

Deep-Sea Harpacticoid Copepod Diversity Maintenance: The Role of Polychaetes*

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Abstract

Several models to account for enhanced diversity in the deep sea have been proposed, but the available natural history information has been inadequate to distinguish among them. In particular, few data exist on patterns of co-occurrence among species. At 1220 m depth in the San Diego Trough (32°35.75'N; 117°29.00'W), harpacticoid copepod species covary significantly with polychaetes when the polychaetes are combined into functional groups on the basis of feeding type and mobility. In particular, harpacticoid species tend to avoid polychaetes which are sessile surface-deposit feeders. The results provide support for models in which disturbance/predation plays an important role in maintaining deep-sea diversity.

Introduction

In the deep sea, certain higher taxa are more diverse than in comparable, shallow-water habitats (Hessler and Sanders, 1967; Coull, 1972; Hessler and Jumars, 1974; Thistle, 1978). Several models (e.g. Sanders, 1968; Dayton and Hessler, 1972; Grassle and Sanders, 1973; Jumars, 1975a; Menge and Sutherland, 1976) have been proposed to explain this enhanced diversity, but the available data do not unequivocally support a particular view (Jumars, 1975a; Thistle, 1977). The paucity of natural history information available hinders our ability to perceive mechanisms maintaining high deep-sea diversity. *In situ* observations have provided some information about the small-scale spatial dispersion and rates of movement of some epibenthic, megafaunal species (Barham *et al.*, 1967; Lafond, 1967; Grassle *et al.*, 1975). Some small-scale dispersion data have been published on the diverse taxa (Hessler and Jumars, 1974; Jumars, 1975a, 1976; Thistle, 1978). Jumars (1975a, 1976) and Thistle (in press) have shown the apparent impact of biogenic structures on macrofaunal and meiofaunal species respectively. However, few data (e.g. Hessler and Jumars, 1974) have been pub-

lished on the patterns of co-occurrence of species on small scales. Although such analyses suffer from the limitations of a correlation approach, they provide a qualitatively different description of pattern in the community and may help limit the set of acceptable models of diversity maintenance in the deep sea (Hessler and Jumars, 1974).

This paper describes the co-occurrence of polychaetes and harpacticoid copepods at a bathyal site in the San Diego Trough. Polychaetes at this locality are the most abundant macrofaunal organisms (Jumars, 1976), and certain species are known harpacticoid predators (Jumars, personal communication). The majority of the species deposit-feed and probably consume harpacticoids as they process sediment. Their activities may alter the environment locally for harpacticoids. This paper reports the impact of polychaetes on harpacticoid species abundances and examines the proposed models in terms of the results.

Materials and Methods

The sample site was located in the San Diego Trough (32°35.75'N; 117°29.00'W) between 1218.3 and 1223.8 m depth (Fig. 1), away from known turbidite channels. The sediment was a green mud. Thistle (1978) presented data on phys-

*Contribution No. 15 from Expedition Quagmire.

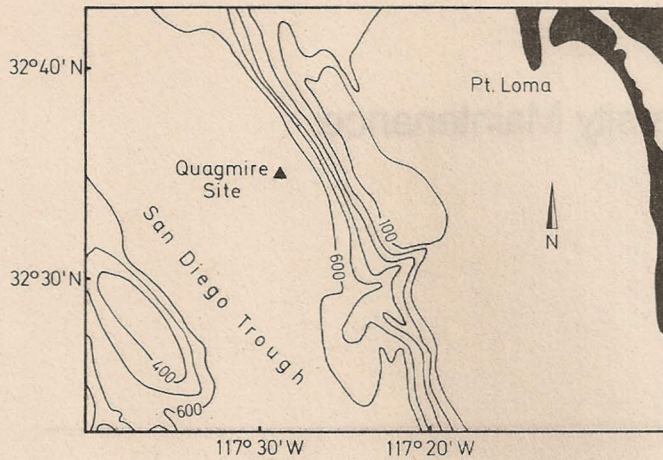


Fig. 1. Chart of sampling area. Filled triangle marks the Quagmire site; depth contours are in fathoms. (Modified from Coast and Geodetic Survey Map No. 5101)

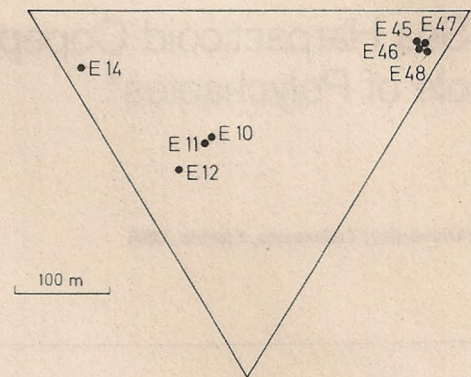


Fig. 2. Quagmire-site sampling triangle. The Ekman cores dealt with in this study are indicated by numbered circles

Table 1. Feeding-mobility classification. (Modified from Jumars and Fauchald, 1977)

Mobility class	Trophic type	
	Subsurface-deposit feeder	Surface-deposit feeder
Motile	Capitellidae	<i>Braniella</i> sp.
	<i>Cossura</i> spp.	Dorvilleidae
	<i>Meiodorvillea apalpata</i>	(excl. <i>Meiodorvillea</i>)
	Orbiniidae	<i>Exogone</i> sp.
	Paraonidae	<i>Flabelligella</i> spp.
Discretely motile		<i>Ophelina</i> sp.
		<i>Polyophthalmus</i> sp.
		Sphaerodoridae
		<i>Artacamella</i> sp.
		Cirratulidae
		(excl. <i>Tharyx luticastellus</i>)
		<i>Myriochele</i> sp.
Sessile	Maldanidae	Sabellidae
		Spionidae
		Ampharetidae
		<i>Fauveliopsis glabra</i>
		<i>Phyllochaetopterus limicola</i>
		Terebellidae
		<i>Terebellides</i> cf. <i>stroemi</i>
<i>Tharyx luticastellus</i>		

Table 2. Summary of significant correlations between harpacticoid species and polychaete functional group. No adjustment has been made for multiple testing

Polychaete functional group	No. of species with significant positive correlations	No. of species with significant negative correlations
Motile subsurface-deposit feeders	6	4
Motile surface-deposit feeders	4	6
Carnivores	5	3
Discretely motile subsurface-deposit feeders	5	3
Discretely motile surface-deposit feeders	3	3
Sessile surface-deposit feeders	3	9

ical parameters and argued that the site had the stability characteristics typical of the deep sea.

The samples were collected as part of Expedition Quagmire (Thiel and Hessler, 1974). The expedition used a remote underwater manipulator to take samples *in situ*. Television monitoring suggested that these samples were free of bias caused by the shock wave which preceded the sampler, in contrast to those taken with ship-based samplers (e.g. Jumars, 1975b). Using transponder navigation, the sample positions were determined to within 1 m.

Fifty-eight samples were taken in a stratified random manner from the study site using a modified Ekman grab (20 x 20 cm) containing four 10 x 10 cm subcores. I analyzed the harpacticoid copepod fauna from 14 subcores (2 from each of 6 cores and 2 single subcores). Fig. 2 shows the distribution of samples in the study site; Thistle (1978, his Table 2) gives the intersample distances. The top 1 cm layer and overlying water for each subcore were fixed in formaldehyde at sea. Each sample was sieved on 0.062 mm opening sieve and transferred to ethanol. The adult harpacticoids were sorted, identified to species and counted.

Because individual polychaete species' abundances were too low to permit correlation statistics to be usefully calculated, species were combined into functional groups. *Aglaophamus paucilamelata*, *Ceratocephale pacifica*, *Glycera* sp. and the members of the Hesioidae, Lumbrineridae, Phyllodocidae and Polynoidae found in the San Diego Trough were grouped together as carnivores. The remaining species were grouped by their feeding type and mobility, following Jumars and Fauchald (1977). Motile forms move freely over the bottom; discretely motile forms move after intervals of remaining still; sessile forms are either fixed-location tube dwellers or species which move only under great provocation. Feeding type is categorized by both method and location. Table 1 gives the taxa assigned to each category. The inconsistency in taxonomic level treated occurs because of the differences in level necessary to specify a feeding mode (K. Fauchald, personal communication). Individuals for all taxa in each category were summed for use in statistical analysis.

Results

Data from all 14 subcores were used to calculate Kendall rank correlation coefficients (Tate and Clelland, 1957) be-

tween the 6 polychaete functional groups and the 124 harpacticoid species which occurred at more than one station. Of the 744 possible correlations, 54 were significant ($\alpha = 0.05$, two-tailed test). This number of significant correlations was more than expected by chance alone (chi square 1 degree of freedom, $DF = 7.9864$, $P < 0.005$). These correlations were distributed among 41 species and all polychaete functional groups. Those harpacticoid species which were significantly correlated with the same functional group varied in the signs of their correlations (Table 2).

To estimate the average strength of harpacticoid species-polychaete functional group correlations, the data set was partitioned into two equal subsets in a stratified random manner. I used significant correlations ($\alpha = 0.10$, two-tailed test) in Subset 1 to predict significant correlations ($\alpha = 0.10$, one-tailed test, direction predicted) in Subset 2. Of the 31 correlations predicted, 4 were significant, approximating what one would expect by chance alone.

Using the same two data subsets, I tested for a tendency for the sign of the correlation between a particular species and a particular polychaete functional group to be the same in both subsets on the average. None of the polychaete functional groups exceeded chance level in the number of matching signs observed between data subsets. The total chi square was also nonsignificant.

The tabulation of matching and mismatching signs for sessile surface-deposit feeders showed that the number of times a negative correlation in the first subset was also negative in the second subset conspicuously exceeded expectation. This observation suggested an *a posteriori* search for negative interactions between polychaete functional groups and harpacticoid species' abundances. Using the data from all 14 subcores, I found 55 significant negative correlations ($\alpha = 0.05$, one-tailed test), significantly more than expected by chance alone (chi square 1 $DF = 8.9655$, $P < 0.005$) and more than that found when both positive and negative correlations were considered at the same overall probability level. However, when the data were partitioned into two subsets, no better than chance level was found when significant ($\alpha = 0.10$, one-tailed test) negative correlations in Subset 1 were used to predict significant negative correlations in Subset 2 (Table 3).

The null hypothesis that the number of negative-negative matches between

Table 3. Contingency table showing that predicted significance of a correlation is independent of its observed significance

Predicted	Observed	
	Significant	Nonsignificant
Significant	2	27
Nonsignificant	44	461

Table 4. Chi square values resulting from comparing number of negative-negative matches of signs of correlation coefficients between harpacticoid species and polychaete functional groups to the 1:4 proportion expected if there were no association between species and polychaete functional groups

Polychaete functional group	Chi square value	Degrees of freedom	Probability
Motile subsurface deposit feeders	0.2541	1	>0.05
Motile surface-deposit feeders	0.3704	1	>0.05
Carnivores	0.8376	1	>0.05
Discretely motile subsurface-deposit feeders	0.1538	1	>0.05
Discretely motile surface-deposit feeders	0.0042	1	>0.05
Sessile surface-deposit feeders	7.0928	1	<0.01
Total	8.7129	6	>0.05

subsets is no greater than would result by chance was tested (Table 4). There is no evidence that negative correlations are maintained on the average over all classes. However, sessile surface-deposit feeders have significantly more negative-negative matches than expected by chance ($P < 0.01$, a *posteriori* test).

Discussion and Conclusions

When 14 samples were used to calculate correlation coefficients between abundances of harpacticoid species and polychaete functional group abundances, the significant covariance indicated an impact of polychaete functional groups on harpacticoid species on the average. When the statistical power of the test was reduced by using only 7 samples, the effect could not be detected, suggesting that individual species-polychaete functional group interactions are weak on the average. However, the size of the sampler was large (100 cm²) relative to the size of the animals involved and may have included other sources of variance which obscured the effect.

Harpacticoid species were negatively correlated with sessile surface-deposit feeders more often than expected by chance. If not a statistical artifact, this result suggests that a portion of the harpacticoid species tends to avoid areas where sessile surface-deposit feeders are abundant, perhaps because of an increase in predation rate.

This apparent avoidance of sessile surface-deposit feeders by harpacticoid

species appears to contrast with previous results (Thistle, in press). The mud ball-making polychaete *Tharyx luticastellus* constitutes 31% of the sessile surface-deposit feeding individuals. Harpacticoid species are positively correlated with the mud balls produced by this species (Thistle, in press). Following Thistle (in press) and using the volume of occupied and unoccupied *T. luticastellus* mud balls as the measure of abundance, there is a significant excess of positive over negative correlations (17 versus 4, $P < 0.01$, two-tailed test). Using the number of *T. luticastellus* individuals as the measure of abundance (as in this paper), there is a trend toward significant negative correlations outnumbering positive correlations (13 versus 7, $0.1 < P < 0.2$, two-tailed test). Most *T. luticastellus* mud balls are unoccupied (66%). The difference in the results of the two analyses may indicate that it is the unoccupied mud balls which account for the positive association previously reported, which was interpreted as evidence that harpacticoids partition their habitat in terms of their response to these mud balls (see also, Jumars, 1975a). This result supports Jumars' (1975a, 1976) argument. He suggests that the physical stability of the deep sea permits relatively delicate mud structures to persist. These structures may increase the exploitable complexity of the habitat and permit a larger number of similar species to coexist than possible in less stable environments.

The lack of apparent impact of the other functional groups may be, in part,

artificial. A sessile polychaete is a fixed feature of a harpacticoid's local environment and could cause distinctive changes in the immediate vicinity over the worm's life span. For these reasons, the impact of sessile surface-deposit feeders may be easier to detect than those of motile and discretely motile forms.

Alternative mechanisms could cause harpacticoid species to covary with polychaete functional groups. Some polychaetes prey upon harpacticoids in the San Diego Trough (P.A. Jumars, personal communication), and elsewhere (e.g. Rees, 1940; Perkins, 1958). Such predation could generate the negative correlations observed. Alternatively, certain harpacticoids and some polychaetes deposit-feed, bringing them at least potentially into competition (Coull, 1973). If harpacticoid species are in active competition with polychaete species, then harpacticoid abundances would be expected to covary negatively with polychaete species' abundances. Positive covariance could arise if in the presence of a particular polychaete species a harpacticoid either enjoyed a refuge from predation or a reduction in competition. Despite this ambiguity, some of the proposed models of deep-sea diversity maintenance can be examined for consistency with the results.

In Grassle and Sanders' (1973) model, disturbance and predation cause small-scale spatial mosaics of out-of-phase successional states. The present data suggest that sessile surface-deposit-feeding polychaetes cause changes in harpacticoid species composition on small scales. Although the mechanism underlying this interaction can not be specified, the pattern is consistent with Grassle and Sanders' concept of deep-sea communities as spatial mosaics.

In Dayton and Hessler's (1972) model, the diversity of small-sized organisms is maintained by predation and disturbance. In Menge and Sutherland's (1976) model, the diversity of low-trophic level species is maintained by predation. Harpacticoids are small, low trophic-level species. If the negative covariance of harpacticoid species and polychaete sessile surface-deposit feeders results from polychaete predation on harpacticoids, this aspect of each model is supported.

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