Aspects of the Natural History of the Harpacticoid Copepods of San Diego Trough

David Thistle

Department of Oceanography
Florida State University
Tallahassee, FL

Abstract   In samples from San Diego Trough (32° 35.75′ N, 117° 29.00′ W, 1,220-m depth), there were significantly more significant correlations between pairs of harpacticoid copepod species than expected by chance. Of these, significant positive correlations were significantly more frequent than negative correlations. By summing the per station abundances for pairs of significantly positively correlated species, it was shown that these correlations appear to be shared responses to five classes of biogenous structures. Also, species with morphological features suggesting that they were functionally similar were combined into groups, i.e., a sediment-covered group, an interstitial group, and a burrowing group. There was no evidence to suggest that the per-core abundance of these functional groups covaried with the per-core volume of classes of biogenous structures. However, the existence of large, apparently surface-dwelling species from three families that covered their dorsa with mud suggested that these species had adapted to a strong selective pressure. The mud covering seems capable of minimizing predation by particle-by-particle feeders, implying that selective predation is an important ecological force acting on deep-sea harpacticoids. Of the models proposed to explain diversity maintenance in the deep sea, those that

have invoked species' responses to habitat structures or selective predation received the strongest support.

The deep-sea, soft-bottom benthos has fascinated biological oceanographers at least since the *Challenger* Expedition. Modern workers have found the high diversity of the infauna of these communities particularly intriguing. A variety of models has been proposed to describe the structure of these diverse communities (Sanders, 1968, 1969; Slobodkin and Sanders, 1969; Dayton and Hessler, 1972; Grassle and Sanders, 1973; Jumars, 1975a,b, 1976; Menge and Sutherland, 1976; Rex, 1976; Osman and Whitlatch, 1978), but no consensus has yet emerged as to the organizing forces (Jumars and Gallagher, in press). Given the inaccessibility of the habitat, it is not surprising that relatively little natural history information has been collected. As a result, the models have been little constrained, and biological systems for experiments on community organization are difficult to specify.

I have reported on several aspects of the natural history of the harpacticoid copepod fauna from a set of high quality, deep-sea samples from San Diego Trough, i.e., species' dispersion patterns (Thistle, 1978), correlations between harpacticoid species and polychaete functional groups (Thistle, 1979a), and correlations between individual harpacticoid species and classes of biogenous structures (Thistle, 1979b). In this paper, I extend the results of my previous work on biogenous structure correlations, using a different analytical approach to show that harpacticoids covary with five rather than three structural classes. Also, I describe three functional groups of harpacticoids and argue that the presence of a sediment-covered group suggests that harpacticoids contend with selective predators.

Materials and Methods

Locality

A site that had the constancy of physical conditions typical of the deep sea was chosen at 1,200-m depth in San Diego Trough, a filled basin in the Southern California continental borderland (32° 35.75′ N, 117°

29.00' W) (Figure 1). The sediment was an oxidized green mud (3% sand, 53% silt, 44% clay; graphic mean grain size equaled 0.004 mm). Literature reports for San Diego Trough and measurements made during the sampling suggest that near-bottom water parameters vary little in time and space (temperature: 3.5 ± 0.3°C; salinity: 34.53 ± 0.02 °/oo; oxygen concentration: 0.71 ml/*l* (see Thistle, 1978, Table 1)). The site was located away from known turbidite channels (Moore, 1969); the granulometric analyses showed no evidence of recent disturbance by turbidity flows (R. R. Hessler, unpublished data).

Sampling

The samples were taken during Expedition Quagmire, which was organized by Dr. Robert R. Hessler. The expedition sampled using a transponder-navigated, remote underwater manipulator (Thiel and Hessler, 1974). This device took Ekman grab samples (20 × 20 cm containing four 10 × 10 cm subcores) *in situ* while being observed via closed-
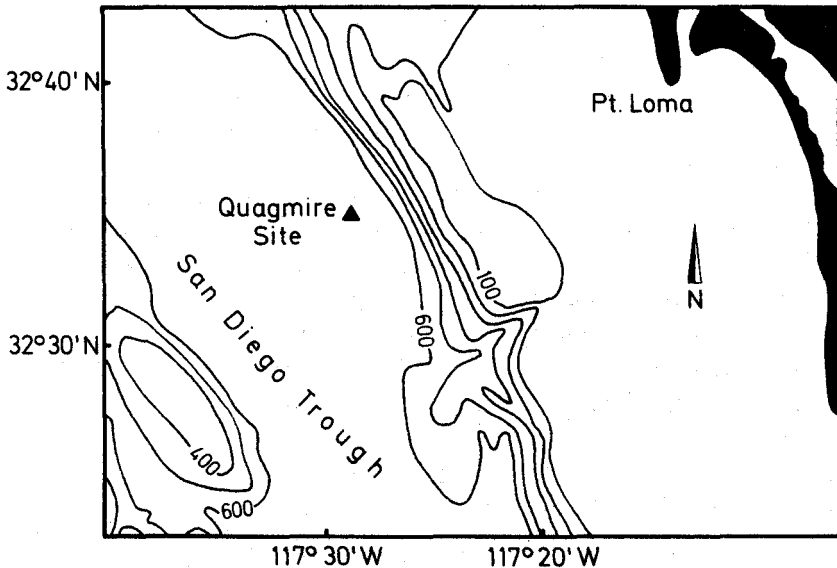

FIGURE 1. Chart of sampling area. The triangle marks the Quagmire site. Depth contours are in fathoms (1 fathom = 1.83 m). Modified from Coast and Geodetic Survey Map N. 5101. Previously published in Marine Biology 52 (4); used by permission.

Table 1

Volume (mm³) of biogenous structures by class from the 0-1-cm layer of 100 cm² subcores from the San Diego Trough.

Subcore				Structural Class			
	Tharyx luticastellus	Tharyx monilaris	Polychaete tubes	Orictoderma	Tube-shaped Foraminifera	Bush-like Foraminifera	Tanaid tubes
E10X	0.00	0.00	55.35	37.00	506.30	257.24	7.03
E11X	0.00	0.00	372.75	169.90	717.05	146.58	44.76
E12W	49394.46	38.97	414.03	152.77	1602.39	31.07	34.41
E12Z	668.52	32.78	193.46	21.58	624.47	1243.64	13.19
E14X	5782.00	0.00	267.12	16.34	1270.43	76.10	0.00
E14Y	6423.81	0.00	271.74	0.00	894.61	791.92	0.77
E45X	0.00	203.15	408.91	674.85	1655.34	354.10	2.11
E45Z	3279.22	426.02	543.78	126.24	2375.86	1247.59	31.80
E46Y	13391.23	0.00	770.46	220.16	3638.50	1019.85	23.22
E46Z	3420.61	48.97	156.76	190.17	1976.05	18.75	29.52
E47W	0.00	84.08	257.17	703.14	1684.00	357.07	0.00
E47Z	307.96	28.10	354.33	720.04	771.87	74.79	29.25
E48Y	763.63	113.84	210.48	117.77	1359.26	114.44	7.23
E48Z	10719.57	47.38	508.01	178.36	2629.75	160.13	7.10

circuit television. As a result, the effect of the bow wave that tends to bias ship-based samples (e.g., Jumars, 1976) was reduced or eliminated. The samples were taken at the locations shown in Figure 2. They consisted of pairs of subcores from six Ekman cores plus one subcore from each of two additional Ekman cores. On deck, the cores were kept at the *in situ* temperature until processed. From each subcore, the topwater and the 0-1-cm layer were removed and fixed in 10% formaldehyde. (On the Quagmire site, the upper 1 cm of sediment contains nearly all the harpacticoid individuals (G. D. Wilson, personal communication)). In the laboratory, each subcore sample was divided into two size classes on nested sieves of 1.0 and 0.062 mm mesh opening.

The samples contained biogenous mud structures. These structures were divided into seven classes: (1) mudballs formed by the cirratulid polychaete *Tharyx luticastellus* (Jumars, 1975c), (2) smaller mudballs made by *T. monilaris* (see Thistle, 1979b), (3) all other polychaete tubes, (4) tests of the agglutinating foraminiferan genus *Orictoderma* (see Thistle, 1979b), (5) tube-shaped agglutinating Foraminifera (see Thistle, 1979b), (6) bushlike agglutinating Foraminifera (see Thistle, 1979b), (7) tanaid crustacean tubes. All structures or fragments of structures that were retained on the 1.0-m sieve and that exceeded 0.5 mm in minimum dimension were considered. The maximum orthogonal length and width were measured, except that the second widest dimen-
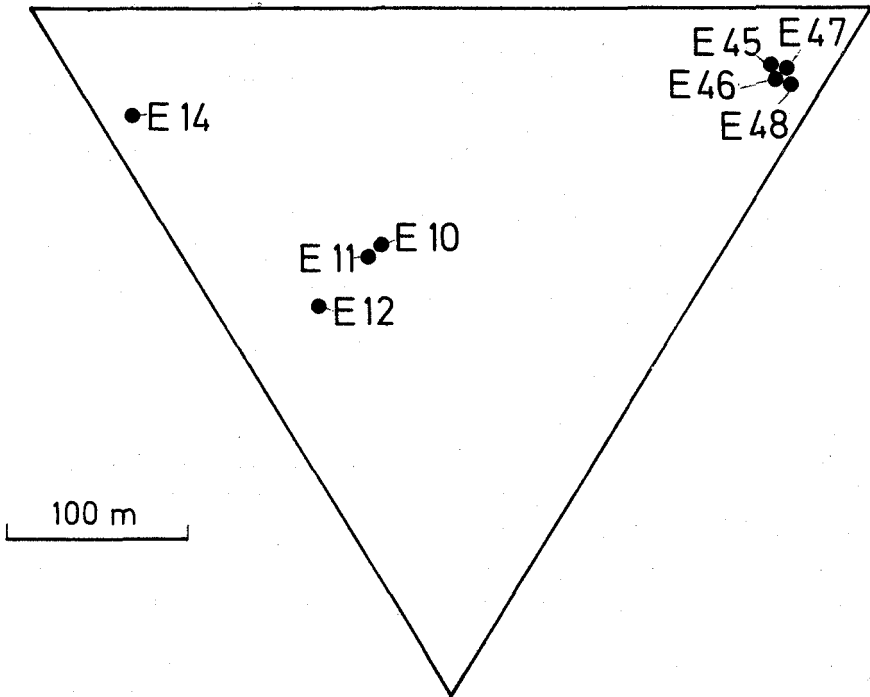
FIGURE 2. The Quagmire-site sampling triangle. The Ekman cores treated in this study are indicated by circles. Previously published in Marine Biology 52 (4); used by permission.

sion was used for branched forms. The shape of each class was approximated as follows: classes 2, 4: a sphere; classes 3, 5, 7: a cylinder; classes 1, 6: a prolate ellipsoid. Volumes for each class were calculated (Table 1).

After rose bengal staining, the harpacticoid copepods from each subcore were sorted from the two sieve fractions under a dissecting microscope. Adults were identified as to working species and counted. Most of the harpacticoids belonged to undescribed species. Preliminary identifications can be found in Thistle (1977); formal taxonomic treatment has begun (e.g., Thistle and Coull, 1979).

Harpacticoid species' length measurements were made as follows. Five adult females (or as many as were available) were selected at random from each species and measured for body length, excluding

rostrum and caudal furca. Measurements were made to ± 0.01 mm in lateral view (correcting for expanded arthrodial membranes), using a compound microscope and camera lucida.

The 95% significance level was used throughout. Nonparametric correlation coefficients (Kendall's tau, Tate and Clelland, 1957) were used. If a species occurred in only one subcore, it was not included in the correlation analysis, because little information about its covariance with other species can be gleaned. One hundred twenty-four species were used in the correlation analysis.

Results

I calculated the 7,626 correlation coefficients between all possible pairs of harpacticoid species, using the 14 samples. Eight hundred seventy-eight coefficients (11.5%) were significant; each species was significantly correlated with at least one other species. Because of the number of tests performed, the significance of a particular coefficient could not be determined, but there were more significant correlations than expected by chance alone ($p \ll 0.0005$). Of the 878 coefficients, 551 were positive. This number of significant positive correlations exceeded that expected by chance alone if the probability of getting a significant correlation of either sign were equal ($p \ll 0.0005$).

The excess of significantly positively correlated species could arise if pairs of species responded similarly to some third factor, in particular, classes of biogenous structures. Biogenous structures were conspicuous both in photographs of the sediment surface in this habitat and in the subcores themselves (personal observation). Because these structures extended into the overlying water, the volumes in Table 1 cannot be used to calculate the proportion of the sample volume each structure comprised. However, an inspection of the entries in Table 1 shows that each structural class varied by at least an order of magnitude among these standardly collected subcores.

To test for a relationship between positively correlated pairs of harpacticoid species and classes of biogenous structure, I first identified the species belonging to each of the 551 positively correlated pairs (all 124 species particpated in at least one pair). For the species in each pair, I summed their abundances in each subcore. I then calculated a correlation coefficient for this new variate with each of the seven classes of

biogenous structure. For each structural class, if there were no correlation between it and the variates, the expected number of significant correlations of either sign would be 5% of the total number calculated. I compared this expected value with the observed number of significant correlations and found that the number of significant correlations significantly exceeded expectation for five of the seven classes (Table 2), suggesting that the covariance of these pairs of harpacticoid species results, at least in part, from their association with these five classes of biogenous structures. However, this approach does not allow me to specify which harpacticoid pairs are associated with which structures.

The morphologies of many of the San Diego Trough harpacticoid species provided information about the manner in which they appeared to make a living. I formed three groups of species by combining species that appeared to be functionally similar. Fifteen species (Table 3) were conspicuous during sorting, because they had sediment firmly attached to and covering their dorsal surfaces. This sediment was consolidated, perhaps with mucus (see Hicks and Grahame, 1979), and was attached to vertically directed projections of the animal's body (Figure 3). In the

Table 2

The number of significant rank correlations between classes of biogenous structure and the variates formed by summing the per station abundances of those species pairs that were significantly positively correlated.

Structural Class	Number of Significant Correlations	p
Tharyx luticastellus	78	<0.0005
Tharyx monilaris	47	<0.0005
Polychaete tubes	63	<0.0005
Orictoderma	56	<0.0005
Tube-shaped Foraminifera	62	<0.0005
Bush-like Foraminifera	25	>0.05
Tanaid tubes	26	>0.05

Table 3

The composition of the three functional groups. Species number is the identifying number in Thistle (1977), Appendix B.

Species Number	Family	Genus
	Sediment-covered Group	
3	Ameiridae	Malacopsyllus
4	Ameiridae	Malacopsyllus
5	Ancorabolidae	Ceratonotus
18	Cletodidae	c.f. Eurycletodes
65	Cletodidae	Eurycletodes
66	Cletodidae	Eurycletodes
67	Cletodidae	Eurycletodes
68	Cletodidae	Eurycletodes
69	Cletodidae	Eurycletodes
76	Ameiridae	Malacopsyllus
104	Anchorabolidae	Echinopsyllus
106	Cletodidae	Eurycletodes
122	Ancorabolidae	c.f. Dorsiceratus
130	Ancorabolidae	Dorsiceratus
	Interstitial Group	
13	Cylindropsyllidae	Stenocaris
71	Paramesochridae	Leptopsyllus
74	Paramesochridae	Paramesochra
75	Paramesochridae	c.f. Scottopsyllus
79	Paramesochridae	Paramesochra
126	Cylindropsyllidae	Stenocaris
	Burrowing Group	
44	Cletodidae	Heteropsyllus
46	Canthocamptidae	Nannomesochra
47	Cletodidae	Hemimesochra
100	Cletodidae	Heteropsyllus
117	Cletodidae	Paranannopus
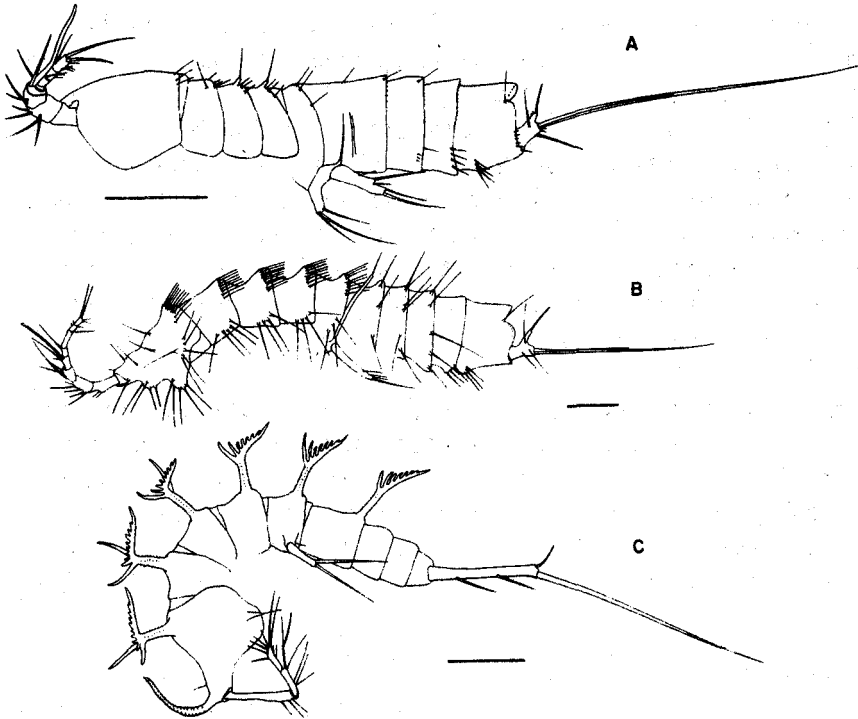
FIGURE 3. Lateral views of representatives of the sediment-covered group: A Cletodidae, B. Ameiridae, C. Ancorabolidae. Scale lines equal 0.1 mm.

Ancorabolidae species, these projections were the horns that characterize the family. In the Cletodidae and Ameiridae species, the sediment was bound to longitudinal rows of long setae on the posterior margins of most segments. The median body length of those "sediment-covered" species was significantly greater than the median body length of the remaining species (0.50 mm versus 0.37 mm; $p < < 0.001$ two-tailed, Mann-Whitney U test, Tate and Clelland, 1957). Only one sediment-covered species had a median size less than the nongroup median size, and five of the ten largest species were sediment-covered group members. From their sediment covering, their large size, and the condition of their pereopods, these species appeared to be surface dwellers (see also Coull, 1972, 1977).

The second functional group contained six vermiform species from families known to contain primarily interstitial species, i.e., Cylindrop-

syllidae and Paramesochridae (Noodt, 1971; Coull, 1977) (Table 3). These "interstitial"-group species have reduced pereopods. The third group contained five species that appeared to be adapted for burrowing (Table 3). The condition of the second antenna unified the group. This robust appendage bore setae that were enlarged and flattened. These setae tended to be arranged in circles around the limb in a manner reminiscent of the pushing foot of *Limulus*. The species' body lengths were smaller than the median, but not significantly so ($0.10 < p < 0.05$, Wilcoxon T test, Tate and Clelland, 1957). The species were similar in size (0.27–0.34 mm versus 0.21–0.87 mm median body length for all harpacticoids measured).

For each functional group, I summed the abundance of each member species in each subcore to give a group abundance. I calculated rank correlation coefficients between the per-core abundances of each harpacticoid group and the per-core volumes of the seven classes of biogenous structures (21 total correlations). The number of significant correlations did not exceed that expected by chance for any group.

Discussion

Natural history data on deep-sea species remain in short supply. In particular, relatively little is known about the patterns of co-occurrence among deep-sea species. In the Quagmire harpacticoid data, significantly more pairs of species are significantly correlated than expected by chance (11.5% versus 5%). Further, because of the significant excess of positive over negative correlations, it seems likely that many of those associations that are biologically real result from agreement between species in their abundance patterns. Jumars (1976) synthesizes arguments of Schoener (1974) and Hairston (1973) to suggest that the most likely result of competition among species in a food-poor environment should be spatial habitat partitioning. To the extent that the results of such competition could be perceived in samples at this scale, one would predict that negative pairwise-correlation coefficients should outnumber positive coefficients. Here, the reverse is true. This result does not fit predictions of competition-based models such as those of Sanders (1968, 1969) and Slobodkin and Sanders (1969).

There is nothing in the life styles of free-living harpacticoids to suggest that two species should positively covary because of an interac-

tion between them. Rather, it seems more likely that the significant excess of positive correlations among harpacticoid species results from shared responses to some third factor. Thistle (1979b), using a procedure where the correlation coefficients were based on seven samples, showed that harpacticoid species individually covary with per-core volumes of three classes of biogenous structures, *Tharyx luticastellus* mud balls, *T. monilaris* mud balls, and tube-shaped Foraminifera. In the analysis presented above, the power of the individual tests was increased because all 14 samples were used and because fewer ties occurred in the per-core abundances. Pairs of positively correlated harpacticoid species were shown to covary significantly with the per-core volume of five structure classes, *T. luticastellus, T. monilaris,* polychaete tubes, *Orictoderma* tests, and tube-shaped Foraminifera. This result suggests that biogenous environmental structures are important for harpacticoid copepods and strengthens the results of Thistle's (1979b) test of the grain-matching model (Jumars, 1975a, b), according to which organisms produce the most important sources of environmental heterogeneity (see also Bernstein et al., 1978). This result contradicts a prediction of the extreme-case formulation of the Dayton and Hessler (1972) model, where species of harpacticoid size and trophic position should not respond to sources of environmental heterogeneity on this scale. The species pairs differ among themselves as to which structural class with which to be correlated; they are partitioning their habitat. This pattern should arise under the Sanders model (1968, 1969), but alternative explanations could also be advanced. Further, this result provides a natural history context for a test of the grain-matching model; an experimentally produced increase in one of the structural classes should result in an increase in the abundance of those species that have been shown to covary with it.

There is no evidence that the harpacticoid functional groups covary with the measured habitat variables. However, the groups themselves provide some insight. The sediment-covered group contains species from three families. The members are larger on the average than the rest of the harpacticoid fauna and appear to be surface dwellers. The species have converged on the habit of anchoring sediment to their dorsal surfaces, suggesting that the covering is adaptive. In the lightless deep sea, it is unlikely that the sediment covering protects individuals from visual predators, nor is the covering likely to protect an individual from

nonselective deposit feeders. Rather, the sediment on an individual's dorsum implies a predator that selects its food particle by particle, e.g., a tentaculate selective deposit feeder, because the covering could fool such a predator into classifying the harpacticoid as an unsuitable particle by providing incorrect tactile or chemical cues or by causing the harpacticoid to be judged to be in a larger, less-preferred size class (see Self and Jumars, 1978). Therefore, the existence of sediment-covered harpacticoids appears to support the idea that selective predators are important in the deep sea, as suggested by Menge and Sutherland (1976) and Rex (1976, 1977).

Sediment-covered group species appear to live on the sediment surface, whereas the infaunal interstitial-group and burrowing-group members appear to live within it. This vertical separation weakens one of Dayton and Hessler's (1972) criticisms of Sanders (1968, 1969), because species have divided the habitat vertically (see also Jumars, 1978) and therefore food need not provide all of the niche separation. This arrangement could have arisen via competitive habitat partitioning, and its presence would lend support to competition-based models of deep-sea community structure. However, recent work in shallow-water soft bottoms has shown that infaunal species enjoy a refuge from predation (Virnstein, 1977, 1979; Peterson, 1979). The vertical separation could reflect two different solutions to predator avoidance and therefore support predation-based models. Similar ambiguities hinder the interpretation of most deep-sea results.

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