

YALE PEABODY MUSEUM

P.O. BOX 208118 | NEW HAVEN CT 06520-8118 USA | PEABODY.YALE. EDU

JOURNAL OF MARINE RESEARCH

The *Journal of Marine Research*, one of the oldest journals in American marine science, published important peer-reviewed original research on a broad array of topics in physical, biological, and chemical oceanography vital to the academic oceanographic community in the long and rich tradition of the Sears Foundation for Marine Research at Yale University.

An archive of all issues from 1937 to 2021 (Volume 1–79) are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at <https://elischolar.library.yale.edu/>.

Requests for permission to clear rights for use of this content should be directed to the authors, their estates, or other representatives. The *Journal of Marine Research* has no contact information beyond the affiliations listed in the published articles. We ask that you provide attribution to the *Journal of Marine Research*.

Yale University provides access to these materials for educational and research purposes only. Copyright or other proprietary rights to content contained in this document may be held by individuals or entities other than, or in addition to, Yale University. You are solely responsible for determining the ownership of the copyright, and for obtaining permission for your intended use. Yale University makes no warranty that your distribution, reproduction, or other use of these materials will not infringe the rights of third parties.



This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License.
<https://creativecommons.org/licenses/by-nc-sa/4.0/>



Nekton falls, low-intensity disturbance and community structure of infaunal benthos in the deep sea

by Craig R. Smith¹

ABSTRACT

A simulation of natural disturbance at the bathyal seafloor evoked rapid response from dominant infaunal species, for the first time providing experimental evidence that similar disturbances structure normal deep-sea communities. Parcels of dead fish (1–40 kg) were placed on the seafloor at a depth of 1310 m in the Santa Catalina Basin and monitored with *Alvin* and free-vehicle cameras for up to 8 wk. Dense aggregations of fish and ophiuroids were rapidly attracted to the baitfalls; in the process of consuming the bait, these megafaunal scavengers disrupted sediment surface structures and resuspended substantial amounts of sediment. The predominant macrofaunal effect was reduction of infaunal species diversity and community abundance around treatments. The most strongly depressed species was the community dominant *Tharyx monilaris*, a near-surface-dwelling cirratulid polychaete. Disturbance effects were low in intensity, however, with a large number of background species persisting within the perturbed area. Three macrofaunal species rapidly colonized the areas of disturbance/enrichment near baitfalls; two of these species, the paraonid polychaete *Levinsenia oculata* and the cirratulid polychaete *Chaetozone* sp. A, were dominant members of the surrounding community, while the third respondent, the cumacean (?) *Cumella* sp. A, was rare in background sediments. *L. oculata* and (?) *Cumella* apparently responded as post-larvae, suggesting that “adult” colonization of disturbed habitats may be important in deep-sea environments. The opportunistic response of two common species indicates that normal components of the Santa Catalina Basin fauna can rapidly exploit disequilibrium conditions, such as those resulting from a variety of low-intensity disturbance sources (e.g., conveyor-belt species, megafaunal “croppers”, skates, flatfish, carcasses of megafauna, kelp falls) commonly observed at the basin floor. Low-intensity disturbance may thus contribute materially to the structure of this, and other, deep-sea communities.

1. Introduction

At present there is circumstantial support for both equilibrium and nonequilibrium views of community organization in deep-sea benthos. Jumars and Eckman (1983), for example, described discordance in the local abundances of infaunal species; such a pattern could indicate a disturbance-induced successional mosaic (cf. Grassle and Sanders, 1973; Osman and Whitlatch, 1978; Jumars and Gallagher, 1982), or could result from more stable habitat partitioning (Sanders, 1968, 1969; Jumars, 1975,

1. School of Oceanography, WB-10, University of Washington, Seattle, Washington, 98195, U.S.A.

1976). Our knowledge of the deep-sea benthos, however, remains largely a snapshot view; we know discouragingly little of the kinematics of observed patterns (Jumars and Eckman, 1983). Pattern analysis thus cannot distinguish the roles of equilibrium processes from disturbance phenomena in structuring the diverse assemblages of the deep-sea floor. To improve our understanding of the deep-ocean ecosystem, we must obtain considerably more data on the dynamics of ecological processes, such as disturbance, succession and competitive exclusion.

Initial studies of community kinematics in the deep sea provided little indication that disturbance is important in the ecology of dominant infaunal species. Trays of azoic sediment placed on the seafloor either were colonized very slowly, or the early colonists belonged primarily to species found infrequently in the surrounding community (Grassle, 1977; Desbruyères *et al.*, 1980). These studies suggested that common deep-sea species are poorly adapted to respond to disturbance, while those opportunistic species which do respond are rare in the background assemblage and hence contribute little to community composition (although they do augment species richness). However, the recruitment, growth and survivorship of many infaunal species may be heavily biased in sediment trays, due to structural and hydrodynamic artifacts (Smith, 1985a). Colonization-tray results must thus be treated cautiously when interpreting the influence of natural disturbance on community structure in the deep sea.

I decided to manipulate nekton falls to study more natural processes of faunal disequilibrium on the ocean floor. Parcels of carrion, derived from pelagic and benthic megafauna, occur in a wide variety of habitats (Stockton and DeLaca, 1982; Smith 1985b). Such "large organic falls" might be expected to induce infaunal community disequilibrium in at least two ways. A 2-kg fish carcass, for example, is a significant parcel of energy and could thus cause substantial organic enrichment of the surrounding seafloor (Stockton and DeLaca, 1982). If bathyal populations are food limited (*cf.* Sanders and Hessler, 1969; Thiel, 1979) this could increase carrying capacities, resulting in changes in population densities or species structure. In any event, short-term enrichment appears to have a destabilizing influence, inducing changes in the composition of many communities, both modeled and real (*e.g.*, Patten, 1962; Williams, 1964; Hurd *et al.*, 1971; Rosenzweig, 1971; Gilpin, 1972; Grassle *et al.*, 1985; Gee *et al.*, 1985).

Alternatively, carcass falls could cause habitat modification and population reductions, resulting from local sediment disturbance. Bait drops in the deep sea attract large aggregations of voracious scavengers whose frenzied feeding raises clouds of sediment from the adjacent seafloor (Dayton and Hessler, 1972; Hessler *et al.*, 1978; Smith, 1985b). Mechanical disruption of the infaunal community is thus a likely consequence of nekton falls in the abyss.

I used the deep-diving submersible *Alvin* to experimentally study community dynamics of bathyal benthos around carrion falls. Parcels of dead fish were placed on

the seafloor, and data collected to assess spatial and temporal scales of (1) organic enrichment of surface sediments, (2) physical disruption of the sediment-water interface and (3) changes in population and community structure of macrobenthos in the vicinity of these artificial carrion parcels. My results suggest that common infaunal species are rapidly attracted to disturbed conditions near nekton falls, and that similar, low-intensity disturbances may play an important role in structuring infaunal communities in at least some bathyal ecosystems.

2. Methods

a. Study site. This study was conducted at a depth of 1310 m on the floor of the Santa Catalina Basin (SCB) (33°16'N, 118°38'W), one of 14 bathyal basins off southern California, U.S.A. The SCB environment and the fauna at this site are described in detail by Emery (1960), Smith and Hamilton (1983) and Smith (1983, 1985b).

Many features of macrofaunal community structure in SCB are typical of bathyal assemblages. Levels of macrofaunal abundance and biomass, and sediment-community respiration, are similar to those from other slope habitats (Smith and Hinga, 1983). As in most deep-sea settings (Jumars and Gallagher, 1982), macrofaunal abundance is dominated by polychaetes (85%), most of which are deposit feeders (Smith, 1983). In addition, macrofaunal species diversity, as evinced by the polychaetes, falls within the envelope of diversities measured for deep-sea communities (Jumars, 1976; Jumars and Gallagher, 1982; Smith, 1983), and well above that measured for a variety of shallow-water, soft-bottom assemblages [calculated from Sanders (1968) by Abele and Walters (1979)]. Consequently, many of the ecological processes characteristic of bathyal habitats are likely to operate in SCB, making it a suitable locality for the study of disequilibrium processes at the bathyal seafloor.

b. Field and laboratory procedures. Two time-lapse camera tripods were used to assess qualitatively the disruptive effects of scavenger aggregations on the sediment surface nearby nekton carcasses (Smith, 1985b). Three photographic time series (4 d, 6 d, and 57 d long) of carrion parcels resting in the sediment were obtained: each series consisting of color photographs, taken at intervals of 1-2 h, of a dead-fish parcel (1-4 kg wet weight) and the surrounding 0.9 m² of seafloor. The stations occupied, and methods used for photographic analysis, are given by Smith (1985b). Structures and organisms ≥ 3 mm in smallest dimension were resolvable in photographs.

The DSRV *Alvin* was used to set up and monitor a transect of experimental treatments (Fig. 1) on the SCB floor as described in Smith (1985b). During the first *Alvin* dive a 40-kg parcel of dead yellowtail (*Seriola dorsalis*) was secured by a 1-m long tether to 30-kg of steel ballast and dropped to the seafloor. The carcasses of this large baitfall landed on the sediment beside the ballast package, causing no discernable

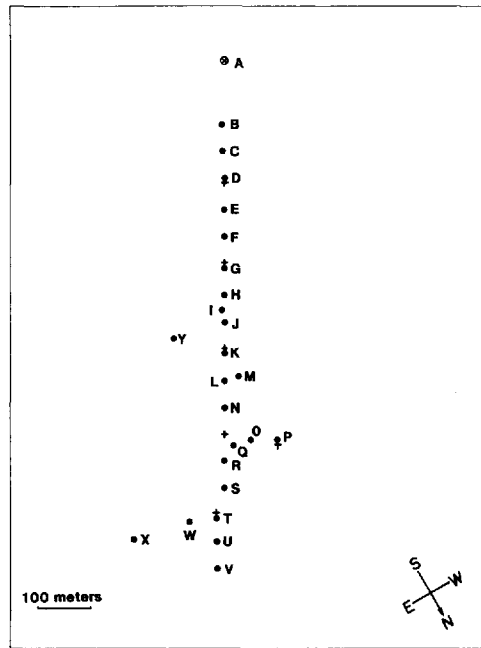


Figure 1. Map of experimental treatments set up by *Alvin* on the floor of the Santa Catalina Basin. A = large (40-kg) fish implantation and station-marker floats located at 33°16'N, 118°38'W; G, K, O, P, R, U and V = 2-kg fish-stake implantations; I = control treatment; Q, W and X = locations of background community cores; B, C, D, E, F, H, J, L, N, S and T = treatments from other experiments (kelp parcels, simulated sediment mound, wood blocks [Smith, 1983]); + = acoustic reflector.

disruption of sediment surface structures on the three sides of the carcasses facing away from the ballast. The position of this large baitfall remained unchanged throughout the 6 wk of the experiment.

The remaining treatments were implanted by *Alvin* along a line normal to near-bottom current observed during the first dive. Treatments were at least 50 m apart (Fig. 1) to prevent interactions. Seven treatments consisted of 2-kg parcels (4 individuals) of mackerel (*Scomber japonicus*) attached to weighted (5-kg) steel stakes, which were pushed slowly into the seafloor until mackerel carcasses rested on the sediment; emplacement caused no detectable disturbance of sediment within 2 m of treatments. Three of these 2-kg treatments, subsequently called small baitfalls, were monitored intensively (see below); their dates of emplacement are given in Table 1. In addition, a control treatment was set up to simulate the disturbance and hydrodynamic effects associated with emplacement and monitoring of experimental treatments. A PVC marker, similar in its size to fish stakes, was pushed into the sediment and an Ekman core sample (described below) taken about 20 cm away. This treatment was then monitored in a manner similar to experimental treatments.

Alvin returned at intervals of 1 d, 2 d, 2 wk, 3 wk and 6 wk after emplacement to collect visual observations, porthole and survey photographs, and sediment core samples in the vicinity of selected treatments (Table 1). Core samples were of two types: 20 × 20 cm Ekman cores (each vertically subdivided *in situ* into four 10 × 10 cm subcores) used to assess macrofauna, and 35-cm² circular *Alvin* cores for sediment CHN analysis. Samples bracketed the spatial scales (Table 1) of processes evident to the naked eye (sediment-surface disruption, scavenger aggregations, etc.). To standardize hydrodynamic artifacts, experimental cores were collected along a constant compass bearing from treatments (~30°), wherever possible. All cores were collected at a constant distance (~2 m) from *Alvin* and its tracks to standardize any biases introduced by the submersible.

Only one large fish parcel was placed on the seafloor, and core samples were taken near this single treatment after 3 wk and 6 wk (Table 1). I collected 6-wk cores at least 50 cm from the sites of cores obtained 3 wk earlier to minimize artifacts resulting from earlier disruptive sampling. For small baitfalls, a separate replicate treatment was sampled at each time interval.

Three Ekman cores from the background community were taken at random distances on randomly selected headings from the end of the experimental transect, with the condition that sample locations be at least 50 m from the nearest fish-implantation treatment. Because of limited dive time, the fourth Ekman core and the two *Alvin* cores collected as background samples were taken at random distances along random headings from haphazard points on the experimental transect.

Upon recovery, the overlying water and top 1-cm layer of sediment from Ekman cores were fixed together in a buffered 10%-formalin solution. This material was then washed carefully on a 420- μ m sieve and transferred to 80% ethanol for storage. The sediment layer occurring at a depth of 1 to 10 cm was washed immediately on a 420- μ m sieve, then fixed and stored as above. In the laboratory, samples were stained with Rose Bengal and sorted using a dissecting microscope. All metazoa, except copepods and nematodes (poorly retained on a 420- μ m sieve), were counted and identified to lowest attainable taxonomic level.

In some cases, about 1 ml of surface sediment was removed from Ekman subcores prior to fixation (Table 1). Dr. Jody Deming made direct counts of bacteria (per gram dry weight of sediment) in these subsamples using the epifluorescence microscopy procedures of Hobbie *et al.* (1977), and Deming and Colwell (1982).

Alvin cores used for CHN analyses of surface sediments were frozen at -30°C immediately following recovery. Prior to analyses, samples were thawed and allowed to sit upright for 3-4 h to ensure particle settling; topwater was then siphoned off. Core samples were subsequently refrozen and several cm³ of sediment cut from the top 1-cm layer; this was acidified to pH 3.5 and dried at 70°C to remove carbonate carbon (Smith *et al.*, 1983). After drying, samples were homogenized, and three replicate subsamples from each processed in a Perkin-Elmer model #204C Elemental Analyzer for percent organic carbon, hydrogen and nitrogen.

Table 1. Samples collected around experimental treatment for this study.

Treatment type	Date of emplacement	Time, after emplacement, of sampling	<i>Alvin</i> dive no.	Core type	Distance from treatment	No. of cores	No. of sub-cores	Comments			
Large baitfall	2/20/82	3 wk	1205	Ekman	adjacent (0.4 m)	2	6	One core subsampled for bacterial counts			
					1.4 m	1	4	Subsampled for bacterial counts			
					2.4 m	1	4	Subsampled for bacterial counts			
					<i>Alvin</i> adjacent (0.2 m)	1	—				
					1.0 m	1	—				
		6 wk	1210	Ekman	adjacent (0.2 m)	1	4				
					1.2 m	1	4				
					2.3 m	1	4				
					<i>Alvin</i> adjacent (0.1 m)	1	—				
					1.1 m	1	—				
Small baitfalls	4/3/82	2 d	1210	Ekman	adjacent (0.2 m)	1	4				
					2/20/82	3 wk	1206	Ekman	adjacent (0.2 m)	2	8
	0.9 m	1	4	Subsampled for bacterial counts							
	1.9 m	1	4	Subsampled for bacterial counts							
	<i>Alvin</i> adjacent (0.2 m)	1	—								
	0.6 m	1	—								
	1.7 m	1	—								
	2/20/82	6 wk	1208	Ekman	adjacent (0.1 m)				2	7	
	1.1 m				1				4		
	2.0 m				1	4					
<i>Alvin</i> adjacent (0.1 m)	1				—						
Control	2/20/82	2 wk	1199	Ekman	adjacent (0.3 m)	1	3				
					0.7 m	1	4				
Background	2/21/82	—	1189	Ekman	—	3	11				
	3/6/82	—	1199	Ekman	—	1	4				
	4/4/82	—	1209	<i>Alvin</i>	—	1	—				
	4/5/82	—	1210	<i>Alvin</i>	—	1	—				

c. *Statistical methods.* Because *Alvin* time is extremely limited, it was possible to deploy only one replicate treatment for each treatment-time combination. The inferential statistics discussed below thus test for "location", rather than "treatment", effects (*sensu* Hurlbert, 1984); i.e., observed significant differences between, for example, treatment and background samples, suggest that sampled localities are different, but these differences cannot be ascribed unequivocally to treatment effects. During subsequent discussions, however, it will be argued that by far the most parsimonious explanations of most faunal patterns around baitfalls invoke treatment effects.

During all analyses of population variations around treatments, Ekman subcores were used as replicate samples. Thus, within-location replicates consisted of all subcores taken at a particular distance and time interval from an initial treatment implantation (Table 1). Distance effects for a given time interval after treatment emplacement were analyzed using Krushal-Wallis (K-W) tests (nonparametric analogs of one-way ANOVA) and *a posteriori* multiple comparisons, at an experiment-wise alpha level of 0.05 (Conover, 1980). A nonparametric approach was employed because normality could not be assured from the obtained sample sizes. For these K-W analyses, the 15 subcores from the four background community Ekman cores were combined as replicates from a single "distance": this was done to obtain a general statement of background community conditions, to be contrasted with conditions at specific distances from treatments. Background (and treatment) *subcores* were not randomly and independently located, and thus the probability levels given for K-W tests (which assume sample independence) are approximate. Single-species abundances for bathyal macrofauna in the SCB area usually show no significant spatial autocorrelation on the 10-cm (i.e., subcore) scale, however, (Jumars, 1978; Jumars and Eckman, 1983), and thus errors resulting from use of these probability levels are likely to be small.

Community variation around treatments was partly assessed by measuring changes with distance in (1) species number per unit area and (2) total faunal density minus those species exhibiting significant single-species patterns ("community abundance"). Single-species patterns of abundance around treatments were analyzed for the five most common macrofaunal species in treatment samples (*Tharyx monilaris*, *Levinsenia oculata*, *Chaetozone* sp. A, *Tharyx* sp. A and (?) *Cumella* sp. A). The remaining species were generally too rare to show significant single-species patterns (i.e., statistical power was low) so they were combined into functional groups based on characteristics of motility, feeding type, life position within the sediment column, and taxonomic affinity. Grouping decisions for polychaetes were based on observations made while sorting species (e.g., occurrence in tubes, types of feeding structures, location in sediment column) and on information from Jumars and Fauchald (1977) and Fauchald and Jumars (1979). Other taxa were grouped on the basis of taxonomy and basic natural-history information. The functional groupings are given in Smith (1983).

Variations in numerical species richness around treatments were assessed using Hurlbert's rarefaction diversity procedure (Hurlbert, 1971; Smith and Grassle, 1977). Entire Ekman cores were used as "samples" in this analysis to provide reasonable numbers of individuals per sample. In conducting diversity analyses, the recommendations of Tipper (1979) were followed. The four background Ekman cores were used to calculate a composite diversity curve for the background community. Each "knot" on the composite curve consisted of the mean expected number of species, at the specified number of individuals, of the four background samples. One-tailed 95% confidence limits were calculated for each knot using the T distribution and the resulting confidence envelope plotted; one-tailed confidence limits were used because pilot experiments suggested that nekton-fall treatments cause infaunal disturbance, yielding *a priori* expectations of reduced diversity. Diversity curves for individual treatment samples (Ekman cores) were then compared to this envelope; if they fell on or below its lower margin, faunal diversity of treatment samples was considered to be significantly lower than background community diversity. All curves plotted were based on 30 or more calculated points.

A similarity analysis using the "normalized expected species shared" measure (NESS) (Grassle and Smith, 1976) was used to investigate variations in the species composition of samples (whole Ekman cores) collected around treatments. The NESS similarity measure is sensitive to both common and rare species and has been used effectively to document seasonal and disturbance-induced variations in the composition of marine benthic communities (Grassle and Smith, 1976; Grassle *et al.*, 1979; Sanders *et al.*, 1980). A similarity matrix was calculated for all Ekman cores from a given treatment type (small or large baitfalls) together with cores from the background community; this matrix was then used to cluster samples with an agglomerative technique (flexible sorting with $\beta = -0.25$ [Williams, 1971; Grassle and Smith, 1976]).

Sizes of *Levinsenia oculata*, *Chaetozone* sp. A and (?)*Cumella* sp. A were measured with an ocular micrometer to determine whether specific size classes were differentially abundant around treatments. *L. oculata* and *Chaetozone* usually were fragmented so either peristomial width (*L. oculata*), or first setiger width (*Chaetozone*) were measured as an index of body size (for *L. oculata*, peristomial width vs. wet weight yields a Spearman's rho = 0.974, $N = 28$; for *Chaetozone*, first-setiger width vs. total length yielded rho = 0.91, $N = 36$). Sizes of (?)*Cumella* sp. A were determined by measurement of carapace length (cf. Bishop, 1982). Size-frequency distributions were compared statistically using the Smirnov test (Conover, 1980).

Throughout the study, an alpha level of 0.05 was used as the criterion for statistical significance.

3. Results

a. Evidence of sediment enrichment. CHN analyses provided no convincing evidence of organically enriched surface sediment in the vicinity of baitfalls. In some cases,

surface sediments near treatments differed significantly in percent organic carbon from background samples; these deviations were all in a negative direction suggesting that sediment carbon was reduced rather than enhanced by experiments. In addition, near treatment values did not exceed the mean organic content of surface sediments (~5.8%) measured by Smith *et al.* (1983) at this station. C:N ratios also provided little indication of higher concentrations of protein-rich organics near baitfalls, with the only marked deviations indicating unusually high C:N ratios.

Epifluorescence counts of bacterial concentrations in surface sediment showed no strong indication of higher microbial standing crops immediately adjacent to baitfalls after 3 wk (J. Deming, personal communication). These analyses were relatively insensitive, however, due to numerous, difficult-to-control sources of error.

b. Evidence of sediment disturbance. Time-lapse photographs obtained from free-vehicle deployments indicated severe disruption of the sediment surface nearby fish parcels within hours after emplacement. Most fine-scale biogenic surface features, such as polychaete tubes, mudballs, and agglutinated tests of foraminifers, were destroyed within a radius of about 50 cm of baitfalls. Hagfish (*Eptatretus deani*) and sablefish (*Anoplopoma fimbria*) were primarily responsible for this sediment disturbance although aggregated brittle stars may also have contributed to surface disruption (Smith, 1985b).

Observations from *Alvin* corroborated the sediment disturbance effect of megafaunal feeding activity. Following hagfish dispersal, a shallow depression 1 to 2 cm deep could be seen around fish-parcel implantations. This zone of sediment-surface disruption extended to about 50 cm from small baitfalls, and to nearly 1 m from the large baitfall.

c. Macrofaunal patterns—community level. The dominant community-level patterns near baitfalls were reduced infaunal diversity and abundance within 1 m of treatments. Examining results from the large baitfall first, 3 wk after implantation species richness per unit area was significantly lower adjacent to the treatment than 1.4 and 2.4 m away (Fig. 2). Adjacent species richness was not significantly lower, after 3 wk, than that of background samples, but this was because rare species (mean abundance $\leq 0.2/100 \text{ cm}^2$ in background samples) were apparently attracted to the treatment (e.g., *Ophiophthalmus normani*, *Orchomene* sp. A and sp. B, (?) *Cumella* sp. A; see "Species Level" results) augmenting the species list. If these four exotic treatment respondents are excluded from the analysis, species richness adjacent to the large baitfall lies significantly below that of background samples (Fig. 2). After 6 wk, species richness near the large baitfall was still reduced, although not significantly so. (The exotic treatment respondents had apparently dispersed by this time and thus did not obscure background community patterns.)

Infaunal species diversity per number of individuals (Hurlbert diversity) followed a similar pattern of reduction around the large baitfall, with near-treatment curves

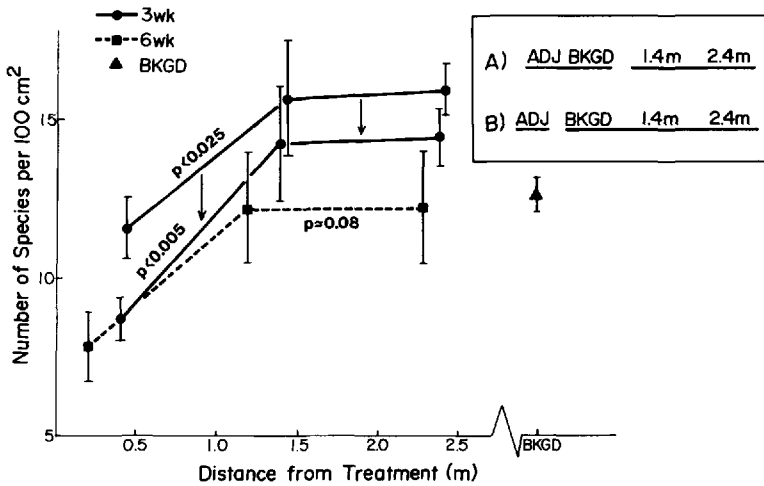


Figure 2. Areal species richness ($\bar{X} \pm 1 \text{ SE}$) around the large baitfall 3 wk and 6 wk after emplacement. The upper solid curve is *total* species richness after 3 wk, while the lower solid curve is species richness at 3 wk with exotic treatment respondents excluded. Probability levels were obtained from K-W tests addressing distance effects for treatment samples from a given time interval in combination with background community samples (BKGD). Inset: *A posteriori* multiple comparisons based on significant K-W tests. Groups of samples collected from distances not underscored by a common line are significantly different. Mean values increase to the right. ADJ = adjacent (i.e., nearest) to treatments; BKGD = background community. (A) 3-wk sampling interval, total species richness; (B) 3-wk sampling interval, exotic treatment respondents excluded.

falling near or below the 95% confidence limit for background community curves, after intervals of both 3 and 6 wk (Fig. 3). Lowered near-treatment diversity appeared to be a consequence of both reduced evenness (lower slopes of curves near the origin) and species richness (lower curve asymptotes). The faunal diversities of core samples taken further from the large baitfall (1.2 to 2.4 m away) fall within the range of background community curves at both sampling intervals.

Macrofaunal “community abundance” also declined nearby the large baitfall. Summing the densities of the 141 study-site species which did not show statistically significant single-species abundance patterns (i.e. excluding in this case *Chaetozone* sp. A, (?) *Cumella* sp. A., *Ophiophthalmus normani*, *Levinsenia oculata* and *Tharyx monilaris* see below), the general community was significantly reduced in abundance within 1 m of the large baitfall at sampling intervals of 3 and 6 wk (Fig. 4). Certain of the organisms excluded from this analysis exhibited a similar negative single-species response to the treatment (i.e., *Chaetozone* sp. A and *Tharyx monilaris*) broadening the generality of reduced infaunal abundance adjacent to the large baitfall.

The community-level patterns around small baitfalls were similar to those of the large baitfall. Species richness per unit area was significantly lower adjacent to

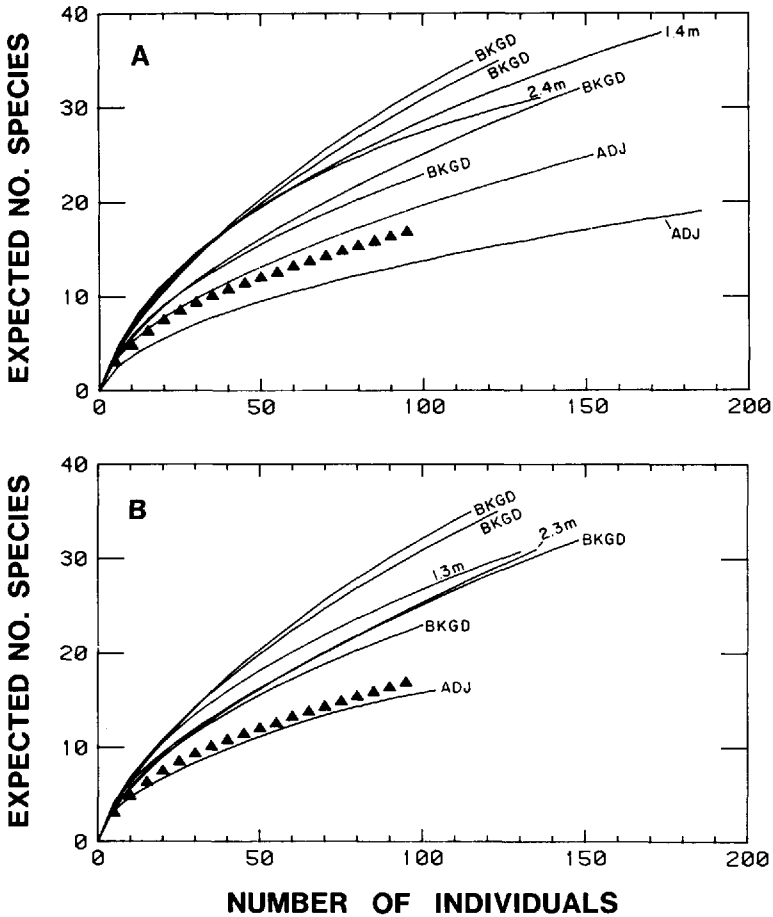


Figure 3. Numerical species richness (Hurlbert diversity) of Ekman cores collected at the indicated distances from the large baitfall. Triangles demark the lower, one-tailed 95% confidence limit for species richness of background community cores. Sample designations as in Figure 2. (A) Treatment cores collected 3 wk after experiment emplacement. (B) Treatment cores collected 6 wk after experiment emplacement.

treatments than (a) 0.8 to 2.0 m away and (b) in the background community after periods of 2 d and 3 wk (Fig. 5). After 6 wk, this pattern was still evident. In addition, Hurlbert diversity was also reduced adjacent to small baitfalls after 2 d and 3 wk (Fig. 6).

Macrofaunal "community abundance" also showed weak evidence of attenuation nearby small baitfalls (Fig. 7). Summing, as before, the densities of those 142 species not exhibiting significant single-species abundance patterns around small falls (here excluding *Chaetozone* sp. A, *O. normani*, *L. oculata* and *T. monilaris*, see below), there was a trend toward lower community abundance nearby treatments at all

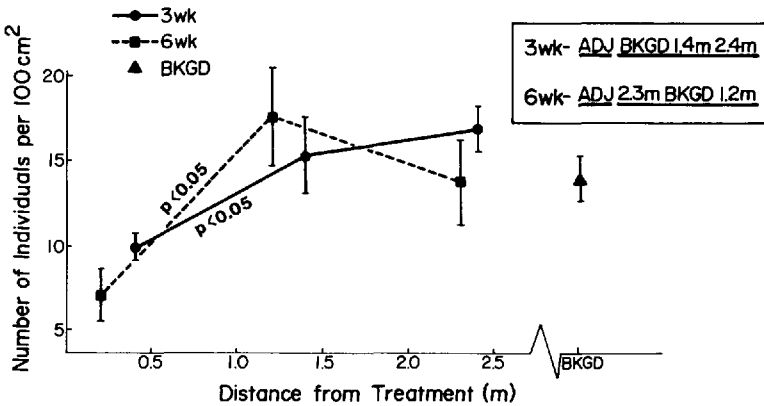


Figure 4. Macrofaunal “community abundance” ($\bar{X} \pm 1$ SE) around the large baitfall 3 wk and 6 wk after emplacement. Probabilities are based on K-W tests as in Figure 2. Inset: *A posteriori* multiple comparisons as in Figure 2.

sampling intervals (2 d, 3 wk, and 6 wk). Individually, these trends were not statistically significant, but combining the probability levels of the three K-W tests using Fisher’s procedure (Sokal and Rohlf, 1969) yields a *p* level of ~0.057. Thus, there is a suggestion of reduced community abundance near small baitfalls, although this tendency is not statistically significant at this level of replication.

The similarity analyses using NESS provide still further evidence that the infaunal

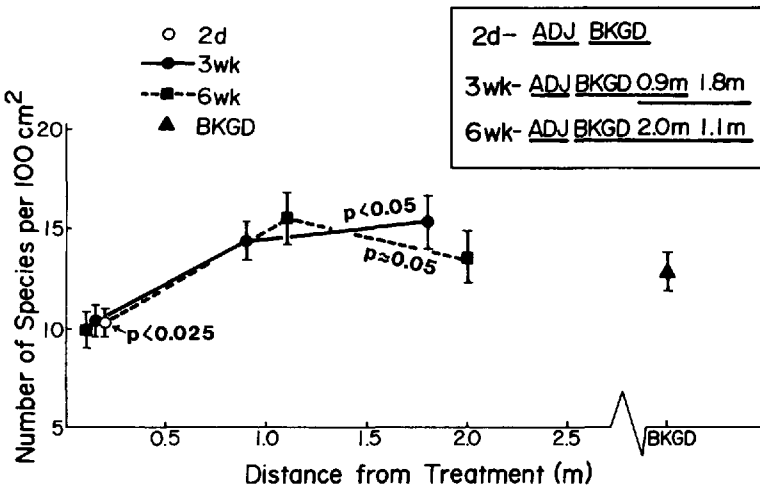


Figure 5. Areal species richness ($\bar{X} \pm 1$ SE) around small baitfalls 2 d, 3 wk and 6 wk after emplacement. Probabilities are based on K-W tests as in Figure 2. Inset: *A posteriori* multiple comparisons as in Figure 2.

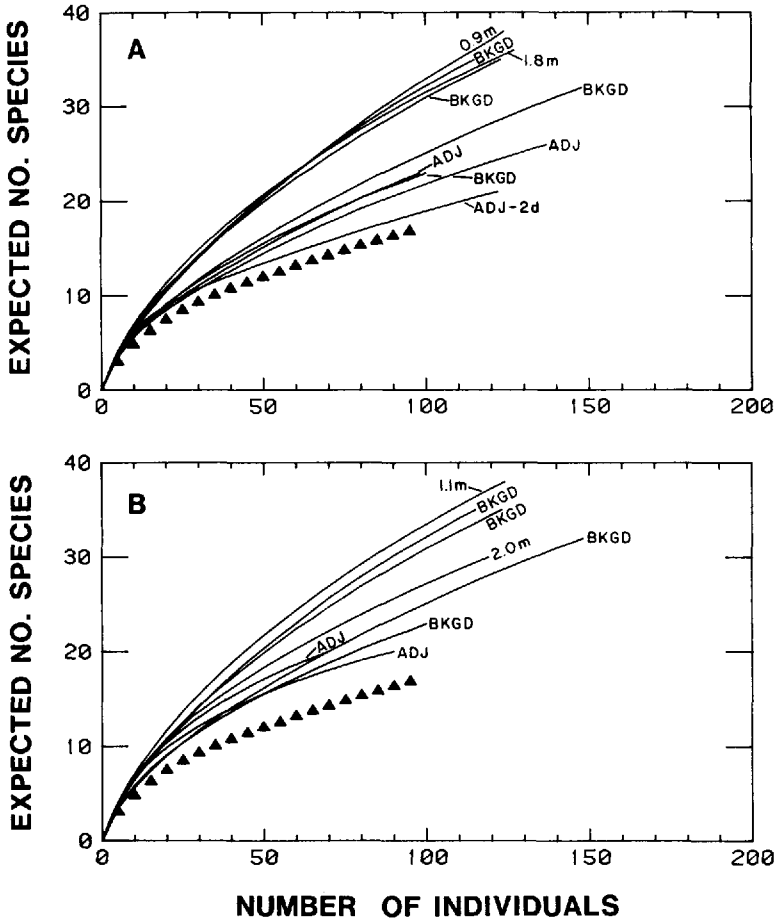


Figure 6. Numerical species richness (Hurlbert diversity) of Ekman cores collected at the indicated distances from small baitfalls, details as in Figure 3. (A) Treatment cores collected 2 d (single curve indicated) and 3 wk after experiment emplacement. Considered singly, each of the curves for the three “adjacent” samples is not significantly different from background diversity. Combining the probabilities of these curves (0.16, 0.13, and 0.09) using Fisher’s method (Sokal and Rohlf, 1969) suggests, however, that as a group, they fall significantly below background levels ($p \approx 0.05$). (B) Treatment cores collected 6 wk after experiment emplacement.

community within 1 m of baitfalls was anomalous. The NESS cluster for the large baitfall (Fig. 8) possesses two well-defined groups: one composed of all samples taken adjacent to the fish parcel, and the other containing the remaining treatment samples and samples from the background community. The NESS clustering of small-baitfall data exhibits a similar, although less marked, pattern (Fig. 8). Again, two clusters are formed, one composed exclusively of samples taken adjacent to small baitfall

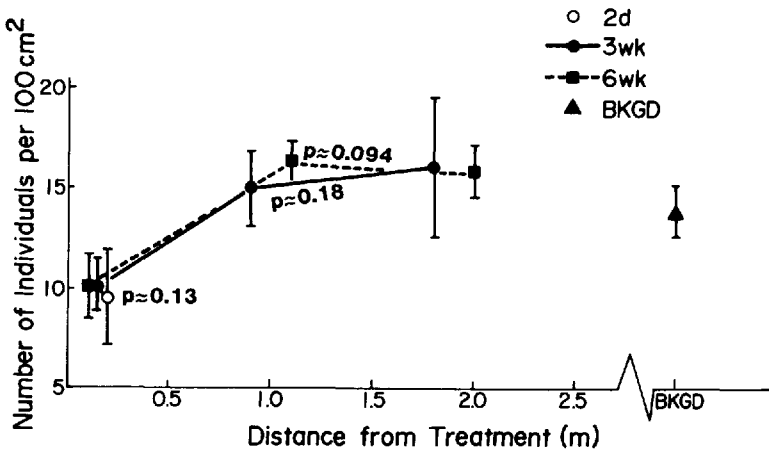


Figure 7. Macrofaunal "community abundance" ($\bar{X} \pm 1$ SE) around small baitfalls 2 d, 3 wk, and 6 wk after emplacement. Probabilities are based on K-W tests as in Figure 2. BKGD = background community samples.

treatments: however, some of the adjacent treatment samples (those taken after 3 wk) are clustered with treatment samples from greater distances, and with background community samples. The message seems to be that composition of the infaunal community within a meter of baitfalls typically was different (in terms of species identities and proportions) from that further away and in background samples, at time intervals ranging from 2 d to 6 wk.

It should be noted that while NESS similarity demonstrated that the faunal composition of near-treatment samples deviated from that of the background community, most of the species collected near treatments were not exotic. At least 64% of the species from subcores taken within a meter of treatments also occurred in background samples.

d. Macrofaunal patterns—single-species level. Two types of single-species patterns occurred around baitfalls: lower density adjacent to treatments, and elevated abundance within a meter or so of experiments. The cirratulid polychaete *Tharyx monilaris* Hartman, the dominant species in the background community (Table 2), showed the most marked decrease in abundance near treatments. Within 0.9 m of baitfalls, the density of *T. monilaris* was lower than that both in more distant treatment samples and in the background community at all sampling intervals (Fig. 9).

Chaetozone sp. A the third most abundant background species (Table 2) and also a cirratulid, followed a similar pattern of decreased abundance nearby the large baitfall (although not near small baitfalls) after 3 wk and 6 wk (Fig. 10). It should be noted however that while the abundances of both *Chaetozone* sp. A and *T. monilaris* were

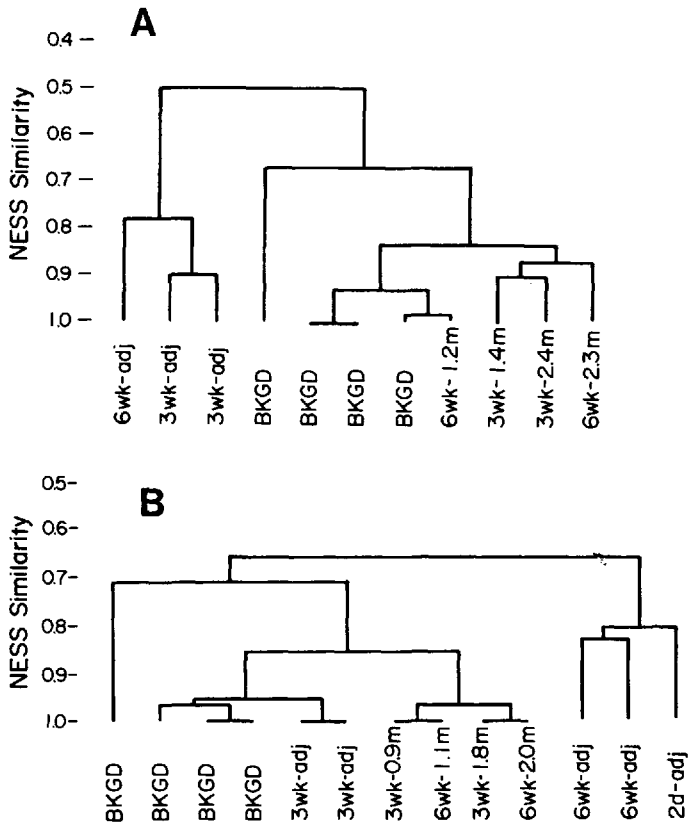


Figure 8. NESS clustering of Ekman cores from the background community (BKGD) with those collected around the large baitfall (A) and around small baitfalls (B) at the sampling intervals and distances indicated. ADJ = adjacent (i.e., nearest) to treatments.

Table 2. Dominant species in SCB background community samples. P = polychaete, B = bivalve, C = cumacean.

Abundance rank	Species	Major taxon	Percent of macrofauna
1	<i>Tharyx monilaris</i>	P	35
2	<i>Levinsenia oculata</i>	P	16
3	<i>Chaetozone</i> sp. A	P	7.1
4	<i>Tharyx</i> sp. A	P	6.7
5	Protobranch sp. A	B	2.4
6	<i>Myriochele gracilis</i>	P	2.0
7	<i>Maldane cristata</i>	P	1.8
8	<i>Lumbriclymene lineus</i>	P	1.4
8	<i>Cossura</i> sp. A	P	1.4
8	<i>Exogone</i> sp. A	P	1.4
21	(?) <i>Cumella</i> sp. A	C	0.6

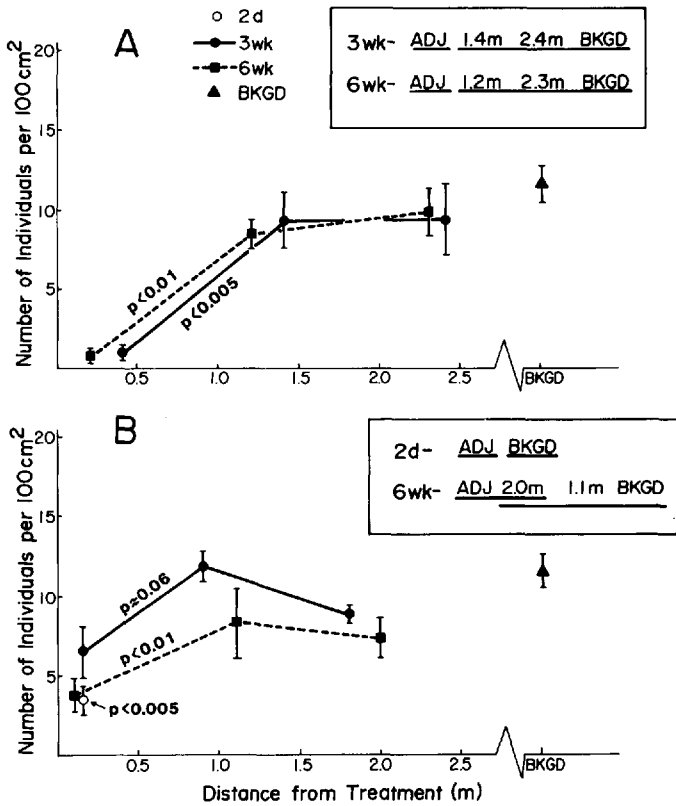


Figure 9. Density of *Tharyx monilaris* ($\bar{X} \pm 1$ SE) around baitfall treatments. Probabilities are based on K-W tests as in Figure 2. BKGD = background community samples. Insets: *A posteriori* multiple comparisons as in Figure 2. (A) Samples from the large baitfall at intervals of 3 wk and 6 wk. (B) Samples from the small baitfalls at intervals of 2 d, 3 wk and 6 wk.

substantially reduced, these species were still present at low levels nearby the treatments.

Several species were elevated in abundance in the vicinity of fish parcel implantations. The brittle star *Opiophthalmus normani* occurred at high densities in treatment samples after 2 d and 3 wk: the pronounced attraction of this megafaunal species to fish parcels is described in detail in Smith (1985b).

The cumacean (?) *Cumella* sp. A was also abundant around baitfalls. This undescribed species (R. Winn, personal communication) occurred rarely in the background community (Table 2), but reached very high densities nearby the large baitfall after 3 wk (Fig. 11). By 6 wk (?) *Cumella* sp. A densities had declined considerably near the large baitfall, but were still significantly above background levels. The high concentra-

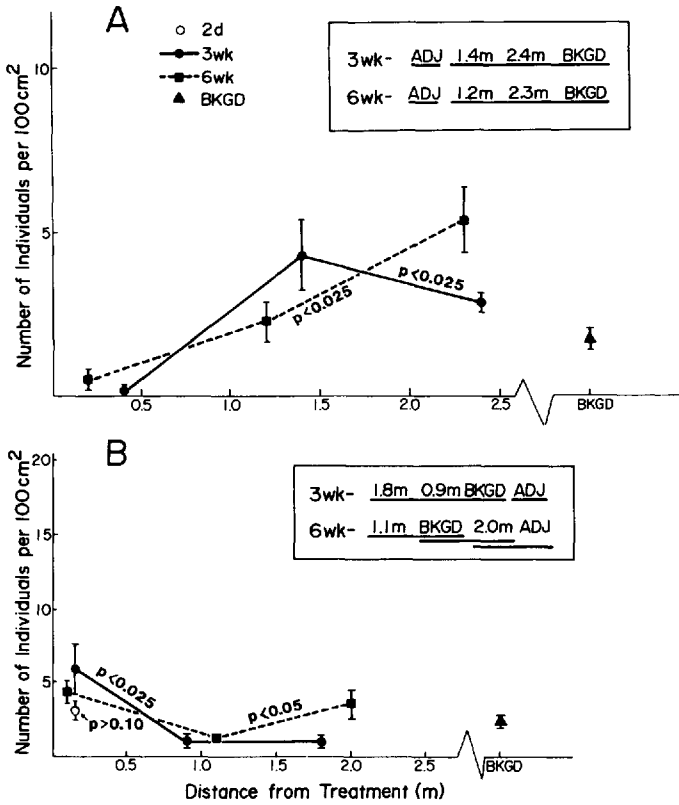


Figure 10. Density of *Chaetozone* sp. A ($\bar{X} \pm 1$ SE) around baitfall treatments. Probabilities are based on K-W tests as in Figure 2. BKGD = background community samples. Insets; *A posteriori* multiple comparisons as in Figure 2. (A) Samples from the large baitfall at intervals of 3 wk and 6 wk. (B) Samples from small baitfalls at intervals of 2 d, 3 wk and 6 wk.

tions of this cumacean comprised individuals from a broad range of size categories including large females with oostegites (although no brooders). In addition, (?)*Cumella* sp. A tended to be more abundant nearby the small baitfalls after 3 wk and 6 wk than in the background community (Fig. 11).

The paraonid polychaete *Levinsenia oculata* (Hartman) (called *Tauberia oculata* in earlier work [Smith, 1983, 1985a,b; Levin and Smith, 1984]) also varied in abundance around baitfalls, but in a more complicated pattern than the species discussed above. In terms of total density, this community dominant (Table 2) tended to be most abundant nearby the small baitfall after 3 wk and near the large baitfall after 6 wk (Figs. 12 and 13). These trends are in agreement with results from a pilot experiment, in which *L. oculata* showed significant enhancement in total abundance around a bait parcel

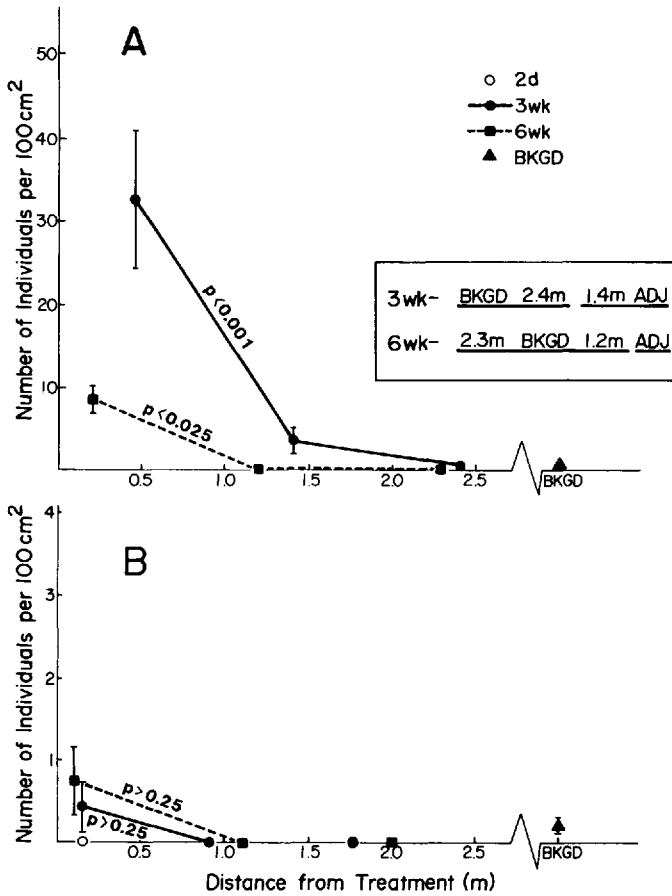


Figure 11. Density of (?)*Cumella* sp. A ($\bar{X} \pm 1$ SE) around baitfall treatments. Probabilities are based on K-W tests as in Figure 2. BKGD = background community samples. Inset: *A posteriori* multiple comparisons as in Figure 2. (A) Samples from the large baitfall at intervals of 3 wk and 6 wk. (B) Samples from small baitfalls at intervals of 2 d, 3 wk and 6 wk.

after 8 days (C. R. Smith, unpublished data). The vertical distributions of this species near treatments showed an additional, significant pattern; *L. oculata's* abundance in the top centimeter of sediment was much greater adjacent to (a) the small baitfalls after 2 d and 3 wk and (b) the large baitfalls after 6 wk, than in samples taken further from treatments or in the background community, where it was rare near the sediment surface. It should be noted that *L. oculata* showed virtually identical abundance patterns around small and large baitfall treatments, except that the large-baitfall pattern was displaced 3 wk later in time.

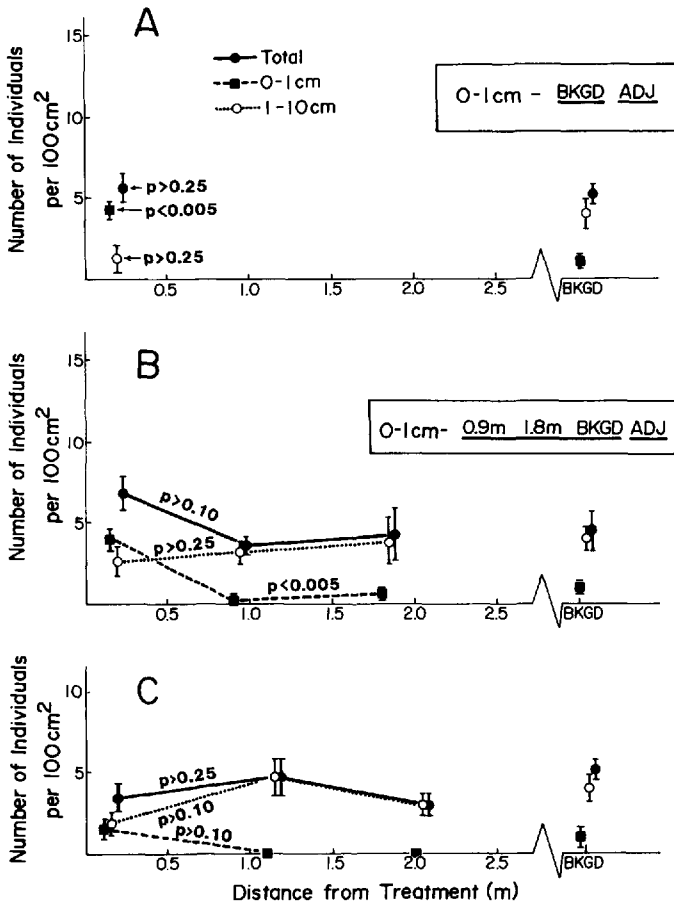


Figure 12. Density of *Levisenia oculata* ($\bar{X} \pm 1$ SE) around small baitfalls in the total, sampled sediment column (Total), and in the 0-1 cm and 1-10 cm layers. Probabilities are based on K-W tests as in Figure 2. BKGD = background community samples. Insets: A *a posteriori* multiple comparisons as in Figure 2. (B) Treatment samples collected 2 d after baitfall emplacement. (C) Treatment samples collected 6 wk after baitfall emplacement.

Smirnov tests of size-frequency distributions of *L. oculata* around treatments provided little indication that samples with enhanced surface-layer abundance had atypical size-frequency distributions; only one of 13 tests showed significance at the 0.05 level, a result likely attributable to alpha error (Smith, 1983). In addition, there was no significant evidence of an increased proportion of gravid females in enhanced samples (probability >0.07 in all cases using the percentage test [Sokal and Rohlf, 1969]). Thus, neither larval recruitment nor immigration of large, reproductive individuals was strongly implicated in near-surface enhancement.

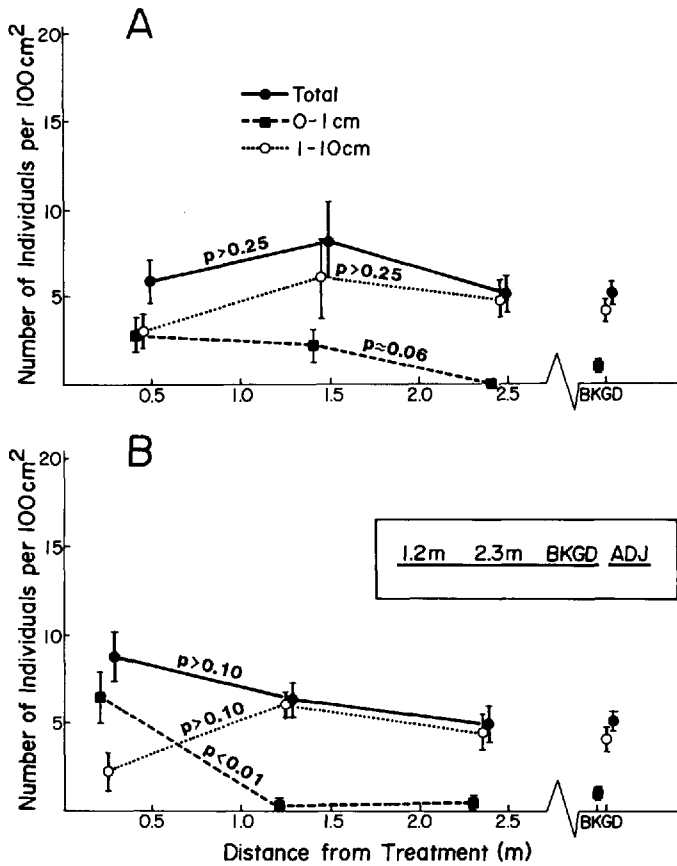


Figure 13. Density of *Levinsenia oculata* ($\bar{X} \pm 1$ SE) around the large baitfall in the total, sampled sediment column (Total), and in the 0–1 cm and 1–10 cm layers. Probabilities are based on K-W tests as in Figure 2. BKGD = background community samples. Inset: *A posteriori* multiple comparisons as in Figure 2. (A) Treatment samples collected 3 wk after baitfall emplacement. (B) Treatment samples collected 6 wk after baitfall emplacement.

There are at least three alternate explanations of *L. oculata*'s distribution around baitfall treatments. Enhanced abundance in the top centimeter of sediment near treatments may derive from downward movement of the sediment-water interface, resulting from the erosive effects of scavengers. Significant sediment resuspension occurred near fish parcels; this may have brought the normal level of *L. oculata* peak abundance to within 1 cm of the sediment surface, requiring no movement by the paraonid. Erosion probably explains the surface-layer enhancement of *Levinsenia* near the small baitfall after 2 d, as this pattern formed very rapidly with no indication of immigration (i.e., no change in total abundance). The near-surface increase at the large baitfall after 3 wk may have been induced similarly. This hypothesis however,

cannot explain *L. oculata*'s dispersion around fish parcels at later sampling times. Surface-layer enhancement required more than 3 wk to fully develop around the large baitfall, whereas sediment erosion occurred within a few days of fish-parcel emplacement (Smith, 1985b). In addition, both treatments exhibited weak increases in total density concomitant with surface-layer enhancement, suggesting that immigration contributed to these patterns.

The remaining explanations of *L. oculata*'s distribution around fish parcels invoke active selection by the worm of near-treatment conditions. The increase in density in the top centimeter of sediment may be due to vertical migration of *Levinsenia* from subsurface layers. Upward burrowing appears to have occurred at least around the large baitfall, as enhanced surface-layer densities coincided with decreased subsurface abundance (Figs. 12 and 13). However, this hypothesis too fails to explain the increase of *L. oculata* in the total sampled sediment column, unless this species occurs in substantial numbers at depths > 10 cm below the sediment-water interface (an unlikely possibility [Jumars, 1978]).

Finally, *L. oculata*'s patterns of abundance around treatments may derive from immigration into the top centimeter of sediment within a meter of experimental sites. This hypothesis is supported by increases in total abundance adjacent to the small baitfall after 3 wk and the large baitfall at 6 wk.

There is thus good evidence of a non-trivial response by *L. oculata* to baitfalls; on time scales of 3 to 6 wk, *Levinsenia* was attracted to surface sediments within a meter of treatments. Attraction apparently occurred by both vertical burrowing and immigration (e.g., recruitment or lateral movements) and new immigrants were not heavily concentrated in particular size classes, implying at least some post-larval attraction. The high desirability of near-treatment sites may have been short-lived (lasting a few weeks), as evinced by the lack of significant response patterns at the small baitfall after 6 wk (Fig. 13).

Chaetozone sp. A provides the final single-species pattern of enhanced abundance around fish parcels. After 3 wk, its density was highest adjacent to the small baitfall (Fig. 10), where it was significantly concentrated ($p < 0.01$ with one-tailed sign test [Conover, 1980]) in the top centimeter of sediment. In more distant treatment samples, this species exhibited no significant vertical differences in abundance, while it was more common per unit area in subsurface (1–10 cm) sediment layers in the background samples ($p < 0.01$). At the 6 wk sampling interval, *Chaetozone* was also significantly more abundant next to the small baitfall than in the background community, while its density 1–2 m away was quite variable. In addition, individuals from proximate samples were significantly smaller than those from more distant treatment samples, or from background samples (Table 3). This suggests larval recruitment or juvenile immigration contributed to near-treatment enhancement.

e. Macrofaunal patterns—functional-group level. Analysis of the abundance of functional groups around baitfalls yielded little evidence of nonrandom distributions;

Table 3. Results from Smirnov tests on size-frequency distributions of *Chaetozone* sp. A collected around the large baitfall after 6 wk. The null hypothesis tested is, "Chaetozone in samples adjacent to treatments (Adj) are similar in size to those from more distant samples, or background community samples (BKGD)." All maximum deviations occurred in the direction indicating adjacent samples had smaller individuals.

Samples compared	Sample sizes	2-tailed probability level
Adj vs 1.1 m	26,5	<0.10
Adj vs 2.0 m	26,15	<0.01
Adj vx BKGD	26,30	<0.05

only one out of 75 K-W tests was statistically significant. Lysianassid amphipods were more abundant ($p < 0.025$) adjacent to the small baitfall after 2 d than in background samples. This result is in agreement with the more detailed findings regarding these scavengers (Smith, 1985b).

f. Controls. Ekman cores were taken adjacent to the control treatment and 0.7 m away, two weeks after treatment emplacement. These samples showed no evidence of the macrofaunal trends which were statistically significant around baitfalls at community, single-species or functional-group levels.

4. Discussion

a. Physical effects of baitfalls: enrichment versus disturbance. Organic enrichment and disruption (by scavengers) of surface sediments are the most likely physical consequences of baitfall treatments in SCB. Current intensification and scour around experimental treatments are also conceivable, but the low current velocities ($\leq 7 \text{ cm s}^{-1}$ one meter above the sea floor, C. R. Smith, personal observations) and absence of erosional features around controls suggest that such effects are small.

CHN analysis and bacterial direct counts provided little evidence of local organic enrichment of sediment around the baitfalls, especially within 1 m of treatments. The most tenable explanation of the lack of sediment enrichment is that epifaunal scavengers, such as hagfish, amphipods and ophiuroids, so efficiently removed fish-fall organics that no detectable amounts reached the local sediment (Smith, 1985b). The infaunal community may thus experience no direct energetic benefit from the occurrence of carcasses on the seafloor. This interpretation must be applied cautiously, however, for at least two reasons: (1) Detritus feeders may respond to sources or levels of organic carbon that are beyond the sensitivities of these analyses. (2) It is conceivable that surface sediments near treatments were detectably enriched, but that this excess carbon was respired by microbiota or assimilated by macrofauna in less than 3 wk (i.e., prior to collection of samples). In this event, changes in infaunal populations could have occurred during the period of enrichment and persisted, or

caused second-order effects, through my sampling intervals. Changes could have included increases in macrofaunal biomass, which probably would not have been detected by small-scale CHN samples. Thus, while baitfalls appear not to have increased sediment organics, enrichment effects from these treatments cannot be completely discounted.

There is strong evidence of mechanical disturbance of surface sediments around baitfalls, resulting from the active feeding of large scavengers. Such disturbance is likely to influence infaunal species dwelling near the sediment surface, especially tube and mud-ball builders (Brenchley, 1981; Smith, 1981). Other species may also decrease in abundance following sediment disruption, due to loss of biogenic habitat structure (Jumars, 1976; Thistle, 1979), increased susceptibility to predation (Woodin, 1978, 1981; Van Blaricom, 1982), or reduced food availability resulting from loss of organic-rich surface sediments. Infaunal disturbance (i.e., population reductions) within 1 m of treatments thus appears to be a likely consequence of the activity of megafaunal scavengers around baitfalls on the SCB floor.

b. Disturbance of infauna around baitfalls. Infaunal patterns around baitfalls strongly suggested disturbance effects. Disturbance at the community level was indicated by (a) reduced areal species richness, (b) lower Hurlbert diversity, and (c) reduced macrofaunal density within a meter of treatments. In addition, the relative dissimilarity between most near-treatment samples and background community cores may have resulted from disproportionate reductions in some infaunal populations. These community disturbance effects were not evident at distances of >1 m from treatments at any of the time intervals sampled (2 d–6 wk).

The abundance of two dominant infaunal species, *T. monilaris* and *Chaetozone* sp. A also suggested disturbance around fish parcels. *Tharyx monilaris* is a surface deposit feeder (Fauchald and Jumars, 1979) which lives in mud balls several mm in diameter located near the sediment-water interface (Thistle, 1979; C. R. Smith, personal observations). Such structures disappear near carrion parcels placed on the SCB floor, as a consequence of the activity of megafaunal scavengers (Smith, 1985b). A decline in *T. monilaris* near baitfalls is thus not surprising, although it is unclear whether it results from mortality or emigration.

The general similarity of disturbance patterns occurring around small baitfalls and the large baitfall indicates a common cause of infaunal change, one which transcends differences between treatments (e.g., local infaunal patchiness, potentially disruptive replicate sampling of only the large baitfall). Moreover, lack of disturbance around the control suggests that these effects do not obtain from treatment emplacement, modification of the hydrodynamic regime near experiments, or movement of *Alvin* around treatment sites.

The most reasonable explanation of macrofaunal disturbance around treatments is that the physical disruption of surface sediments, resulting from scavenger activity,

leads to mortality and/or emigration of infaunal benthos. This is supported by agreement in scale between sediment disruption and infaunal change. In both cases disturbance occurred within several days of experiment emplacements and was restricted to within one meter of treatments. In addition, there was correspondence between the relative intensities of surface disruption and faunal disturbance; the large baitfall attracted larger aggregations of necrophages for longer periods than did small falls (Smith, 1985b), and the infaunal community near this large parcel showed more marked and consistent disturbance.

While infaunal disturbance around treatments was readily detectable, perturbational effects were of relatively low intensity, compared to the macrofauna-eliminating disturbances studied by most soft-substratum workers (Thistle, 1981; Zajac and Whitlatch, 1982 a, b; Gallagher *et al.*, 1983; Whitlatch and Zajac, 1985). Population densities of many species apparently were reduced, but individuals from a large number of background species persisted within the perturbed area, as evinced by retention of the bulk of species richness and the low proportion of exotic species. This low-intensity disturbance was broad-based, eliciting a variety of community-level effects (e.g. decreased species richness, diversity and faunal density), yet it was not completely density independent; the community dominant, *T. monilaris*, suffered the greatest reduction. One might expect other species dwelling in near-surface structures (e.g., tube-builders) to suffer differentially from megafaunal disturbance. Failure to detect such a trend in functional group analysis may have resulted from weak statistical tests due to low faunal densities (*sensu* Jumars and Eckman, 1983).

The effects of infaunal disturbance near treatments remained largely unmitigated throughout the study, a period of six weeks. Several species colonized the disturbed patches during this interval, but even after 6 wk (42 d) near-treatment microcommunities had not returned to background conditions of faunal density, species diversity and community composition. The macrofaunal effects of natural disturbances of similar scale and intensity have rarely been studied in shallow marine sediments (see Dayton and Oliver, 1980; and Thistle, 1981, for recent reviews), so only limited comparisons of shallow-water and deep-sea recovery rates are possible here. Van Blaricom (1982) analyzed recolonization of rat pits ~50 cm diameter in a subtidal, sandy habitat and observed macrofaunal recovery from near-complete defaunation in ≤ 42 d. Levin (1984) dug 0.4 m² pits in an intertidal mudflat to simulate defaunation resulting from ray disturbance; she observed community re-establishment in 40 to 75 d. It thus appears that infaunal community recovery following meter-scale mechanical disturbance may be slow in SCB relative to shallow habitats, although perhaps not as slow as suggested by colonization-tray experiments from bathyal localities (Smith, 1985a).

c. Infaunal attraction to baitfall treatments. The abundance of three species near fish parcels suggested attraction to treatments. Each of these species exhibited a different "response" pattern.

The cumacean (?)*Cumella* sp. A appeared to be very strongly and rapidly (within 3 weeks) attracted to at least some baitfall treatments. Rapid response of a cumacean to disequilibrium conditions in the deep sea is not surprising, as these crustaceans are common disturbance respondents in shallow marine habitats (e.g. Leppakoski, 1971; Rumohr, 1978; Van Blaricom, 1982; L. Levin, unpublished data from False Bay, Washington). In fact, (?)*Cumella*'s response parallels that of several shallow-water species which achieve high densities in small disturbed patches within days, disappearing after a few weeks (Van Blaricom, 1982; R. Winn, personal communication). For shallow-water species, it is unclear whether exploitation of perturbed sites is keyed to a reduction of superior competitors, to enhancement of food or other resources (Thistle, 1981; Van Blaricom, 1982), or to avoidance of infaunal predators (cf. Commito and Ambrose, 1985). This uncertainty also applies to (?)*Cumella*, which may have responded to (a) fish-fall enrichment, (b) the release of indigenous resources or (c) reduced predation.

Whether an enrichment or disturbance respondent, (?)*Cumella* appears capable of moving rapidly between sites of community disequilibrium. Such patches may be necessary for its persistence, enabling it to obtain resources unavailable in more advanced stages of succession. The collection of (?)*Cumella* as isolated individuals in background cores suggests that such exploitation of community disequilibrium can occur naturally on very small spatial scales in SCB (cf. Jumars, 1975, 1976).

There is also good evidence that the paraonid *Levinsenia oculata* was rapidly attracted to near-surface sediment around baitfalls, responding both by upward burrowing, and immigration. As with (?)*Cumella* sp. A, *L. oculata* may be drawn to conditions resulting either from organic enrichment or infaunal disturbance, although evidence favoring a disturbance response is perhaps more convincing. *Levinsenia* enhancement corresponded in spatial scale to the effects of both sediment and community disruption. In addition, *L. oculata*'s response pattern required more than 3 wk to develop around the large baitfall; by this time most of the enrichment effects from the carrion parcel likely had disappeared (Smith, 1985b). Even if one assumes organic enrichment near treatments, as a purported subsurface-deposit feeder (Jumars and Fauchald, 1977; Fauchald and Jumars, 1979) *L. oculata* would seem poorly adapted to exploit such a bonanza, because carrion particles likely remain at or very near the sediment-water interface.

At least one other study suggests *L. oculata* attraction to enrichment/disturbance conditions. Jumars (1974, 1976; Jumars and Eckman, 1983) found unusually high densities of *Paraonis gracilis oculata* (= *L. oculata*) in association with hexactinellid spicules. High concentrations of spicules may have indicated recent death of a large sponge (cf. Smith and Hamilton, 1983) leading to local sediment enrichment. Alternatively, hexactinellid spicules may have altered sedimentation patterns or inhibited predators (Jumars, 1976; and Jumars and Eckman, 1983) increasing food supplies or disturbing portions of the benthos.

Finally, the cirratulid *Chaetozone* sp. A showed evidence of attraction, as larvae or juveniles, to the vicinity of small baitfalls. Once again, it is difficult to determine whether attraction resulted from sediment enrichment or infaunal disturbance, although an enrichment response is perhaps more tenable. As a palpate surface-deposit feeder (Fauchald and Jumars, 1979), this species seems capable of exploiting enriched surface sediments near carrion parcels. In addition, the rapidity of *Chaetozone*'s response (strong attraction occurring after ≤ 3 wk) and its concentration in the sediment surface layer are consistent with the probable space and time scales of greatest food-resource enhancement.

d. Disequilibrium and infaunal community structure in the deep sea. These nekton-fall experiments suggest that three infaunal species, two of which are abundant in the surrounding community, are capable of rapid response to disequilibrium conditions on the SCB floor. Levin and Smith (1984) observed a similar (albeit slower) response by common background species. Both studies suggest that disturbance/enrichment events may be important in the ecology of at least some community dominants in SCB.

Under natural circumstances, (?) *Cumella*, *L. oculata* and *Chaetozone* may exploit infaunal disturbance from a variety of sources routinely observed on the SCB floor, including (a) sediment mounds and pits (Smith and Hamilton, 1983; Smith, 1985b; Smith *et al.*, 1986), (b) large skates and flatfish (Smith and Hamilton, 1983), (c) invertebrate megafaunal "croppers" (Dayton and Hessler, 1972; Smith and Hamilton, 1983), (d) carcasses of sponges and other megafauna (Jumars, 1976; Smith, 1985b); and (e) kelp falls (Smith, 1983). All of these are expected to produce low-intensity community disequilibrium through sediment-surface disruption and burial, cropping of infauna or organic enrichment. Megafaunal cropping may be especially important, as indicated by the high respiration rates of populations of omnivorous ophiuroids in SCB (high enough to respire the macrofaunal biomass within ~ 75 d [Smith, 1983]), but rarer perturbation agents may also be significant (cf. Huston, 1979) considering the slow growth and population recovery rates of some deep-sea infauna (Turekian *et al.*, 1975; Grassle, 1977; Desbruyères *et al.*, 1980; Levin and Smith, 1984). The common occurrence of two disequilibrium respondents in the SCB benthos is consistent with the hypothesis that community disturbance and disequilibrium are widespread on the basin floor (cf. the chronically disturbed shallow-water habitats discussed in Oliver (1980), Thistle (1981), Levin (1984) and Nichols and Thompson [1985]). *Levinsenia oculata* and *Chaetozone* sp. A are also common in the bathyal San Diego Trough (Jumars, 1974), suggesting that disequilibrium may play a role in structuring this remarkably diverse community (Jumars, 1976) as well.

The impact of these sources of disequilibrium should be patchy, as they appear to differentially affect circumscribed areas (0.01 to 1.0 m²) of the seafloor. If much of the community is held in disequilibrium by such perturbations, one might expect high levels of patchiness and interspecific discordance in dispersion patterns of infauna,

particularly on the spatial scales at which these perturbations occur. Jumars (1975, 1976, 1978) and Thistle (1978) looked for evidence of such community heterogeneity in SCB, and in the nearby San Diego Trough, and found relatively low levels of patchiness and species discordance on all horizontal scales studied (0.10 m to 100 km). They thus inferred, in the form of the "grain-matching" hypothesis (Jumars, 1975, 1976), that the processes dominating diversity maintenance in the bathyal deep sea occur on the scale of macrofaunal individuals (i.e., $<0.01 \text{ m}^2$).

The grain-matching hypothesis has failed a recent test, however (Thistle, 1983b), and there are at least two alternate reasons why weak evidence of patchiness does not negate the importance of meter-scale sources of disequilibrium (e.g., mounds, pits, epibenthic megafauna) in structuring the SCB and other bathyal communities. First, the low faunal densities and sampling intensities of most deep-sea studies result in weak statistical tests, making infaunal patchiness very difficult to detect (Jumars and Eckman, 1983). Secondly, these sources of meter-scale disequilibrium are relatively mild, presumably leading to low-intensity effects. For example, megafaunal disturbance (resulting either from sediment disruption or cropping) may be expected to reduce the densities of many populations, while leaving some individuals of most species alive within the area of perturbation. Recently disturbed patches should thus maintain faunal similarities with sites which are not freshly disturbed, and hence in later stages of succession. This effect is well illustrated by the small baitfall which was monitored 3 wk after emplacement; there was significant evidence of infaunal disturbance in the form of reductions in areal species richness (Fig. 5) and Hurlbert diversity (Fig. 6). Nonetheless, only one species showed a statistically detectable density decrease (i.e., "patchiness"), and these near-treatment samples were compositionally "similar" to background community cores (Fig. 8), even with the addition of colonizing opportunists.

Such low-intensity disturbance and the resultant community disequilibrium may help to explain the high local (within "patch") species diversity of the deep sea relative to shallow-water systems, in terms of equitability and species richness (Hessler and Jumars, 1974; Jumars, 1975, 1976; Jumars and Hessler, 1976; Thistle, 1978, 1983a). As Connell (1978) noted, low-intensity disturbance, which leaves some of the residents living within an influenced patch, leads to unusually high local diversity by combining species from both early and late successional stages at a single site. If a community were dynamically balanced by low-intensity disturbance at a nonequilibrium state (*sensu* Caswell, 1978; Huston, 1979), within-patch species diversity would be expected to be particularly high.

Disturbance (i.e., population reduction) in the SCB appears to be exclusively of the low-intensity type. Formation of sediment mounds and shallow pits, megafaunal disruption of sediment surface structures, cropping of infauna by ophiuroids and holothurians, etc., should all yield only partial mortality of infauna (Dayton and Hessler, 1972; Wilson, 1981; Brenchley, 1981; Smith, 1981; Turk and Risk, 1981;

Jumars and Gallagher, 1982; Smith *et al.*, 1986), and sources of total defaunation (e.g., anoxia, sediment slumps) appear to be rare at this site (based on personal observations of many individuals from S.I.O. during more than 40 submersible dives in SCB between 1979 and 1985). Predominance of low-intensity disturbance is probably characteristic of deep-sea systems in general (cf. the "biological disturbance" of Dayton and Hessler [1972]), even some of those subjected to large-scale physical perturbations (Thistle, 1983a, b; Thistle *et al.*, 1985). Thus, if deep-sea communities are maintained at a state of nonequilibrium by disturbance (Huston, 1979), one would expect them to exhibit high local species diversity.

A variety of shallow-water systems appear to be structured by disturbance, but these are typically high-intensity perturbations which result in near-total extinction of macrofaunal populations. For example, storm-waves (McCall, 1977; Rees *et al.*, 1977) anoxia (Leppakoski, 1971; Santos and Simon, 1980a, b; Nichols and Thompson, 1985), red tides (Dauer and Simon, 1976a, b), ray digging (Van Blaricom, 1982), sediment slumping (Van Blaricom, 1977), storm induced salinity fluctuations (Boesch *et al.*, 1976), anchor-ice formation (Oliver, 1980), and gray whale feeding (Oliver *et al.*, 1985) all cause extreme damage to infaunal communities. Variations in the intensity of disturbance may thus partially explain the differences between many shallow-water and deep-sea macrofaunal communities in terms of infaunal patchiness and local species diversity.

Low-intensity disturbance and Huston's (1979) dynamic disequilibrium model may partially explain the high local (within patch) diversity of deep-sea communities, but they are insufficient to explicate the elevated regional (i.e., integrating over many patches) diversity of the deep sea, such as that sampled by sleds and dredges (e.g., Sanders and Hessler, 1969; Rex, 1973; 1983). If deep-sea ecosystems are, in fact, mosaics of patches intermittently disturbed on ecologically relevant time scales (cf. the systems discussed in Caswell [1978], Sousa [1979, 1984] and Paine and Levin [1981]), large regional area and relatively small patch size may contribute to their elevated species richness (Osman and Whitlatch, 1978; Abele and Walters, 1979). The recent probabilistic model of Hanski (1983) suggests additional elements which may be of significance. Hanski demonstrated that if local time scales (i.e., growth rates of populations within patches) are slower than regional time scales (i.e., colonization of freshly disturbed patches) many competitors may coexist within a region. The low rates of growth and reproduction of deep-sea infauna (e.g., Allen and Sanders, 1973; Grassle and Sanders, 1973; Turekian *et al.*, 1975; Grassle, 1977; Allen, 1979) coupled with relatively high meter-scale adult mobility (Jumars and Fauchald, 1977; Levin and Smith, 1984) suggest that such a mismatch of time scales may indeed occur in the deep-ocean benthos, especially if disturbed patches are 0.1 to 10 m in size. My disturbance/enrichment studies with dead-fish parcels provide experimental confirmation of fast-regional versus slow-local time scales within the SCB community; two of three treatment respondents colonized experimental vicinities rapidly without exhibiting evidence of reproduction on the time scales studied. Thus, dispersal rates between

meter-scale patches may be high relative to general population growth rates in SCB and other deep-sea areas, promoting unusually high regional species richness.

Although discussed separately, regional and local species diversity are not independent. In a disturbance mosaic, high regional species richness may inflate within-patch diversity by providing a larger species pool of post-perturbational colonists (Osman and Whitlatch, 1978). Local processes may also affect regional diversity. For example, variations in the phasing of patch disturbances may affect the number and equitability of species within the community (Abugov, 1982). Knowledge of the interplay of such disequilibrium factors, and their contribution to benthic community structure, awaits further elucidation of a host of ecological processes. Data concerning (a) the rates and scales of natural infaunal disturbance, and (b) the patterns and mechanisms of species successions following such perturbations, are especially lacking. Manipulative studies of indigenous sources of infaunal disequilibrium, such as sediment mounds or megafaunal "croppers", could provide much of the requisite data, greatly improving our understanding of the deep-sea floor.

5. Conclusions

Attraction of megafaunal scavengers to nekton falls causes disruption of surface sediments within a meter of carrion parcels in SCB. This disruption yields significant disturbance of the infaunal community, decreasing species diversity and faunal densities near carrion parcels; surface-dwelling species are differentially affected. While many macrofaunal populations are reduced below carrying capacity, these disturbances are of relatively low intensity, with few species completely eliminated from the site. Re-establishment of background community conditions following such low-intensity disturbance requires more than 6 wk: this is slow relative to the recovery rate of several shallow-water, soft-bottom communities following more intense perturbations on similar spatial scales.

Three macrofaunal species, two of which are common, rapidly colonize areas of disturbance/enrichment near nekton falls. Rapid attraction to nekton-fall treatments implies that these animals are well adapted for exploiting patches of infaunal community disequilibrium occurring naturally on the SCB floor.

Sources of low-intensity, meter-scale disturbance are commonly observed in SCB and include mounds, pits and active megafauna. Considering the low rate of infaunal recovery following experimental perturbations, much of the SCB community may be in disequilibrium resulting from natural disturbances. The widespread occurrence of species adapted to exploit disequilibrium conditions is consistent with this hypothesis. Low-intensity disturbance may thus contribute materially to the structure of this, and other, deep-sea communities.

Acknowledgments. I am indebted to the many people who helped with this project. R. R. Hessler, K. L. Smith, A. A. Yyanos, C. Ingram, W. Smithey and L. McCann provided advice, logistical support and elbow grease during critical stages. The skill and cooperation of the

entire *Alvin-Lulu* group, particularly Chief Pilot R. Hollis, made the submersible portions of the project successful. The NESS program was generously provided by J. F. Grassle. R. R. Hessler, P. A. Jumars, J. F. Grassle, P. K. Dayton, K. L. Smith, G. D. Lange, J. Collie, and R. A. Wheatcroft read and improved various versions of the manuscript. The paper also benefitted greatly from numerous discussions with H. L. Sanders. The research, and manuscript preparation, were supported by ONR Contract N-00014-80-C-0440 to R. Hessler and C. R. Smith, several contracts to R. Hessler from Sandia National Laboratories, the University of California Ship Funds Committee, a Woods Hole Oceanographic Institution postdoctoral fellowship, and NSF Grant OCE 84-07478. This paper is derived from a chapter of a doctoral dissertation submitted to Scripps Institution of Oceanography, University of California at San Diego. Contribution no. 1635 from the School of Oceanography, University of Washington.

REFERENCES

- Abele, L. G. and K. Walters. 1979. Marine benthic diversity: a critique and alternative explanation. *J. Biogeogr.*, *6*, 115–126.
- Abugov, R. 1982. Species diversity and phasing of disturbance. *Ecology*, *63*, 289–293.
- Allen, J. A. 1979. The adaptations and radiation of deep-sea bivalves. *Sarsia*, *64*, 19–27.
- Allen, J. A. and H. L. Sanders. 1973. Studies on deep-sea Protobranchia (Bivalvia); the families Siliculidae and Lametilidae. *Bull. Mus. Comp. Zool.*, *145*, 263–310.
- Bishop, J. D. 1982. The growth, development and reproduction of a deep-sea cumacean (Crustacea: Peracarida). *Zool. J. Linnean Soc.*, *74*, 359–380.
- Boesch, D. F., R. J. Diaz and R. W. Virnstein. 1976. Effects of tropical storm Agnes on soft-bottom macrobenthic communities of the James and York Estuaries, and the lower Chesapeake Bay. *Ches. Sci.*, *17*, 246–259.
- Brenchley, G. A. 1981. Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. *J. Mar. Res.*, *39*, 767–790.
- Caswell H. 1978. Predator-mediated coexistence: a nonequilibrium model. *Am. Nat.*, *112*, 127–155.
- Commito J. A. and W. G. Ambrose. 1985. Predatory infauna and trophic complexity in soft-bottom communities, *in* Proceedings of the 19th European Marine Biological Symposium, P. E. Gibbs, ed., Cambridge University Press, Cambridge, 323–333.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science*, *199*, 1302–1310.
- Conover, W. J. 1980. Practical Nonparametric Statistics, Wiley, NY, 493 pp.
- Dauer, D. M. and J. L. Simon. 1976a. Repopulation of the polychaete fauna of an intertidal habitat following natural defaunation: species equilibrium. *Oecologia*, *22*, 99–117.
- 1976b. Habitat expansion among polychaetous annelids repopulating a defaunated marine habitat. *Mar. Biol.*, *37*, 169–177.
- Dayton, P. K. and R. R. Hessler, 1972. Role of biological disturbance in maintaining diversity in the deep sea. *Deep-Sea Res.*, *19*, 199–208.
- Dayton, P. K. and J. S. Oliver. 1980. An evaluation of experimental analyses of population and community patterns in benthic marine environments, *in* Marine Benthic Dynamics, K. Tenore and B. Coull, eds., South Carolina Press, Columbia, SC, 93–120.
- Deming, J. W. and R. R. Colwell. 1982. Barophilic bacteria associated with digestive tracts of abyssal holothurians. *Appl. Environ. Microbiol.*, *44*, 1222–1230.
- Desbruyères, D., J. Y. Bervas and A. Khripounoff. 1980. Un cas de colonisation rapide d'un sediment profond. *Oceanologica Acta*, *3*, 285–291.
- Emery, K. O. 1960. The Sea Off Southern California, Wiley, NY, 366 pp.
- Fauchald, K. and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Ann. Rev.*, *17*, 193–284.

- Gallagher, E. D., P. A. Jumars and D. D. Trueblood. 1983. Facilitation of soft-bottom benthic succession by tube builders. *Ecology*, *64*, 1200–1216.
- Gee, J. M., R. M. Warwick, M. Schaaning, J. A. Berge and W. G. Ambrose, Jr. 1985. Effects of organic enrichment on meiofaunal abundance and community structure in sublittoral soft sediments. *J. Exp. Mar. Biol. Ecol.*, *91*, 247–262.
- Gilpin, M. E. 1972. Enriched predator-prey systems: theoretical stability. *Science*, *177*, 902–904.
- Grassle, J. F. 1977. Slow recolonisation of deep-sea sediment. *Nature*, *265*, 618–619.
- Grassle, J. F., J. P. Grassle, L. S. Brown-Leger, R. F. Petrecca and N. J. Copley. 1985. Subtidal macrobenthos of Narragansett Bay: Field and mesocosm studies of the effect of eutrophication and organic input on benthic populations, *in* *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms*, J. S. Gray and M. E. Christiansen, eds., Wiley-Interscience, NY, 421–434.
- Grassle, J. F. and H. L. Sanders. 1973. Life histories and the role of disturbance. *Deep-Sea Res.*, *20*, 643–655.
- Grassle, J. F., H. L. Sanders and W. K. Smith. 1979. Faunal changes with depth in the deep-sea benthos. *Ambio Spec. Rpt. No. 6*, 47–50.
- Grassle, J. F. and W. Smith. 1976. A similarity measure sensitive to the contribution of rare species and its use in investigation of variation in marine benthic communities. *Oecologia*, *25*, 13–22.
- Hanski, I. 1983. Coexistence of competitors in a patchy environment. *Ecology*, *64*, 493–500.
- Hessler, R. R., C. L. Ingram, A. A. Yayanos and B. R. Burnett. 1978. Scavenging amphipods from the floor of the Philippine Trench. *Deep-Sea Res.*, *25*, 1029–1047.
- Hessler, R. R. and P. A. Jumars. 1974. Abyssal community analysis from replicate box cores in the central North Pacific. *Deep-Sea Res.*, *21*, 185–209.
- Hobbie, J. E., R. J. Daley and S. Jasper. 1977. Use of Nuclepore filters for counting bacteria by fluorescence microscopy. *Appl. Env. Microbiol.*, *33*, 1225–1228.
- Hurd L. E., M. V. Mellinger, L. L. Wolf and S. J. McNaughton. 1971. Stability and diversity at three trophic levels in terrestrial successional ecosystems. *Science*, *173*, 1134–1136.
- Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, *52*, 577–586.
- 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Mangr.*, *54*, 187–211.
- Huston, M. 1979. A general hypothesis of species diversity. *Am. Nat.*, *113*, 81–101.
- Jumars, P. A. 1974. Dispersion patterns and species diversity of macrobenthos in two bathyal communities. Ph.D. dissertation, University of California, San Diego, 204 pp.
- 1975. Environmental grain and polychaete species diversity in a bathyal benthic community. *Mar. Biol.*, *30*, 253–266.
- 1976. Deep-sea species diversity: does it have a characteristic scale? *J. Mar. Res.*, *34*, 217–246.
- 1978. Spatial autocorrelation with RUM (Remote Underwater Manipulator): vertical and horizontal structure of a bathyal benthic community. *Deep-Sea Res.*, *25*, 589–604.
- Jumars, P. A. and J. E. Eckman. 1983. Spatial structure within deep-sea benthic communities, *in* *Deep-Sea Biology, The Sea*, Vo. 8, G. T. Rowe, ed., Wiley-Interscience, NY, 399–451.
- Jumars, P. A. and K. Fauchald. 1977. Between-community contrasts in successful polychaete feeding strategies, *in* *Ecology of Marine Benthos*, B. C. Coull, ed., University of South Carolina Press, Columbia, SC, 1–20.
- Jumars, P. A. and E. D. Gallagher. 1982. Deep-sea community structure: three plays on the

- benthic proscenium, in *The Environment of the Deep Sea*, W. G. Ernst and J. G. Morin, eds., Prentice Hall, Englewood Cliffs, NJ, 217–255.
- Jumars, P. A. and R. R. Hessler. 1976. Hadal community structure: implications from the Aleutian Trench. *J. Mar. Res.*, *34*, 547–560.
- Leppakoski, E. 1971. Benthic recolonization of the Bornholm Basin (Southern Baltic) in 1969–71. *Thalassia Jugoslavia*, *7*, 171–179.
- Levin, L. A. 1984. Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. *Ecology*, *65*, 1185–1200.
- Levin, L. A. and C. R. Smith. 1984. Response of background fauna to disturbance and enrichment in the deep sea: a sediment tray experiment. *Deep-Sea Res.*, *31*, 1279–1285.
- McCall, P. L. 1977. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *J. Mar. Res.*, *35*, 221–266.
- Nichols, F. H. and J. K. Thompson. 1985. Persistence of an introduced mudflat community in south San Francisco Bay, California. *Mar. Ecol. Prog. Ser.*, *24*, 83–97.
- Oliver, J. S. 1980. Processes affecting the organization of marine soft-bottom communities in Monterey Bay, California and McMurdo Sound, Antarctic. Ph.D. dissertation, University of California, San Diego, 300 pp.
- Oliver, J. S., R. G. Kvitck and P. N. Slattery. 1985. Walrus feeding disturbance: scavenging habits and recolonization of the Bering Sea benthos. *J. Exp. Mar. Biol. Ecol.*, *91*, 233–246.
- Osman, R. W. and R. B. Whitlatch. 1978. Patterns of species diversity: fact or artifact? *Paleobiology*, *4*, 41–54.
- Paine, R. T. and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.*, *1*, 145–178.
- Patten, B. C. 1962. Species diversity in net phytoplankton of Raritan Bay. *J. Mar. Res.*, *20*, 57–75.
- Rees, E. I. S., A. Nicholaidou and P. Laskaridou. 1977. The effects of storms on the dynamics of shallow water benthic associations, in *Biology of Benthic Organisms*, B. F. Keegan, P. O. Ceidigh and P. J. S. Boaden, eds., Pergamon Press, 465–474.
- Rex, M. A. 1973. Deep-sea species diversity: decreased gastropod diversity at abyssal depths. *Science*, *181*, 1051–1053.
- 1983. Geographic patterns of species diversity in the deep-sea benthos, in *Deep-Sea Biology, The Sea*, Vol 8., G. T. Rowe, ed., Wiley-Interscience, NY, 453–472.
- Rosenzweig, M. L. 1971. Paradox of enrichment destabilization of exploitation ecosystems in ecological time. *Science*, *171*, 385–387.
- Rumohr, H. 1978. The “Benthosgarten”, field experiment on benthic colonization in the western Baltic. 1. Initial Colonization. *Kieler Meeresforschungen*, *4*, 96.
- Sanders H. L. 1968. Marine benthic diversity: a comparative study. *Am. Nat.*, *102*, 243–281.
- 1969. Benthic marine diversity and the stability-time hypothesis. *Brookhaven Symp. Biol.*, *22*, 71–80.
- Sanders, H. L., J. F. Grassle, G. R. Hampson, L. S. Morse, S. Garner-Price and C. C. Jones. 1980. Anatomy of an oil spill: long-term effects from the grounding of the barge *Florida* off West Falmouth, Massachusetts. *J. Mar. Res.*, *38*, 265–380.
- Sanders, H. L. and R. R. Hessler. 1969. Diversity and composition of abyssal benthos. *Science* *166*, 1074.
- Santos, S. L. and J. L. Simon. 1980a. Marine soft-bottom community establishment following annual defaunation: larval or adult recruitment? *Mar. Ecol. Prog. Ser.*, *2*, 235–241.
- 1980b. Response of soft-bottom benthos to annual catastrophic disturbance in a South Florida estuary. *Mar. Ecol. Prog. Ser.*, *3*, 347–355.

- Smith, A. L. 1981. Comparison of macrofaunal invertebrates in sand dollar (*Dendroaster exentricus*) beds and in adjacent areas free of sand dollars. *Mar. Biol.*, *65*, 191–198.
- Smith, C. R. 1983. Enrichment, disturbance and deep-sea community structure: the significance of large organic falls to bathyal benthos in Santa Catalina Basin. Ph. D dissertation, University of California, San Diego, 310 pp.
- 1985a. Colonization studies in the deep-sea: are results biased by experimental designs? *in* Proceedings of the 19th European Marine Biological Symposium, P. E. Gibbs, ed., Cambridge University Press, Cambridge, 183–189.
- 1985b. Food for the deep sea: utilization, dispersal and flux of nekton falls at the Santa Catalina Basin floor. *Deep-Sea Res.*, *32*, 417–442.
- Smith, C. R. and S. C. Hamilton. 1983. Epibenthic megafauna of a bathyal basin off southern California: patterns of abundance, biomass and dispersion. *Deep-Sea Res.*, *30*, 907–928.
- Smith, C. R., P. A. Jumars and D. J. DeMaster. 1986. *In situ* studies of megafaunal mounds indicate rapid sediment turnover and community response at the deep-sea floor. *Nature*, (in press).
- Smith, K. L. Jr. and K. R. Hinga. 1983. Sediment community respiration in the deep sea, *in* The Sea, Volume 8: Deep-Sea Biology, G. T. Rowe, ed., J. Wiley, NY, 331–370.
- Smith, K. L. Jr., M. B. Laver and N. O. Brown. 1983. Sediment community oxygen consumption and nutrient exchange in the central and eastern North Pacific. *Limnol. Oceanogr.*, *28*, 882–898.
- Smith, W. and J. F. Grassle. 1977. Sampling properties of a family of diversity measures. *Biometrics*, *33*, 283–292.
- Sokal, R. R. and F. J. Rohlf. 1969. *Biometry*. W. H. Freeman, San Francisco, 77 pp.
- Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, *60*, 1225–1239.
- 1984. The role of disturbance in natural communities. *Ann. Rev. Ecol. System*, *15*, 353–391.
- Stockton, W. L. and T. E. DeLaca. 1982. Food falls in the deep sea: occurrence, quality and significance. *Deep-Sea Res.*, *29*, 157–169.
- Theil, H. 1979. Structural aspect of the deep-sea benthos. *Ambio Spec. Rpt.*, *6*, 25–31.
- Thistle, D. 1978. Harpacticoid dispersion patterns: implication for deep-sea diversity maintenance. *J. Mar. Res.*, *36*, 377–397.
- 1979. Harpacticoid copepods and biogenic structures: implications for deep-sea diversity maintenance, *in* Ecological Processes in Coastal and Marine Systems, A. J. Livingston, ed., Plenum, NY, 217–231.
- 1981. Natural physical disturbances and communities of marine soft bottoms. *Mar. Ecol. Prog. Ser.*, *6*, 223–228.
- 1983a. The stability-time hypothesis as a predictor of diversity in deep-sea soft-bottom communities: a test. *Deep-Sea Res.*, *30*, 267–277.
- 1983b. Diversity maintenance in a deep-sea community exposed to energetic near-bottom current: a role for biologically produced habit heterogeneity? *Deep-Sea Res.*, *30*, 1235–1245.
- Thistle, D., J. Y. Yingst and K. Fauchald. 1985. A deep-sea benthic community exposed to strong near-bottom currents on the Scotian rise (western Atlantic). *Mar. Geol.*, *66*, 91–112.
- Tipper, J. C. 1979. Rarefaction and rarefaction—the use and abuse of a method in paleoecology. *Paleobiology*, *5*, 423–434.
- Turekian, K. K., J. K. Cochran, D. P. Kharkar, R. M. Cerrato, J. R. Vaisnys, H. L. Sanders,

- J. F. Grassle and J. A. Allen. 1975. Slow growth rate of a deep-sea clam determined by ^{228}Ra chronology. *Proc. Nat. Acad. Sci.*, *72*, 2829–2832.
- Turk, T. R. and M. J. Risk. 1981. Effect of sedimentation on infaunal invertebrate populations of Cobequid Bay, Bay of Fundy. *Can. J. Fish. Aquat. Sci.*, *38*, 642–648.
- Van Blaricom, G. R. 1977. Disturbance, predation, and resource allocation in a high-energy sublittoral sand-bottom ecosystem: experimental analyses of critical structuring processes for the infaunal community. Ph.D. Dissertation, University of California, San Diego.
- 1982. Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. *Ecol. Monogr.*, *5*, 83–305.
- Whitlatch, R. B. and R. N. Zajac. 1985. Biotic interactions among estuarine infaunal opportunistic species. *Mar. Ecol. Prog. Ser.*, *21*, 299–311.
- Williams, L. G. 1964. Possible relationships between plankton-diatom numbers and water-quality estimates. *Ecology*, *45*, 809–823.
- Williams, W. T. 1971. Principles of clustering. *Ann. Rev. Ecol. Syst.*, *2*, 303–326.
- Wilson, W. H. Jr. 1981. Sediment-mediated interactions in a densely populated infaunal assemblage: the effects of the polychaete *Aberenicola pacifica*. *J. Mar. Res.*, *39*, 735–748.
- Wiltse, W. I. 1980. Effects of *Polinices duplicatus* (Gastropoda: Naticidae) on infaunal community structure at Barnstable Harbor, Massachusetts, U.S.A. *Mar. Bio.*, *56*, 301–310.
- Woodin, S. A. 1978. Refuges, disturbance and community structure: a marine soft-bottom example. *Ecology*, *59*, 274–284.
- 1981. Disturbance and community structure in a shallow water sand flat. *Ecology*, *62*, 1052–1066.
- Zajac, R. N. and R. B. Whitlatch. 1982a. Responses of estuarine infauna to disturbance. I. Spatial and temporal variation of initial recolonization. *Mar. Ecol. Prog. Ser.*, *10*, 1–14.
- 1982b. Responses of estuarine infauna to disturbance. II. Spatial and temporal variation of succession. *Mar. Ecol. Prog. Serv.*, *10*, 12–27.