figure 5). Since many of the replicates were lost (Table 3), especially at the more exposed sites, the power of the statistical tests was low.

Worm transplants

When transplanted to the inner edge of the bed, worms got larger than controls replaced in the middle of the bed. However, worms transplanted to the middle of the bed decreased slightly in size relative to worms replaced at the inner edge. Six months after transplantation, there was a significant difference in density at Site 2 between the worms transplanted to the inner edge and control worms replaced in the middle of the bed (p = 0.0001). All other treatments had non significant differences between transplant and control densities. The worm sizes were significantly different between transplants to the inner edge and their controls, and between transplants to the middle and their controls, at Site 1. At Site 2, there were no significant differences between transplants and controls in either direction. Though the differences are not statistically significant, the pattern at Site 1 is repeated at Site 2 (Figure 6). In six months, small worms transplanted closer to the reef, where more food is available, grew noticeably.

Food manipulations

Was the amount of food available to the worms dependent only on the amount of drift kelp available, or was it also dependent on the degree of fouling of the tube cap? Manipulations of

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these two factors, separately and in combination, showed no significant difference in the number of worms in treated quadrats. The sizes of worms in experimental treatment plots were pooled and compared by a non parametric multiple comparison test of control to experimental groups, with unequal sample sizes (Zar 1984, p. 201), except for February samples from Site 1, which were too heterogeneous to pool. This test for mean rank size showed no significant differences, probably because the mean square error is so large - the samples are not count data but sizes and the average size therefore has a large error term. Unfortunately, there is no non parametric statistical test available for comparing frequency distributions with unequal sample sizes (Conover 1980, p. 377). Graphic comparisons showed slight differences in worm size depending on treatment, adding kelp and removing epifaunal algae created the largest difference in worm sizes when compared with controls (Figure 7). Removing algae or adding kelp alone also increased the worm sizes slightly. Though the differences were small, the pattern becomes more evident after twelve months than at six months, suggesting that the worms were responding to the treatments. As with many biological systems, the high variability often gave results that were not statistically significant, though trends were evident. This variability could be reduced by more extensive replication, but this would also make the study more difficult and costly. More obvious growth effects might also be seen by running the experiments for longer time periods, but again, increased replication would be needed to offset the loss of treatments.

Artificial reefs

Diopatra ornata mats around artificial reefs of varying ages showed differences in the density and size of the worms and the extent of the bed around the reef (Table 4, Figure 8). *D. ornata* were densest around the old Marina del Rey Artificial Reef and thin around the new Marina del Rey Artificial Reef, the youngest reef sampled. Worms were largest around Pendleton Artificial Reef and smallest around Hermosa Beach Artificial Reef, the oldest reef. The bed extended the least

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distance from the new Marina del Rey Artificial Reef, the youngest reef.

DISCUSSION

Worm size patterns

Food was the factor that determined worm size distribution patterns. Large worms were prevalent in areas where more food was available. Experimental manipulations that increased potential food resulted in greater growth of the worms.

At the protected sites, the worms were larger close to rock reef edges, where drift kelp was trapped and concentrated, and at the exposed sites, where drift kelp was evenly distributed, worms were the same size throughout the mat. When equal amounts of kelp were made available, the large worms at the edges of the protected sites ate more than the smaller worms in the middle of the bed. Worms at exposed sites ate equivalent amounts throughout the bed.

Experiments at the protected sites suggest that the worms grow larger when transplanted to areas where more food is available or when provided with an easily accessible food source. Unfortunately, it was not feasible to do similar experiments in the exposed areas because the sea conditions were too rough to maintain the manipulations (Table 3). Making food accessible by removing fouling algae from *Diopatra ornata* tubes or abundant by adding drift kelp resulted in larger average worm sizes. Food that was both abundant and readily accessible resulted in the greatest worm growth of all. Differences were noticeable after six months and more obvious after twelve. The growth of *Diopatra ornata* seen in the transplant experiments indicated that food items falling off the reef may result in faster worm growth and larger size close to the reef. Small worms, transplanted from the middle of the bed to the inner edge, grew more than small worms replanted in the middle of the bed. Large worms transplanted from the inner edge to the middle

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of the bed did not grow as much as large worms replanted at the edge. The relative difference in size between worms in the transplant experiments after only six months was greater than that seen between worms in the food availability experiments after six or twelve months (Figures 7 and 8). All differences in size, though detectable after six months, were relatively small even after twelve months and suggest that these worms are slow growing.

Species distributions

Once established, the mat community appears to be regulated by disturbance, primarily physical. The most consistent differences in species abundances were among the sites sampled along an exposure gradient. Most species were more abundant at the protected sites, although none were completely absent from even the most exposed site. Food availability is also a structuring force in this community, influencing the areal distribution of abundant species within the mat. The differences between areas of the mat, seen in half the species censused, correlated with increased food availability close to the rock reef. The animals present at equal densities throughout the mat were either infaunal suspension feeders or known to forage on food items abundant in all areas of the mat, while organisms abundant adjacent to the reef may have been utilizing detritus fallen from the reef as a food resource. The five species which showed a seasonal fluctuation in abundance were likely responding to differences in water and sediment motion.

Along an exposure gradient, nine of the twelve species sampled were more abundant at the protected sites (Table 2). *Diopatra ornata, Chaetopterus variopedatus, Phyllochaetopterus prolifica, Thelepus crispus,* and *Pachycerianthus fimbriatus* are all soft bodied tube dwelling infauna. Reduced scour, burial, and erosion at the more protected sites would be advantageous for these species. Magnum *et al.* (1968) and Rhodes *et al.* (1968) found that congeneric *Diopatra cuprea* preferred habitats with high current flow, rather than the protected sites favored by

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Diopatra ornata. Dense *D. cuprea* mats are found concentrated in areas of high water velocity with the tubes oriented perpendicular to flow (Barwis 1985). Field studies done by Magnum *et al.* (1968) suggest that a greater abundance of drifting food results in higher worm densities. In the absence of a rock reef nearby to trap and concentrate drift algae, *D. cuprea* may rely on high water flow to bring food items which are then trapped by the tube caps and attached to the tubes by the worms (Fauchald and Jumars 1979, Rhoads *et al.* 1978).

Pycnopodia helianthoides, Cryptochiton stelleri, Asterina miniata, and *Loxorhynchus crispatus* may find more abundant food in the protected habitats, as trapped detritus and drift as well as the dense epibionts that flourish on the tubes of the infauna (Day and Osman 1981, Harrold 1981, Herrlinger 1983, Hines 1982, Webster 1968). Reduced water motion may be responsible, directly or indirectly, for the increased densities of these species at protected sites. Two species, Laminariales and *Tegula* spp., were more abundant at the exposed sites. They were also among the few organisms with significant seasonal changes in abundance. Stronger water movement at the exposed sites may be enough to knock *Tegula* spp. off the kelp plants where it is usually found and into the *Diopatra ornata* mat (Watanabe 1984). The greater flow of water could also increase the number of Laminariales spores available to settle in the exposed habitats (Foster and Schiel 1985).

Half of the species were most abundant at the inner edge of the mat. *Pycnopodia helianthoides, Cryptochiton stelleri, Asterina miniata, Pachycerianthus fimbriatus* and *Diopatra ornata* were concentrated at the edges of the community, close to the rock reef. Increased availability of potential food items dislodged from the rocks may concentrate these species near the reef. *Tegula* spp., knocked from kelp plants on adjacent reefs, would naturally be concentrated at the inner edges of the mat.

The other six species were evenly distributed throughout the mat. The infaunal suspension feeders *Chaetopterus variopedatus, Phyllochaetopterus prolifica* and *Thelepus crispus* (from

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Fauchald and Jumars 1979) were spread evenly throughout the mat, as were the seasonal recruits of Laminariales. Highly mobile *Loxorhynchus crispatus* seemed to wander through the community at will, leaving when the conditions became too rough. *Pisaster giganteus* was also evenly distributed in the mat community and has been observed feeding on *Diopatra ornata* (Rosenthal *et al.* 1974). Its distribution may be due to the abundant availability of potential food items.

Most of the species found showed no seasonal change in abundance. Significant seasonal differences were found only for Laminariales, *Loxorhynchus crispatus, Tegula* spp., and *Pachycerianthus fimbriatus*. Laminariales and *L. crispatus* were most abundant in the fall, *Tegula* spp. in the winter, and *P. fimbriatus* in the spring. In Laminariales a pattern of seasonal recruitment was obvious, with many small plants appearing in late fall. Because older plants did not persist in the bed once they grew large enough to be ripped out by water motion, in winter density declined to zero. *L. crispatus* may shelter in reef crevices from winter storm surge, or the difference in numbers may reflect an actual change in abundance. Hines (1982) found reduced numbers of *L. crispatus* on reefs in winter months, due to mortality from storms. The seasonal storm pattern was possibly responsible for the date effect seen in *Tegula* spp. By knocking *Tegula* spp. off the kelp plants and ripping away blades where the snails are often found (Watanabe 1984) storms may force the snails into the *Diopatra ornata* mat. The number of *P. fimbriatus* was high during the first month of sampling only, this was probably due to investigator error. Generally, the mat community was remarkably stable and non-seasonal. This is consistent with the results of Peckol and Baxter (1986), who found no changes in density in a *Diopatra cuprea* assemblage over three years.

For species where the interactive effects could be examined, there was usually an interactive date and site effect. This was possibly due to the difference in intensity and effects of seasonal storms at exposed versus protected sites. Date and area showed no interactive effect except for *Diopatra ornata*. Again, seasonal weather patterns may be the causal factor, tearing up the outer

edges of the mat seasonally when storms are the strongest.

The abundant species in the ecotone community seem to be responding to a combination of factors within the *Diopatra ornata* mat. Reduced sediment scour and mobility would be advantageous for soft bodied, non-motile organisms. Stable substrate availability would allow settlement of sessile species, and sediment stability might increase the numbers of associated infauna. Abundant food would be attractive to grazers, omnivores and detritivores. Whether effects are directly or indirectly due to the presence of *D. ornata*, the densities of all ecotone species decline rapidly at the sand edge of the community (Figure 2).

Ecotone development

The *Diopatra ornata* dominated ecotone community around natural reefs also develops around artificial reefs placed on soft bottoms. Davis *et al.* (1982) found that within 18 months, *D. ornata* had begun to form a halo around artificial reefs in southern California. As a *D. ornata* bed develops around artificial reefs, it becomes denser and extends further away from the reef (Davis *et al.* 1982). Juveniles show a settling response to sediments conditioned with *Macrocystis pyrifera* or with extracts from adults (Fauchald and Emerson 1975), and in the field *Diopatra cuprea* recruits more heavily in areas where adults are present (Peckol and Baxter 1986, Woodin 1981).

Relative ages of artificial reefs can be determined by examining the ecotone community around them. Since *D. ornata* density increases with time around newly deployed artificial reefs, the relative ages of reefs sampled can be ordered based on the number of worms around them. This relative order of reef age can also be determined from the distance away from the reef of maximum worm density (Figure 8). A third method of determining relative reef age is by comparing the average size of *D. ornata* around the reef; once a few *D. ornata* establish themselves, they will stabilize the substrate and increase recruitment of small juvenile worms (Fauchald and Emerson 1975, Peckol and Baxter 1986, Woodin 1981). Table 4 shows the relative reef ages determined

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by these methods, compared with the known ages of the reefs. Each of the aging methods distinguished the two oldest reefs from the two newest reefs, recognizing differences between reefs whose ages differed by more than 15 years, but not between reefs with age differences of less than five years.

These time scales indicate that development of the ecotone community is a slow process. Establishment of a kelp forest on the new hard substrate can be a slow process as well (Turner *et al.* 1969), and perhaps it is the slow development of an abundant food resource that limits the rate of development of the ecotone. Drift kelp trapped against the reef may encourage development of a dense tube mat which further allows migration or recruitment of species generally associated with rocky reefs, as well as some species usually found in relatively undisturbed sand bottoms. This becomes a distinct ecotone community. The differences in abundance of the dominant species along an exposure gradient indicate the importance of disturbance as a structuring force in the established ecotone community. Higher densities of many species and larger sizes of *Diopatra ornata* at the inner edge of the mat, next to the reef, indicate the continued importance of food supply in structuring the ecotone community.

Artificial reef locations can be wisely chosen with more information on the changes that occur in the surrounding soft sediments. Unfortunately, monitoring of artificial reefs is usually only concerned with the development of a rocky bottom community. However, development of an ecotone community can be equally important to the health and persistence of the reef and its community, because as the fringing mat stabilizes the sediment it reduces scour stress on soft bodied animals and prevents the reef material from being buried or sinking into shifting sediments (Orth 1977). Prior knowledge of the hydrography in areas where artificial reefs are planned can be used to advantage to increase the stability of the reef, as *Diopatra ornata* will generally arrange their tubes in rows perpendicular to the current, and will concentrate at the upcurrent end of a structure, where kelp and other detritus is caught (Barwis 1985, Brenchley and Tidball 1980,

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Fager 1971, Myers 1972).

Summary

In the *Diopatra ornata* ecotone community, recovery from natural or man-made disturbance is likely to be slow. Growth rates seen in the experimental manipulations indicate that *D.ornata* is a slow growing species, and artificial reef data that the tube mat takes a long time to develop. The differences in the community seen along an exposure gradient indicate that the primary source of disturbance is physical, but feeding disturbances may also play an important role. Predators range from crabs (*Cancer magister*) and fish (*Damalichthys vacca*), through bat rays (*Myliobatus californica*) to grey whales (*Eschrichtius robustus*) (pers. obs.). These animals create disturbances which vary from displacing one worm tube to decimating several hundred square meters of mat (Fager 1964, Oliver *et al.* 1984).

Diopatra ornata could be called the "anchor species" in this ecotone; its absence would result in significant changes in the community structure. The abrupt decrease of all associated species densities at the edge where *D. ornata* abundance decreases and the absence of these species from mobile sand communities, even adjacent to rock reefs (ABA Consultants 1985, Davis *et al.* 1982), indicate that they are dependent on *D. ornata* for the underlying structure of the community. Species from the adjacent habitats, both rocky reef/kelp forest and sand bottom, utilize the tube mat as a hospitable habitat. While the relative abundances of the associated species change depending on the degree of exposure, the species composition of the community remains constant.

The *Diopatra ornata* community is similar to coastal dunes, seagrass beds, salt marshes and mangrove forests, all systems where sediment stabilization by primarily one species plays a major role in structuring the community. The factors that control initial establishment of the stabilizing species in these communities are not well known (Bradstock 1985, Brewer and Grace 1988,

Phillips and McRoy 1980, Ranwell 1972, Stewart 1988). Once established, factors important in maintaining ecotone communities may be very different, but in *D. ornata* mats, disturbance and food availability appear to be the dominant structuring forces. Because of the recent realization of man's impact on various interface communities, much research is currently being conducted in these habitats. The *D. ornata* tube mat is an interface community like the threatened ecosystems and understanding how important ecological factors affect it can aid our understanding of other ecotones.

ACKNOWLEDGEMENTS

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Table 1.   Correlation matrix of r values for sizes of *Diopatra ornata* tubes and worms.
N = 40.

	Worm diameter	Worm length	Worm weight
Worm length	0.73	-	
Worm weight	0.79	0.86	-
Tube diameter	0.69	0.59	0.60

Table 2. P values from statistical comparisons of density by date, site and area (nested within site), for dominant species in the *Diopatra ornata* community. Three way ANOVAs with one nested factor were performed whenever possible. The complete data set from (field) was too large for the computer capacity to allow calculations to be performed by Statview II, so (field) data were pooled over date and analyzed by two way ANOVA if Scheffe's test was non significant, otherwise data were split into two six month time segments for a three way ANOVA, one nested factor. Data are from field counts, except (lab), which indicates lab counts from infaunal cores. NS = not significant at the P = 0.05 level.

Species	Site effect	Area (site) effect	Date effect	Site x Date effect	Area (site) x Date effect
Tegula spp.	<0.002	<0.001	<0.001	<0.001	NS (>0.1)
Pachycerianthus fimbriatus	<0.001	<0.001	<0.001	<0.001	NS (>0.2)
Thelepus crispus (field)	<0.001	<0.001	NS (>0.2)	NS (>0.5)	<0.001
	<0.001	<0.001	<0.001	<0.001	NS (>0.1)
Pycnopodia helianthoides	<0.001	<0.001	NS (>0.2)	<0.005	NS (>0.5)
Cryptochiton stelleri	<0.001	<0.02	NS (>0.1)	<0.02	NS (>0.5)
Asterina miniata	<0.001	<0.001	NS (>0.5)	<0.001	NS (>0.5)
Diopatra ornata (lab)	<0.001	<0.05	NS (>0.2)	NS (>0.5)	<0.001
Diopatra ornata (field)	<0.001	NS(>0.5)	<0.05	NS(>0.5)	<0.001
	<0.001	<0.001	<0.001	<0.001	NS(>0.5)
Loxorhynchus crispatus	<0.001	NS (>0.5)	<0.001	<0.001	NS (>0.5)
Chaetopterus variopedatus (lab)	<0.001	NS (>0.5)	<0.001	<0.005	NS (>0.5)
Laminariales	<0.001	NS (>0.5)	<0.001	<0.001	NS (>0.5)
Thelepus crispus (lab)	<0.001	NS (>0.5)	<0.02	NS (>0.5)	NS (>0.5)
Phyllochaetopterus prolifica (lab)	<0.001	NS (>0.2)	NS (>0.05)	<0.05	NS (>0.2)
Pisaster giganteus	NS (>0.2)	<0.001	NS (>0.05)	<0.001	NS (>0.5)
Phyllochaetopterus prolifica (field)	NS (>0.5)	<0.001	NS (>0.2)		
Chaetopterus variopedatus (field)	NS (>0.2)	<0.002	NS (>0.2)		

Table 3. Percent of kelp samples lost from each of five sites.
N = 10.

Protected		Exposed		
Site 1	Site 2	Site 3	Site 4	Site 5
10%	50%	90%	70%	90%

Table 4.   Relative ages of artificial reefs determined by the *Diopatra ornata* mat around them, and compared to known ages. Reef ages from Carlisle 1977. PAR, Pendleton Artificial Reef; MDR, Marina del Rey Artificial Reef; HBAR, Hermosa Beach Artificial Reef.

METHOD OF AGING REEF	REEF AGE FROM YOUNGEST TO OLDEST			
Field density (overall)	new MDR	PAR	HBAR	old MDR
#/0.175 m^2	0.56	1.72	2.73	5.62
Lab density (overall)	new MDR	PAR	HBAR	old MDR
#/0.0075 m^3	2.0	2.0	4.0	9.8
Field density with distance	new MDR	PAR	old MDR	HBAR
Lab density with distance	new MDR	PAR	HBAR	old MDR
Average worm size	PAR	new MDR	old MDR	HBAR
mm	2.67	2.40	1.49	1.27
Known age	new MDR	PAR	old MDR	HBAR
year built	1985	1980	1965	1960
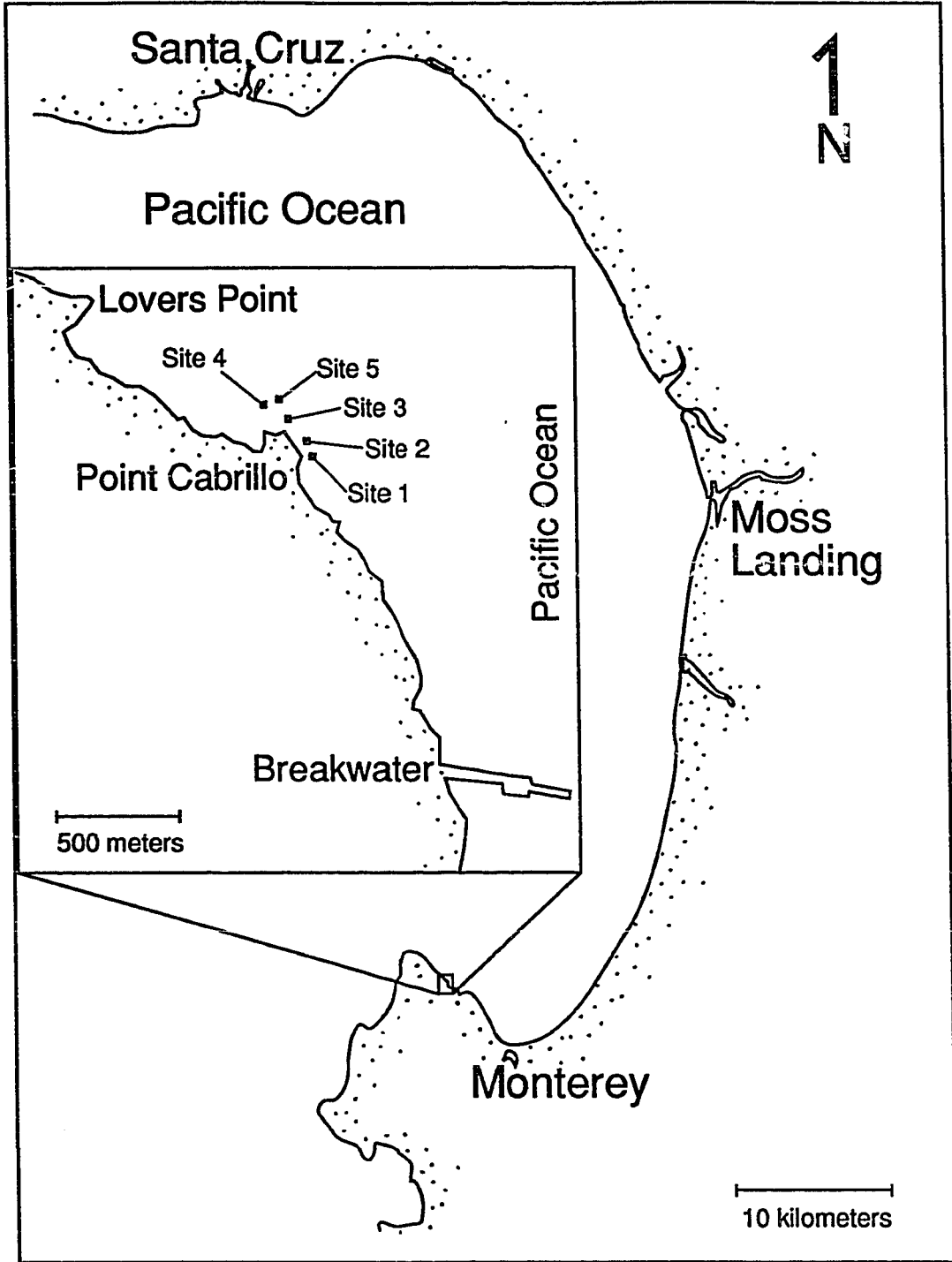
Figure 1. Map of study sites in Monterey Bay. Sites 1 and 2 are protected, sites 3 and 4 are exposed, and site 5 is very exposed.
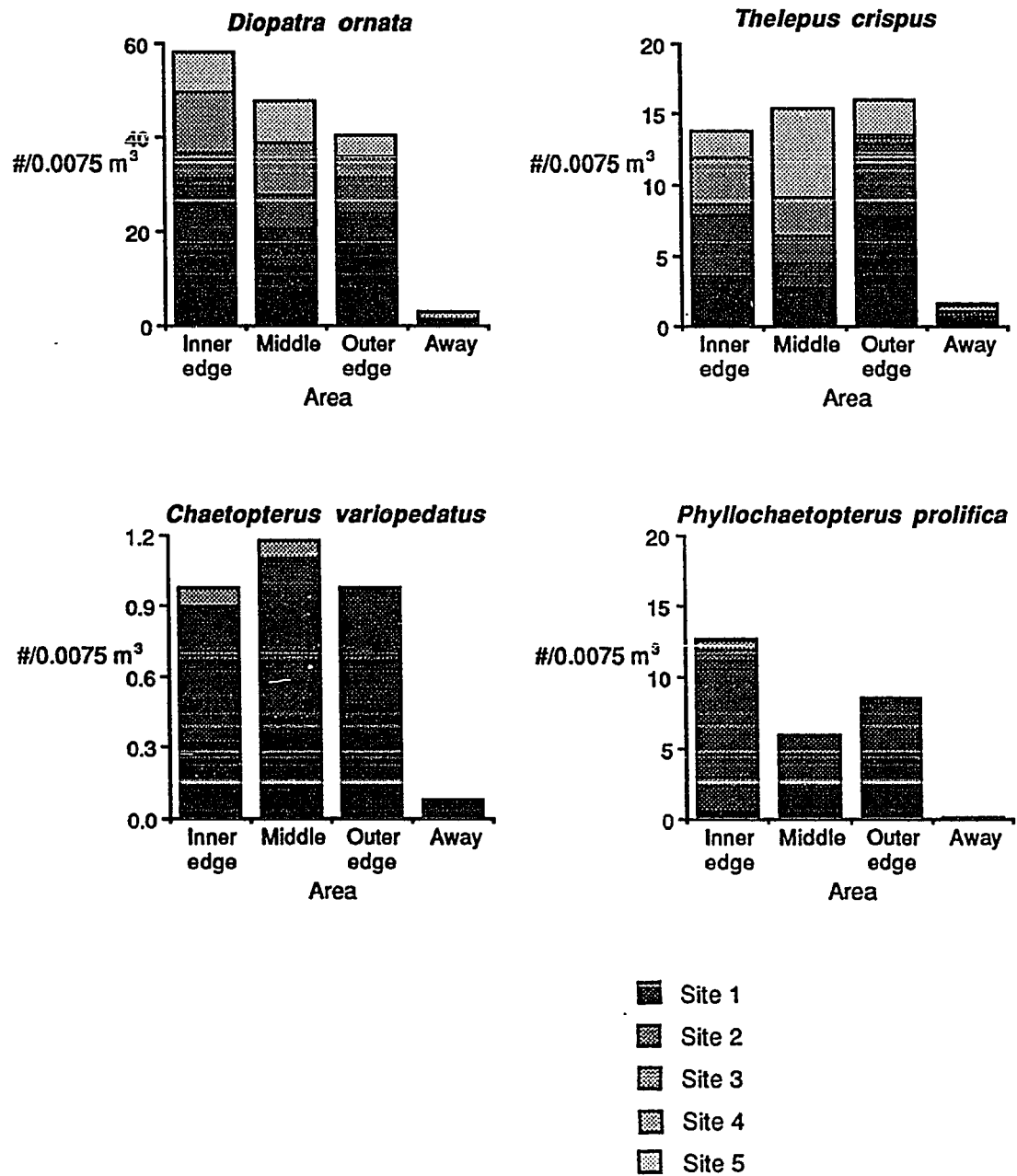
Figure 2. Average density of four infaunal species: *Diopatra ornata*, *Thelepus crispus*, *Chaetopterus variopedatus*, and *Phyllochaetopterus prolifica*, at five sites and four areas in and near a *D. ornata* community. N = 3.
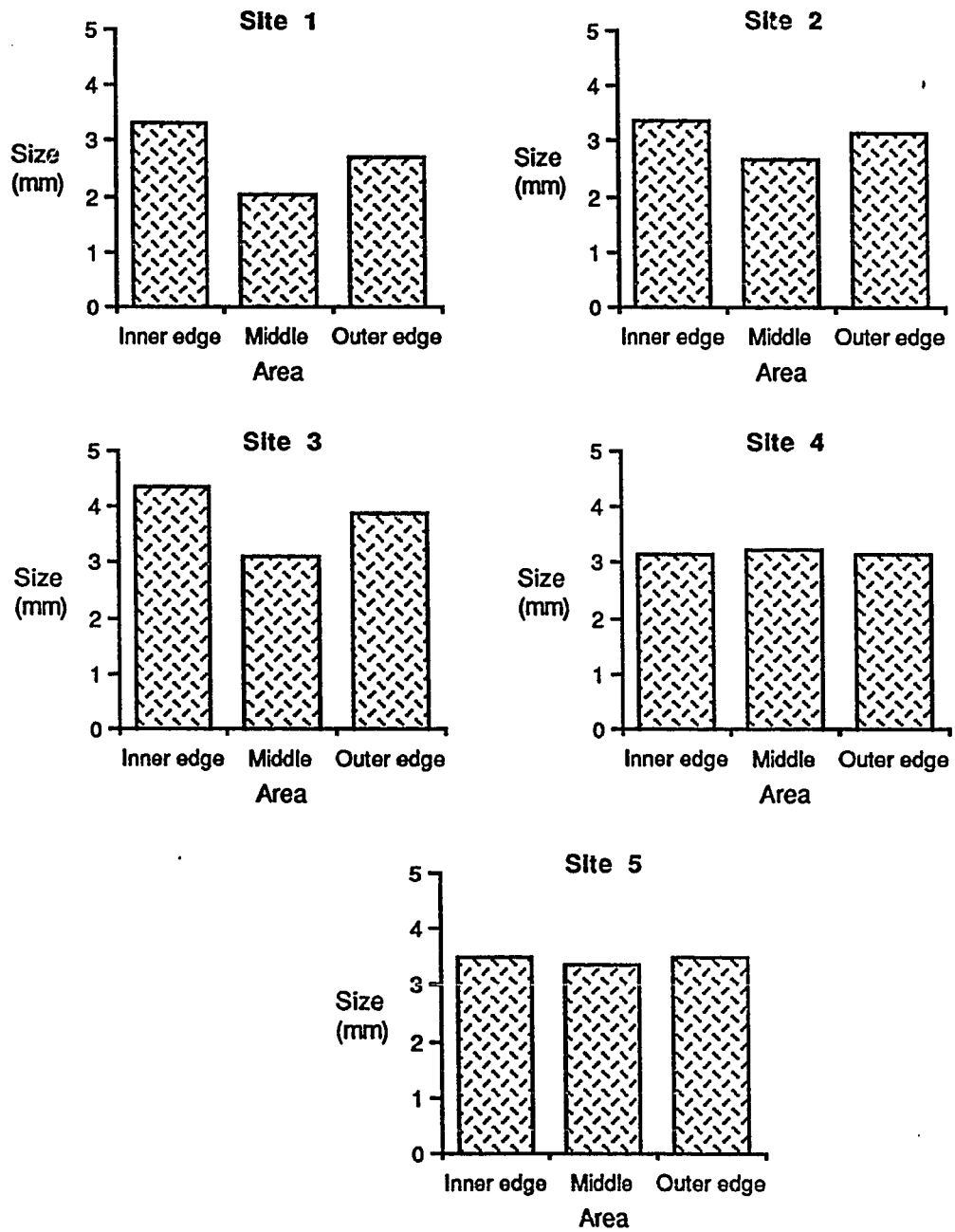
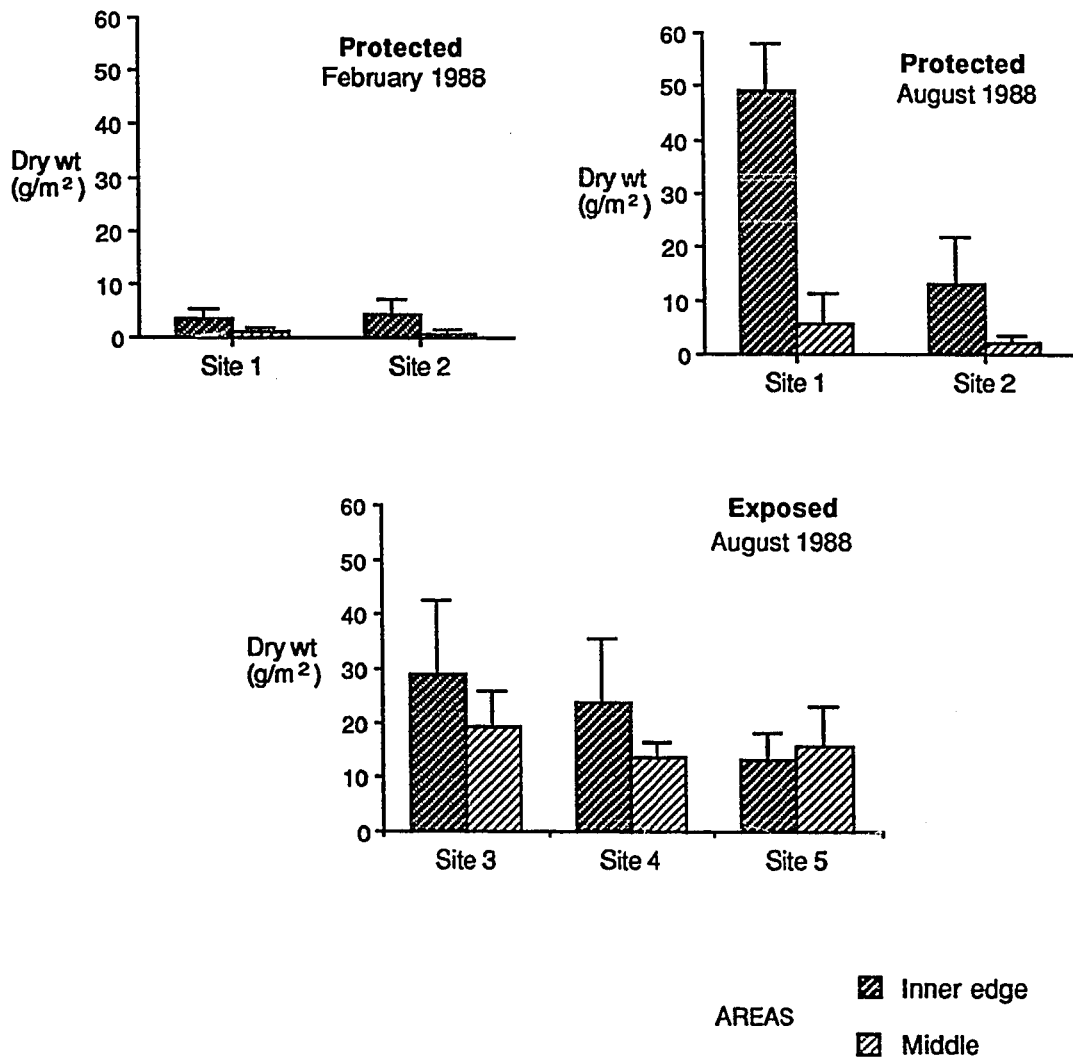Figure 3. Average size of *Diopatra ornata* at three areas within five sites.

Figure 4.   Amount of drift kelp available at five sites and two areas within *Diopatra ornata* beds. Protected sites were sampled at two times. Mean and one standard error, N = 3.
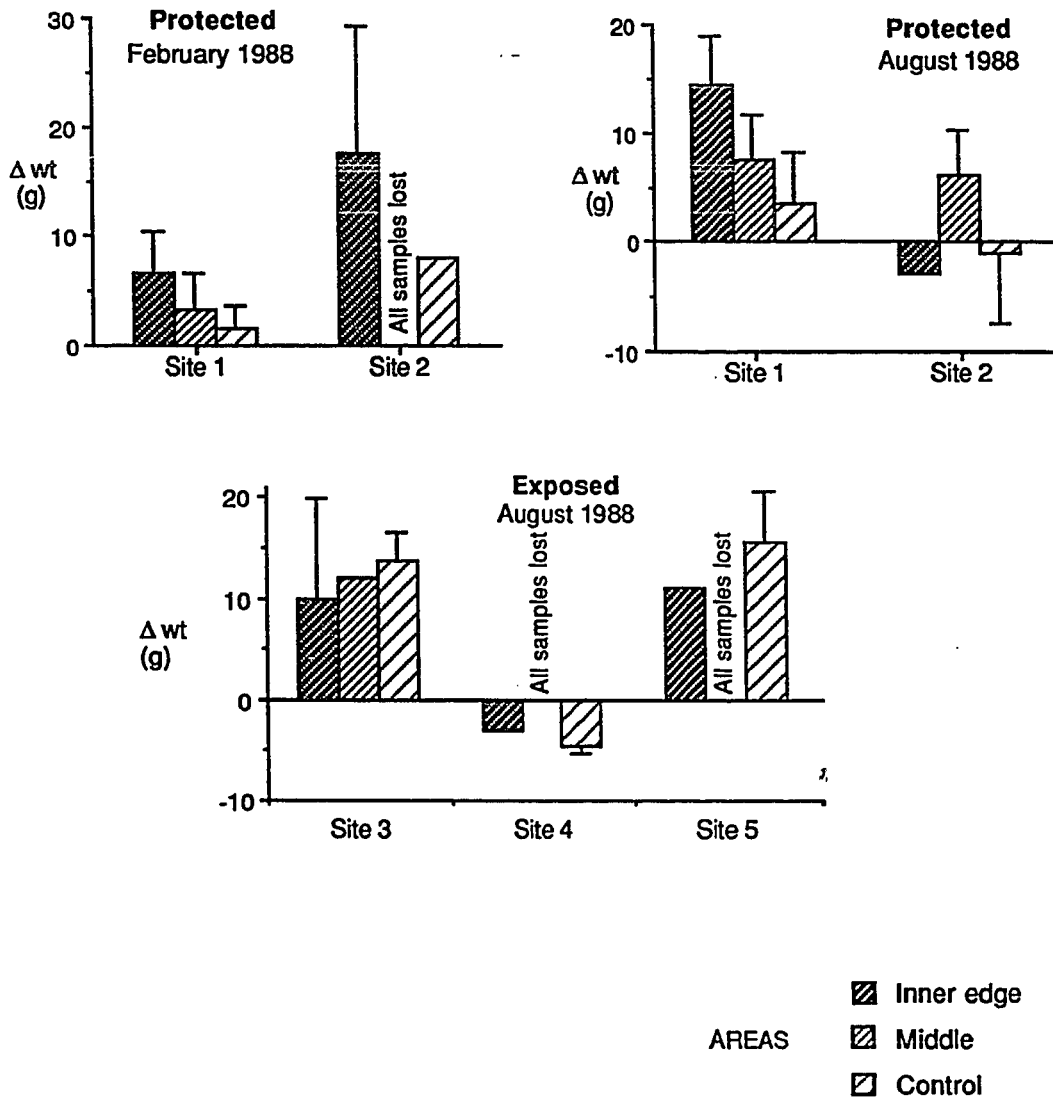
Figure 5. Amount of kelp eaten in one week by *Diopatra ornata*. Experiments performed at five sites along an exposure gradient. At each site, the areas were: at the inner edge, in the middle of the mat, and controls. Experiments were done twice at protected sites. Negative values indicate kelp grew more than it was eaten. Mean and one standard error, see Table 3 for sample sizes.
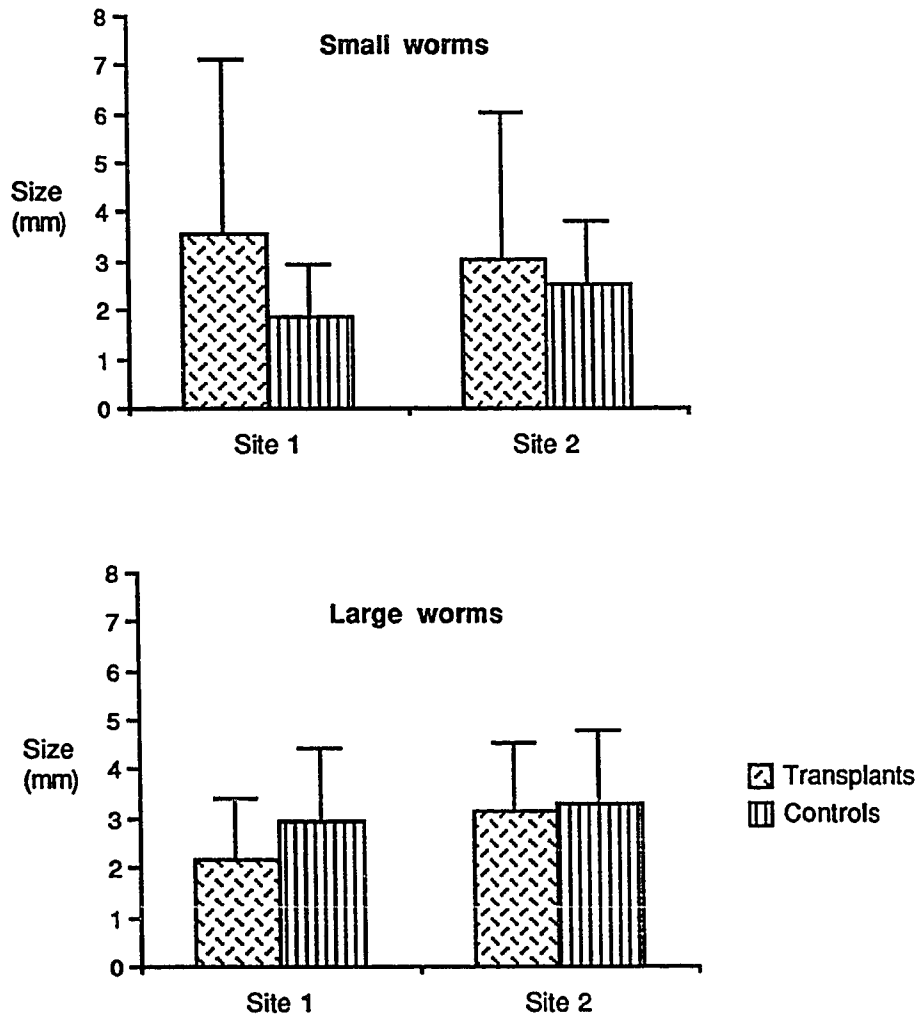
Figure 6.   Average tube diameter of *Diopatra ornata* transplants and controls after six months at two sites. **Small worms** - transplants from the middle to the inner edge of the mat, compared with controls (small worms replaced in the middle of the mat); **Large worms** - transplants from the inner edge to the middle of the mat, compared with controls (large worms replaced at the inner edge of the mat). Mean and one standard error, N = 6.
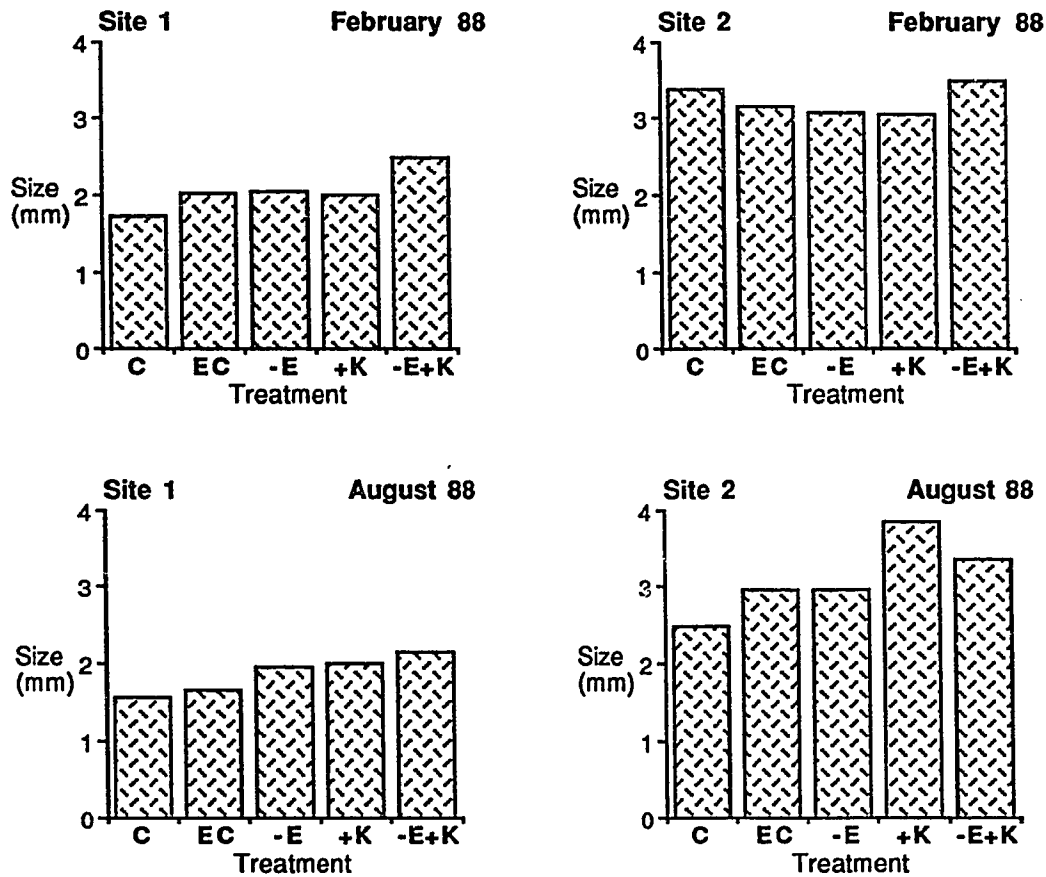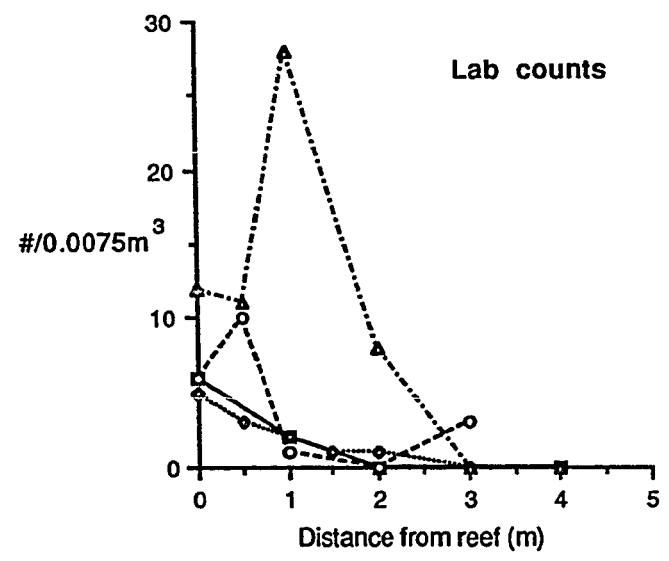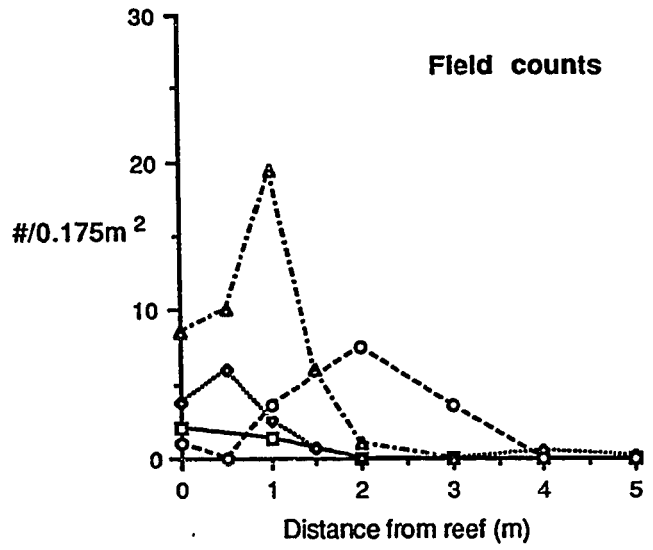
Figure 7.   Average tube diameter of *Diopatra ornata* under three experimental food
manipulations at two sites and two dates. C, untouched control; EC, experimental
control; -E, epifaunal fouling algae removed; +K, drift kelp added as food; -E+K,
both epifauna removed and food added. N = 5.

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Field counts

#/0.175m^2

Distance from reef (m)

Lab counts

#/0.0075m^3

Distance from reef (m)

———□——— new Marina del Rey Artificial Reef

············◇············ Pendleton Artificial Reef

---·-▲-·-- old Marina del Rey Artificial Reef

----o---- Hermosa Beach Artificial Reef

Figure 8. Densities of *Diopatra ornata* at different distances from four artificial reefs in southern California.