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Hadal community structure: implications from the Aleutian Trench

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ABSTRACT

A 0.25-m² box core from the Aleutian Trench (50°58.0′N, 171°37.5′W) was used to generate hypotheses concerning the regulation of benthic community structure in oceanic trenches. High food supply and the concentrating effects of trench topography are suggested by the unexpectedly high standing crop (1272 individuals of macrofaunal taxa m⁻²) and by the feeding modes of the captured polychaetes. Sediment instability caused by rapid sedimentation and frequent seismic activity, in turn, appears to maintain low species diversity and to prevent sessile polychaetes from comprising a large portion of the fauna. As is typical of deep-sea soft bottoms, polychaetes dominate (49% of macrofaunal individuals), but the unusually large contribution of aplacophorans, enteropneusts, and echiurids (respectively 10%, 8%, and 3% of macrofaunal individuals), cannot be readily explained.

1. Introduction

On Leg 7, Expedition *Seventow* (R.V. *Thomas Washington*), in July 1970, we succeeded in collecting a single 0.25-m² box core from the axis of the Aleutian Trench. We have chosen to discuss this single available core because its contents fall well outside the range of variation observed in previous hadal samples. Its standing crop, diversity, and faunal composition differ markedly from what has been seen in comparably collected abyssal samples, and in some respects bathyal samples as well. Additional justification for treating a single core is the relatively low degree of spatial variability observed among replicate box cores to date in the deep sea (Hessler and Jumars, 1974; Jumars, 1975b, 1976). Our comparisons will give special attention to the stable, oligotrophic central North Pacific abyss (Hessler and Jumars, 1974) and to the eutrophic, bathyal basins off southern California (Jumars, 1975b, 1976), where sampling methods have been most closely comparable.

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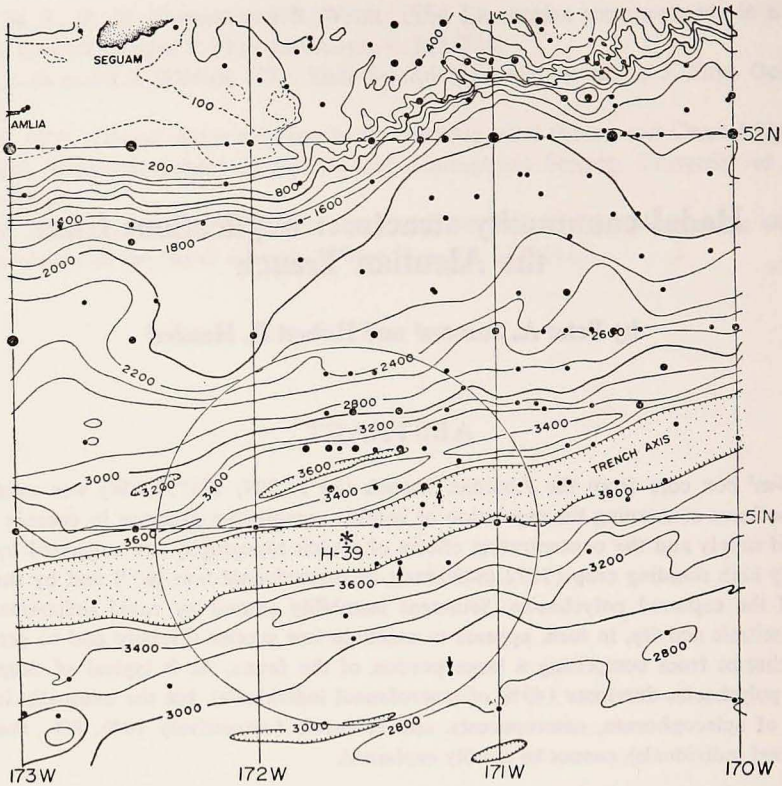
Figure 1. The location of station H-39 (asterisk), showing bathymetry (200-fathom contour interval) and seismic activity during the last 25 years. Flat sedimentary floor of trench axis lightly stippled. Black dots: earthquake epicenters, larger dots indicating more than one event (1, 2-5, 6-10, >10, respectively, with increasing size); arrows: Richter values in excess of 6.0 within 30 nautical miles (circle) of H-39.

2. Locality

The Aleutian Trench is one of the shallower trenches, its depth generally ranging between 7000 and 7500 m. It is one of the few trenches which is so filled with sediment that its axis forms a continuous, wide, relatively flat sedimentary surface for most of its length (Hayes and Ewing, 1971; Fisher, 1974; Scholl, 1974).

Station H-39 (50°58.0′N, 171°37.5′W) is located in the central portion of the Aleutian Trench and just north of the center of the axial sediment pond in an area where the pond is about 16 km wide (Fig. 1). Depth at the core site is 7298 m. The trench wall to the south climbs up to the abyssal hills with a slope of about 4.5-6.0%. To the north, the trench wall is more complicated. While its slope is much steeper, it is subdivided by the broad, relatively flat, sediment-covered Aleutian Terrace at about 3700-4000 m. In addition, a small ridge runs along the base of the northern wall (Marlow, et al., 1973, Fig. 1). The terrace and ridge would

both act to minimize the contribution of sediment directly from the north to the sample locality.

3. Methods

The sample at station H-39 was collected with a 0.25-m² box corer. Details of the technique can be found in Hessler and Jumars (1974). The smooth operation and the condition of the core upon retrieval led us to believe that it was an excellent sample. Immediately upon recovery, the sediment was washed through a 0.297-mm screen with a gentle elutriation technique (Sanders *et al.*, 1965). The core sample was processed in three layers, 0-3 cm, 3-8 cm, and 8-18 cm. Deeper sediment was not utilized.

The residue on the screen was fixed for two days in a buffered 10% formalin solution and was subsequently preserved in 70% ethanol. In the laboratory, the subsamples were stained with rose bengal and were inspected under a dissecting microscope. All benthic organisms were picked out and sorted into major taxa.

Two surface samples, each of 17.7-cm² area, were taken. One was frozen and analyzed for organic carbon content with a Leco® analyzer. The other was dried and measured for grain size by screening the sand fraction and pipetting the silt-clay fraction.

After sorting and identification, species diversity was treated in two ways, both as numerical species richness and as areal species richness (*sensu* Hurlbert, 1971, p. 581). Hurlbert's expected number of species, $E(S_n)$, was calculated by means of his combinatorial formula in each case. For presenting numerical species richness, $E(S_n)$ was plotted against numbers of individuals, while for areal species richness (species density), $E(S_n)$ was plotted against surface area of the sample. The former format is the more frequently used, but the latter treatment may be more informative in dealing with the intensity of interspecific interaction when species are considered to search or to occupy a given area (Hurlbert, 1971). The intensity of interspecific interaction is clearly influenced by the total standing crop of individuals, by species density, and by mobility of the species involved (e.g., Jumars, 1975a,b).

Among those Polychaeta which are not primarily carnivorous, Jumars and Fauchald (1976) have developed provisional classificatory schemes for mobility and for feeding type. Polychaete species included are considered either sessile, motile, or "discretely motile." The latter group contains those species in which moving from place to place is punctuated by periods of apparent sessility. A similar partitioning is made among filter-feeding, surface deposit-feeding, and subsurface deposit-feeding (burrowing) classes. Triangular charting provides a convenient means of displaying observed sample proportions of these various groupings as well as of showing confidence regions about these proportions (Snee, 1974). The polychaetes of core H-39 were classified on these feeding and mobility parameters and the resulting data were analyzed with the help of Snee's methods.

Table 1. Gross taxonomic composition of sample H-39, taxa listed in decreasing rank order of abundance. * = except Incertae Sedis and non-allogromiinid Foraminifera.

	Number of individuals in indicated (cm) layer				Percent of
Macrofaunal taxon	0-3	3-8	8-18	0-18	total
Polychaeta	117	25	3	145	49.0
Bivalvia	33	1	—	34	11.5
Aplacophora	28	3	—	31	10.5
Enteropneusta	24	—	—	24	8.1
Bryozoa	19	—	—	19	6.4
Tanaidacea	16	2	—	18	6.1
Echiurida	9	—	—	9	3.0
Amphipoda	4	—	—	4	1.4
Oligochaeta	4	—	—	4	1.4
Gastropoda	2	—	—	2	0.7
Isopoda	2	—	—	2	0.7
Priapulida	2	—	—	2	0.7
Pycnogonida	—	1	—	1	0.3
Sipunculida	1	—	—	1	0.3
Incertae Sedis	16	5	1	22	*
Total Macrofauna	277	37	4	318	100.0*
Meiofaunal taxon					
Allogromiinid Foraminifera	203	14	4	221	41.08
Other Foraminifera	?*	?*	?*	?*	?*
Nematoda	168	24	2	194	36.06
Harpacticoida	77	2	4	83	15.43
Turbellaria	35	1	1	37	6.88
Ostracoda	3	—	—	3	0.56
Total Meiofauna	486	41	11	538	100.00*

4. Results and discussion

Standing crop. Table 1 lists the numbers of individuals of major taxa found in core H-39. The abundance of organisms dropped by roughly an order of magnitude from one layer to the next. Thus, the great majority of specimens was found in the top 3 cm. There was a total of 318 individuals (1272 ind. m^{-2}) within macrofaunal taxa as defined by Hessler and Jumars (1974), and there were at least 538 specimens (2152 ind. m^{-2}) of meiofaunal taxa.

The standing crop seen in H-39 is very high in comparison to values given for hadal depths in the past (Table 2). All previous samples, covering seven trenches at depths between 6135 m and 7286 m (except the Philippine at 10120 m) yielded 15-200 ind. m^{-2} (except the Philippine at 5 ind. m^{-2}). The H-39 value exceeds the largest of these numbers by a factor of six or more. It is an order of magnitude greater than observed in the oligotrophic abyss, as typified by the central North

Table 2. Standing crops reported from hadal trench soft bottoms.

Trench	Depth (m)	Standing crop (ind. m^{-2})	Source
Philippine	10120	5	Spärck, 1956
Java	6730	15	"
Vityaz	6135	20	Belyaev, 1966
Banda	6580, 7280	30, 55	Spärck, 1956
Java	6487, 6841	50, 55	Belyaev, 1966
Peru-Chile	6229	63.5	Frankenberg & Menzies, 1968
Aleutian	6460, 7286	35, 100	Belyaev, 1966
Kurile-Kamchatka	6150, 6938	120, 200	"
Aleutian	7298	1272	Jumars & Hessler, herein

Pacific (92-148 ind. m^{-2}; Hessler and Jumars, 1974), or by the central North Atlantic (33-126 ind. m^{-2}; Sanders *et al.*, 1965).

Coastal shallow abyssal samples have produced standing crops similar to that of H-39, although they too have often been lower. Carey (unpublished) found 7-1937 ind. m^{-2} at approximately 2800 m near the base of the continental slope off Oregon. Sanders *et al.* (1965) collected 467-1003 ind. m^{-2} from 2500-3752 m on the continental rise of the Gay Head-Bermuda transect off the eastern coast of the United States.

Numerical density at H-39 is only slightly lower than that often seen at eutrophic bathyal depths. Jumars (1976) reported averages of 1880 and 2251 ind. m^{-2} for two localities at 1100-1250 m off the coast of southern California. On the Gay Head-Bermuda transect, two stations at 1500 and 2100 m yielded 1719 and 2154 ind. m^{-2}, respectively. However, much lower values have also been observed at bathyal depths. Carey (1965) reported 565 ind. m^{-2} at 2000 m.

As always, such comparisons must be made with caution. Only the central North Pacific samples were collected and processed in precisely the same way as was H-39. Jumars (1974) also used a 0.25-m^2 box corer but washed the samples through a 0.42-mm screen. Sanders *et al.* (1965) and Carey (1965 and unpublished) used anchor dredges and 0.42-mm screens. Frankenberg and Menzies (1968), Belyaev (1966), and Spärck (1956) all used grab samplers; the former two studies employed 0.5-mm screens (mesh size for Spärck's samples not reported but presumably 1.75 mm). Different samplers are bound to yield somewhat different results. Poorly vented samplers tend to have especially pronounced bow waves, whose action strongly reduces the number of animals captured (Wigley, 1967). We suspect such bow waves may provide a partial explanation for the composition of many of the previous trench samples.

The use of a standard screen size in such comparisons would, at first sight, appear desirable. In between-area comparisons of numerical density and numerical species richness, however, the validity of the comparison hinges on the assumption that a

similar, large proportion of individuals in the taxa of concern has been retained in each region. Because the proportion of individuals remaining on the screen does not vary linearly with the width of the meshes (Reish, 1959) and because average animal size within a given taxon varies from place to place, use of a standard mesh size would be either misleading (large standard mesh) or unnecessarily tedious (small standard mesh). In particular, Rowe and Menzel (1971) have observed that the average size of a macrofaunal individual decreases with overlying water depth along sublittoral to abyssal transects. What clearly is desirable is some assurance that a large portion of the entity of concern, be it biomass, number of individuals or number of species, is retained by the procedure employed. For assessing numbers of individuals of macrofaunal taxa, the 0.42-mm screen appears adequate in the eutrophic bathyal studies cited above, and the 0.297-mm suffices in the oligo-trophic abyss. We used a 0.297-mm screen to insure that nearly all the taxonomi-cally valuable specimens in H-39 would be retained. If experimental manipulations with the preserved Polychaeta are indicative, however, fewer than 10% of the macrofaunal individuals would have been lost by using a 0.42-mm mesh; screen size alone does not appear to be a sufficient explanation for the discrepancy between our results and earlier trench findings, with the possible exception of those reported by Spärck (1956).

Several additional observations corroborate the finding of a high standing crop in the region of H-39. Pamatmat (1973) reported higher oxygen uptake in Aleutian Trench samples than in abyssal samples taken far from shore. The explanation appears to rest in the high productivity of surface waters in that portion of the North Pacific (Larrance, 1971). As Rowe *et al.* (1974) have most recently demon-strated, benthic standing crop reflects surface productivity even in several kilometers of water and in spite of the absence of a fixed, theoretical relationship between standing crop and productivity (e.g., Buchanan, 1967). Furthermore, average stand-ing crop in the axis of the Aleutian Trench may be even higher than estimated from H-39, which is isolated from the north wall of the trench by a topographic rise (Fig. 1). If food is transported down the north wall, its effects should be dis-cernible to the east and west of our sample locality, where the rise is absent. Baker (1976) has shown the channeling effects of topography on the near-bottom nephe-loid layer of the Washington continental slope and Nitinat deep-sea fan, and the apparent concentrating effect of trench topography on standing crop has been demonstrated by Vinogradova *et al.* (1974).

Species diversity. We have assessed species diversity only in Polychaeta and Har-pacticoida. Various problems preclude such analyses in other taxa. Testaceous Foraminifera are excluded by our inability to reliably recognize living individuals, and other taxa are either poorly represented or their specific taxonomic discrimina-tion is incomplete. In comparisons, only those deep-sea Hurlbert rarefaction curves
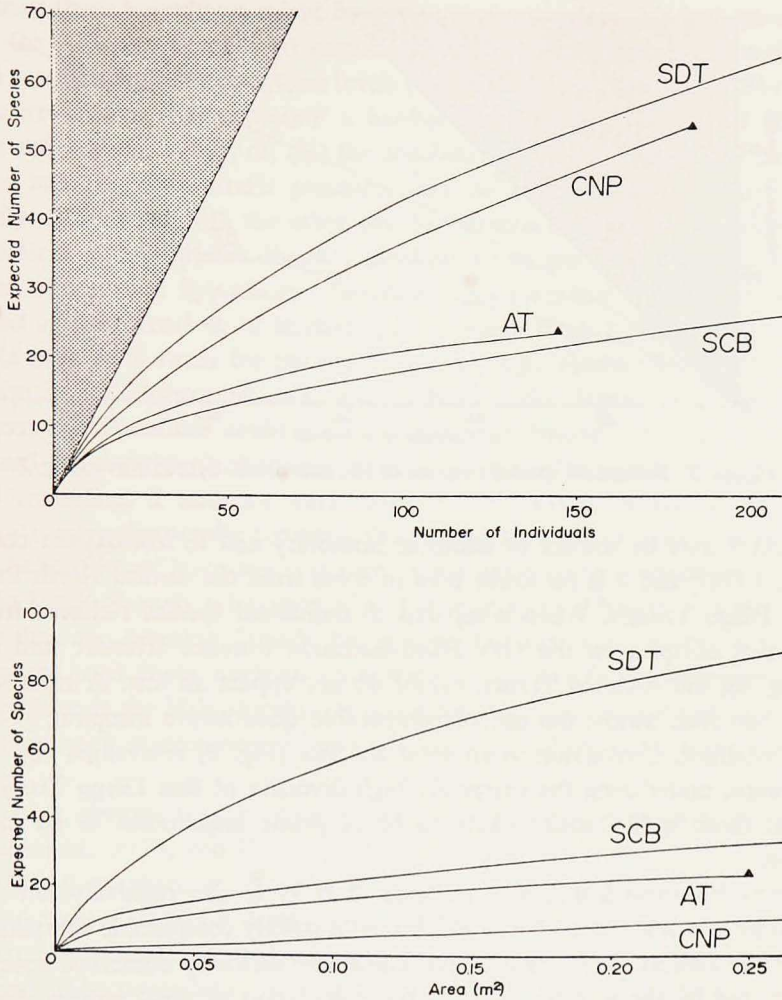
Figure 2. Polychaete numerical and areal species richness of Aleutian Trench (AT) sample H-39 by Hurlbert rarefaction. Triangles: total numbers of species observed; stippling: region cannot be occupied. Comparative data from summed box cores in the San Diego Trough (SDT), Santa Catalina Basin (SCB), and central North Pacific (CNP).

which have been made from box cores are figured. Intergear comparisons are difficult to interpret because they may not give similar results even when applied to the same community (e.g., Hessler and Jumars, 1974; Gage, 1975). Strictly comparable data for deep-sea Polychaeta are thus limited to the central North Pacific at 5600 m (Hessler and Jumars, 1974), to the San Diego Trough at 1230 m (Jumars, 1975b), and to the Santa Catalina Basin at 1130 m (Jumars, 1976).

Numerical species richness of Aleutian Trench Polychaeta proves to be relatively low (Fig. 2). It is nearly as low as in samples from the Santa Catalina Basin, a
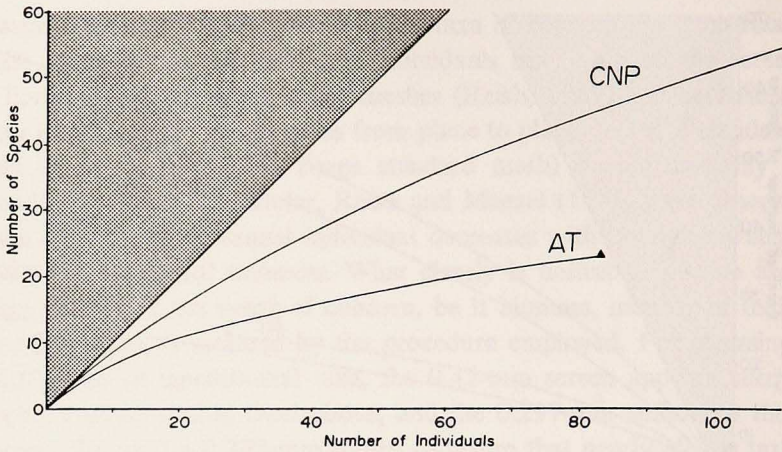
Figure 3. Numerical species richness of Harpacticoida. Symbols as in Fig. 2.

region which may be subject to sediment instability and to low-oxygen conditions (Jumars, 1976), and it is far lower than in cores from the central North Pacific or the San Diego Trough. When compared to numerical species richness from epibenthic sled samples on the Gay Head-Bermuda transect (Hessler and Jumars, 1974, fig. 8), the Aleutian Trench values do not appear so low. A rigorous comparison, however, awaits the use of comparable quantitative sampling procedures at both localities. Conversion to an areal abscissa (Fig. 2) rearranges the diversity relationships, underlining the extremely high diversity of San Diego Trough Polychaeta at those spatial scales likely to be of prime importance to an individual organism.

Harpacticoid numerical species richness in H-39 is also relatively low (Fig. 3), though only one study is available which used a strictly comparable sampling device (Hessler and Jumars, 1974). We do not know how seriously numerical species richness is biased by the screen size used, but calculation of areal species diversity is certainly unwarranted because adults of many harpacticoid species doubtless passed through the meshes. Although Coull (1972) also found higher harpacticoid species diversity in deep-sea samples from the United States east coast than we observed in H-39, the screening problem makes the comparison difficult to interpret.

Other portions of the fauna also exhibit low species diversity, however, which suggests that this situation is characteristic of the fauna as a whole. For example, all the aplacophorans belong to one species; the 17 tanaids belong to no more than five species, and probably only three; the abundant allogromiinid Foraminifera all appear to belong to one species. Unlike our standing crop data, these results are in good accord with past findings of low species diversity and high dominance in hadal faunas—in spite of the use of different, often qualitative samplers in past comparisons (Menzies *et al.*, 1973).

At least three hypotheses might be entertained to explain this low species diversity in the Aleutian Trench: (i) environmental instability may cause extinction of species maintaining low population levels (Grassle, 1972; May, 1974; Smith, 1974); (ii) the trench axis may represent a habitat island of relatively small size (MacArthur and Wilson, 1967); or, (iii) the absolute value of environmental parameters, perhaps including hydrostatic pressure, may be stressful. The last hypothesis is probably confounded with the other two for reasons detailed by Terborgh (1973). Explanations of low species diversity invoking stress are often semantic variants of the first and second hypotheses; "stressful" environments can almost always be classified as ephemeral or of limited spatial extent. High hydrostatic pressure, for example may be a stress for particular species (e.g., Hochachka, 1975) and may thus explain the absence of *these* species from hadal depths. It is not clear that analogous considerations could control the species diversity of a hadal community composed (by definition) of species adapted to such high pressures. By Terborgh's (1973) reasoning, if trenches were more spatially extensive and if conditions in them were more temporally constant, they would have higher species diversities.

The habitat island hypothesis, in turn, is not likely to be a complete explanation. The San Diego Trough, albeit part of an "archipelago" of basins, is a much smaller feature than the Aleutian Trench, but species diversity is not correspondingly low. If, as seems most likely, environmental stability is a key factor controlling community structure at the H-39 locality, it is appropriate to inquire about those ways in which the trench environment is less stable than that of the other regions mentioned above.

The most obvious source of environmental instability is sporadic sedimentation (Menzies *et al.,* 1973; von Huene, 1974). Trench walls are steep, and any sediment accumulating on them gradually achieves an unstable configuration, resulting in slumping and/or turbidity flows. Such flows not only result in locally very rapid sedimentation rates and therefore burial of much of the fauna, but may initially be accompanied by powerful erosive currents. That this form of deposition does occur in the area of H-39 is documented by the presence of layers of graded bedding in the core itself. The surface layer consisted of a soupy, greenish-gray silt-clay (9.6% sand, 56.5% silt, 43.8% clay). At about 3 cm down, the sediment was more consolidated and graded into a coarser composition. Below this layer, it became looser again. At 8 cm it again became more consolidated, and the color was more brownish. In corroboration, Ewing and Thorndike (1966) reported a nepheloid layer possibly due to turbidity currents 100 mi to the east.

If sporadic sedimentation is to have a continuing effect on community structure, it must obviously occur at a rate which is appreciable in comparison to the potential recovery rate of the affected populations. In particular, Southwood *et al.* (1974) suggested that one generation's likelihood of influencing the resources available to the next generation would determine the *"r"* versus *"K"* selected aspect of the
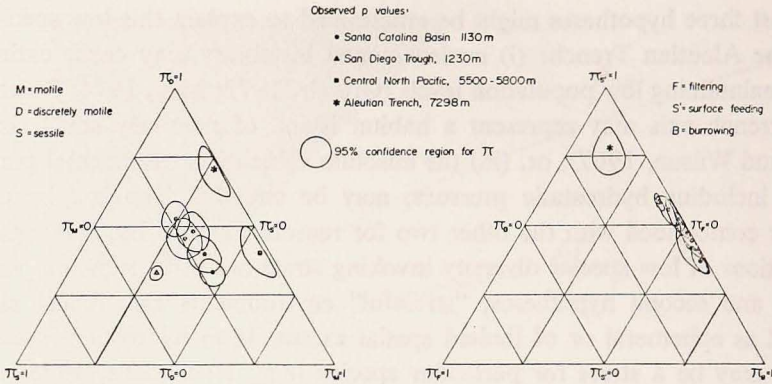
Figure 4. Proportions of noncarnivorous polychaete individuals displaying the indicated forag-
ing patterns, all taken from Pacific deep-sea box core samples. 95% confidence regions for
these proportions are also shown (see text).

populations, and sporadic sedimentation would decrease this likelihood. Such sedi-
mentary events would also impede "grain matching" of temporal and spatial scales
of environmental variation with those most likely to prevent competitive exclusion
(Jumars, 1975b). Just as avalanches are most common in areas of high snowfall,
the frequency of sporadic sedimentary events is increased if the regional sedimentation
rate is high. At Deep Sea Drilling Project Hole 180, in the axis of the trench at
147.75°W in the Gulf of Alaska, the deposition rate has been estimated at 0.35 mm
yr^{-1} during interglacial times and at 2.85 mm yr^{-1} during glacial periods (von
Huene and Kulm, 1973). To the west, at about 178.5°E, trench sedimentation is
thought to be 0.1 mm yr^{-1} (Marlow *et al.,* 1973). At H-39, most sediment must,
then, have come along the trench axis from the east; the volume of sediment fill is
at a maximum yet the adjacent denudation area is at a minimum (Marlow, 1972).

Thus there is good evidence for a high sedimentation rate at H-39, but is it
sporadic? As Menzies *et al.* (1973) have noted, the intense seismic activity charac-
teristic of island arc-trench systems provides the triggering mechanism for frequent
sediment redistribution. Within a 30-mi radius of H-39 (Fig. 1), 53 earthquakes
have been detected in the last 25 years (National Earthquake Information Service,
Boulder, Colorado). Three of these disturbances have exceeded 6.0 on the Richter
scale. It therefore appears likely that the trench community at H-39 and in other
tectonically active trenches is subject to relatively frequent bursts of sedimentation.
We doubt, however, whether these events are severe, frequent, or extensive enough
to cause extinction of entire faunas (Menzies *et al.,* 1973). If the lifespan of deep-
sea species can be measured in decades, as seems to be the case for at least one
species (Turekian *et al.,* 1975), then such disturbances at any one locality would
probably be felt every few generations, a rate more than ample to have continuous
effect on community composition and on species' life history parameters. The logi-

cal test of these ideas would be in the examination of community structure in trench areas of varying sedimentary regimes.

Polychaete foraging patterns. Jumars and Fauchald (1976) suggested that high proportions of sessile polychaetes would occur only where sediment stability and rate of food supply were both high. Figure 4 shows that the polychaetes of core H-39 differ significantly from all deep-sea samples characterized in this manner to date. H-39 has few sessile polychaetes and a very high proportion of surface deposit-feeding forms. In these aspects, it closely resembles samples taken from 10-m depth off southern California (Jumars and Fauchald, 1976, fig. 5).

The high surface productivity and the high standing crop of suspension-feeding polychaetes in particular and of polychaetes in general in H-39 suggest that low food supply is not the reason for a poor representation of sessile polychaetes. In addition, organic carbon concentration in the sediments of the trench axis is comparable with that observed at much shallower depths (Pamatmat, 1973); we found 0.62% in H-39, and Pamatmat (1973) recorded 0.86% in surface sediments from the same area. (In support of our earlier arguments, Pamatmat found 1.08% 110 mi to the west of H-39.) Local sediment instability appears to be the most likely explanation because it places a premium on the capacity to move (Purdy, 1964; Stanley, 1970).

General taxonomic composition. Polychaetes contained half the macrofaunal individuals; bivalves, aplacophorans, enteropneusts, and bryozoans were the next four most abundant macrofaunal taxa. Among the meiofaunal taxa, allogromiinid Foraminifera were somewhat more abundant than were nematodes. Together, the latter two taxa comprised over 75% of the meiofaunal individuals. Harpacticoid copepods and turbellarians were next in abundance. Certain aspects of this gross taxonomic composition are typical of soft-bottom communities, particularly with regard to the deep sea. The high percentage of polychaetes in the macrofaunal taxa and of nematodes in the meiofaunal taxa, as well as the secondarily high abundances of tanaids, bivalves, and copepods, are all common relationships (Hessler and Jumars, 1974).

In other respects, however, the composition of H-39 is quite unusual. Among the macrofaunal taxa, aplacophorans (31 ind., 10%) and enteropneusts (24 ind., 8%) are much more common than has been noted for deep-water communities in general (Hartman and Barnard, 1958, 1960; Emery, 1960; Wolff, 1961; Menzies, 1963, 1964; Sanders *et al.*, 1965; Belyaev, 1966; Menzies and Rowe, 1968; Hessler and Jumars, 1974). Echiurida (9 ind., 3%) are certainly more abundant than is the case for abyssal or bathyal communities, but are common components of hadal samples (Belyaev, 1966). Within the meiofaunal taxa, turbellarians (37 ind., 7%) and the allogromiinid Foraminifera (211 ind., 41%) have not been previously reported as components of so coarse a screen fraction in the deep sea. The tolerances

and life styles of deep-sea taxa are so poorly known that any explanation must be tenuous.

5. Conclusions

The soft bottom of trenches displays a set of environmental features whose combination is unique. The great depth and volume of water insures high stability in temperature, salinity, and oxygen concentration. However, unlike many abyssal regimes, complete environmental stability is not achieved. The confined conditions resulting from the configuration of the trench may cause complex sedimentation patterns, and the steep walls plus the frequent seismic activity insure that sedimentation in the axis will be sporadic and potentially catastrophic. The high productivity of the overlying waters of many trenches means that moderately large amounts of food reach the bottom, in spite of the great depth.

Not surprisingly, the trench community, to the extent that it may be exemplified by H-39 in the Aleutian Trench, displays characteristics which seem to be in response to at least some of these features. The high standing crop reflects high surface productivity. The low diversity is probably a response to environmental instability, which is also suggested by the life styles of resident polychaetes. Finally, the unusual gross taxonomic composition of the community may be a response to these same factors or to a variety of others, which may well include hydrostatic pressure.

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