Low Variability in Planktonic and Micronektonic Populations at 1,000m Depth in the Vicinity of 42°N, 17°W; Evidence Against Diel Migratory Behavior in the Majority of Species

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Abstract Twenty-four repeated samples were collected using an RMT (1+8) M sampler from a depth of 1,000m in the vicinity of 42°N, 17°W in May 1978, most within a single 36h period. Data for 194 species belonging to eight micronektonic and planktonic groups were analyzed. Variability in standing crops of both micronekton and plankton and the numerical abundance of individual species showed that single sample estimates at such depths are within a factor of two or three of the mean estimates from repeated samples. Only one species, a myctophid fish *Notoscopelus elongatus kroyeri,* showed the cyclic changes in abundance that would be expected from diel vertical migration. Discussed is the possible significance of this lack of diel vertical migration at depths below 1,000m, as compared to plankton biomass and the high relative abundance of micronekton, to our

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understanding of the fluxes of organic matter to deep-living population.

KEY WORDS: *Plankton, micronekton, diel migration, Northeast Atlantic, bathypelagic.*

Introduction

Diel vertical migration is a well-documented phenomenon in the surface few hundred meters of the ocean (e.g., Longhurst, 1976). The lower depth limit for such migrations has never been established, although Waterman et al. (1939) claimed to have demonstrated diel migrations in a range of species at depths of 1,000m. Wiebe et al. (1978) published vertical abundance profiles of the salp *Salpa aspera,* which they interpreted as showing migration by this salp to depths of 2,000m. In an attempt to explain how organic material reaches the deep-living communities both in midwater and on the seabed, Vinogradov (1968) put forward his ladder of migration theory. It is in this context that it is very important to establish the lower limit of diel migration. Organisms regularly migrating between the productive near-surface layers and the relatively poor bathypelagic depths would provide a route whereby organic material could be very rapidly transported downward.

The approach of Wiebe and his colleagues in comparing day and night profiles of vertical distribution runs into problems created by the sparseness of the deep-living communities. Even a moderate degree of patchiness in the abundance of these sparse organisms can create enough sampling noise to mask the cyclic variability produced by diel migration. Efforts to increase the sample sizes run into problems of timing. An alternative approach is to collect series of repeat samples within as short a time period as possible, but spanning at least one-and-a-half cycles of any suspected cycle. The problem is then to segregate variability resulting from cyclic behavior patterns, such as diel vertical migration, from variability resulting from spatial pattern (i.e., patchiness) of scales within the sampling range which may also have specific temporal characteristics (Angel, 1976; Haury et al., 1978). This approach assumes that any diel migration is synchronized throughout the population (Pearre, 1979) and will have a similar periodicity to the light cycle, although at such depths the organisms may not be able to detect any changes in light intensity. Confirmatory data on vertical profiles are

necessary to determine unequivocably in which direction the organisms move when they disappear from the sampling zone.

Methods

During Discovery Cruise 92 in May 1978 a station 9801 was occupied in the vicinity of 42°N, 17°W over a period of nine days. Three main sets of observations were conducted at this station: (a) a series of repeated tows at a depth of 1,000m, (b) a series of tows to look at the vertical profiles of plankton and micronekton from the surface down to 3,900m, and (c) a series of tows to study the relationship between isolumes and the vertical distribution of organisms. The sampler used for these observations was the RMT 1+8M (Roe and Shale, 1979), which is an opening/closing net system collecting three successive plankton and micronekton samples, and it continuously monitors via an acoustic link the depth of fishing, the in situ water temperature, the speed of the net through the water, and the operational state of the net (i.e., which nets are fishing). The speed indicator also provides a measure of distance run from which the average speed during the tow can be calculated. Using this average speed together with measurements of net angle at different speeds (Roe et. al., 1980), the volume of water filtered during the course of a tow was estimated. All the data has been normalized and expressed as amount per 1,000 (or 10,000)m^3 water filtered. The plankton nets (the RMT 1's) have a mesh of 0.3mm and at 2 knots filter around 2,800m^3 per hour, and the micronekton nets (the RMT 8's) have 5mm mesh and filter around 28,000m^3 per hour at 2 knots; the drag characteristics of the nets change slightly depending on whether the first, second, or third series are being fished, so the volumes of water filtered vary slightly.

The repeat tows at 1,000m consisted of an initial haul giving a triad of samples and was made over the period of sunset on May 14th (Samples 24–26). This was followed by seven further hauls taken within a 36h period between 2306h/May 16 to 1122h/May 18, giving a total of 24 micronekton and plankton samples. The start and finish positions for each of the samples are plotted in Figure 1. Haul data on the time of fishing, the distance traveled, the estimated volume of water filtered, and the range and mode of the in situ temperature are listed in Appendix 1.

The hydrographic structure of the water column was investigated

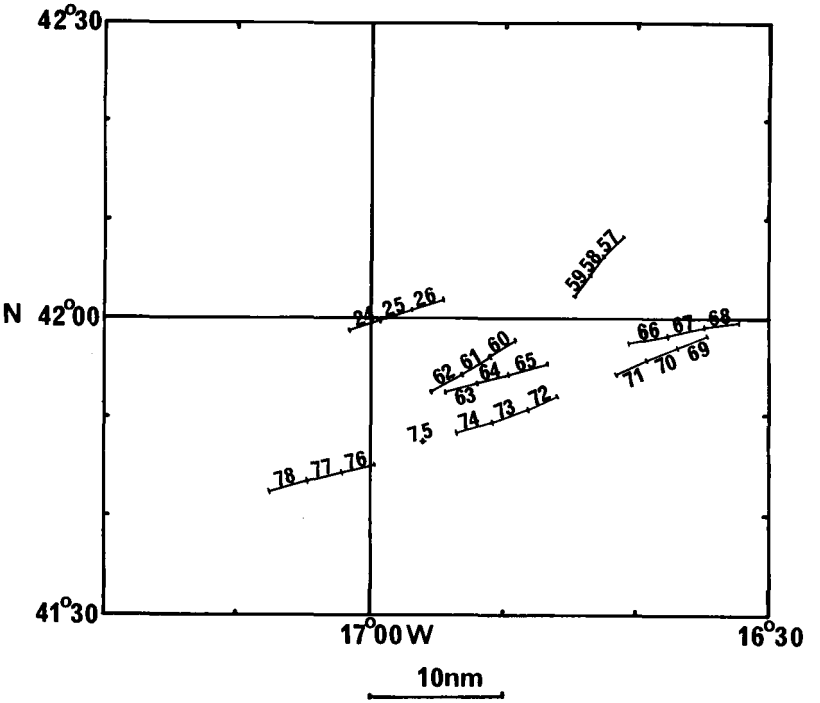

FIGURE 1. The ship's tracks during the course of the 1,000m repeat sampling at a depth of 1,000m in the vicinity of 42°N, 17°W. The numbers refer to the sample numbers at Discovery station 9801 (see Appendix 1).

down to a depth of 2,000m using a conductivity–temperature–depth probe (CTD) on May 18th (observation #75), and additional observations were made in the area on May 13th (#2) and May 21st (#94).

The biological samples were preserved in 5% neutralized formalin in sea water (100% formalin = 40% solution of formaldehyde buffered with 6.g.l^{-1} borax). During some of the nighttime tows very dense swarms of the scyphomedusan *Pelagia noctiluca* occurred at the surface and contaminated the samples as the nets surged at the surface during recovery. Specimens of *Pelagia* were removed, counted, volumed, and discarded. All data presented below are exclusive of *Pelagia* data. The displacement volumes of the total samples were measured 48 to 60h after collection, when any rapid shrinkage resulting from initial fixation had been completed. The change into fresh preservative reduces sub-

sequent shrinkage. Back at the laboratory the RMT 8 samples were totally sorted into the main taxonomic groupings, and the displacement volume of each group was measured. The RMT 1 samples were sorted only for fish, mysids, euphausiids, and planktonic ostracods.

The data interpretation has been aided by some of the initial results of the vertical profile samples from the surface to 3,900m. Angel and Baker (in press) have described the biomass profiles and how the contributions of the main taxonomic groups fluctuated with depth. Some of the data of the specific analyses have been used to confirm that conventional patterns of migration occurred in some of the species at shallower depths; these data are not yet sufficiently complete to be published.

Results

Physical Structure of the Water Column

The temperature and salinity profiles from the three sets of CTD observations are plotted in Figure 2 (A, B). Two of the profiles extended down to 2,000m, the third (#94) to 4,000m. There was some stratification in the surface 100m. The salinity minimum was at around 600m of $<35.5^0/_{00}$, where $\sigma^t \approx 27.3$ marked the top of the influence of Gulf of Guinea (or Mediterranean) Water. Water above 600m can be considered to be North Atlantic Central Water, which is increasingly mixed with Gulf of Gibraltar Water below 600m. There are the two salinity maxima, at around 860m ($\approx$10°C; 35.75%; σ^t27.53) and at around 1,020m (8.92°C; $35.6^0/_{00}$; σ^t 27.67), which are typical features of Gulf of Gibraltar Water (Figure 2) in the region. Hence, the sampling at 1,000m occurred within the core of the lower stratum of Gulf of Gibraltar Water.

The profiles from 1,000m down to the inflection in the salinity profile at about 2,300m in the #94 profile is a typical mixing profile between Gulf of Gibraltar Water and North Atlantic Deep Water. The inflection may be related to the marked decrease in the "porosity" of the Mid-Atlantic Ridge at that depth (J. Swallow, personal communication), or it may relate to the influence of Labrador Sea Water. The profiles indicate that at the time scale of the biological sampling there is no evidence of major perturbations in the physical structure of the water column, although the T.S. relationship in the Gulf of Gibraltar Water is noisy.

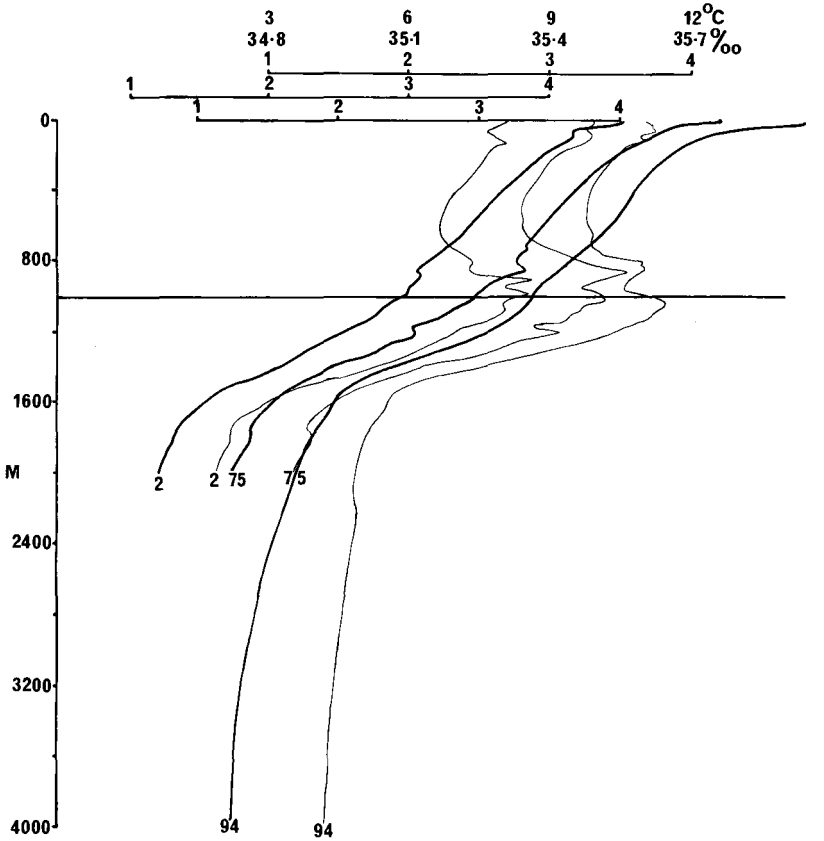

FIGURE 2. A. The temperature and salinity profiles observed by CTD on May 13 (#2), May 18 (#75), and May 21 (#94). B. (opposite page.) The T/S profiles from these three CTD observations. The box indicates the envelope of properties of typical "Deep Water."

Variability in Standing Crops

The displacement volumes per 1,000m^3 water filtered are shown both for the RMT 1 samples (macroplankton) and the RMT 8 sample (micronekton) in Figure 3. The accuracy of individual estimates is probably around ± 5%. The relative uniformity of the community structure within the samples (see below) will probably have resulted in relatively small differences in shrinkage between samples. The mean of the values for micronekton was 28.03 ± 6.52 mls per 1,000m^3 and for the

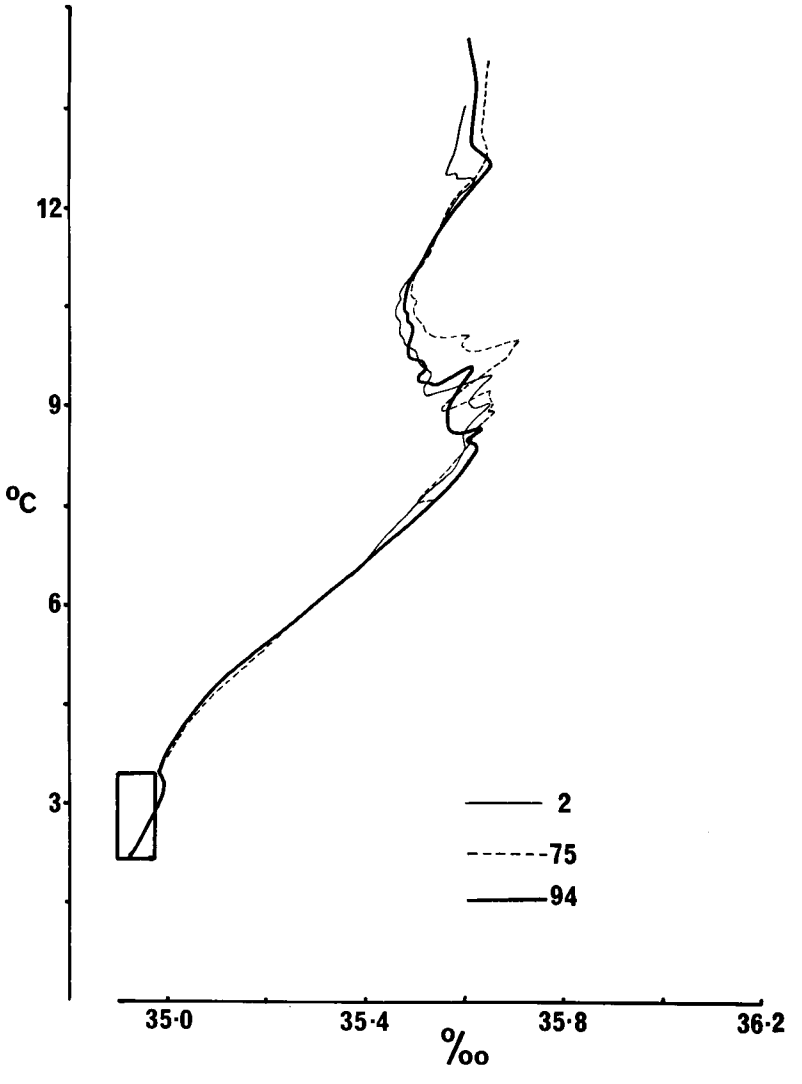

FIGURE 2.B.

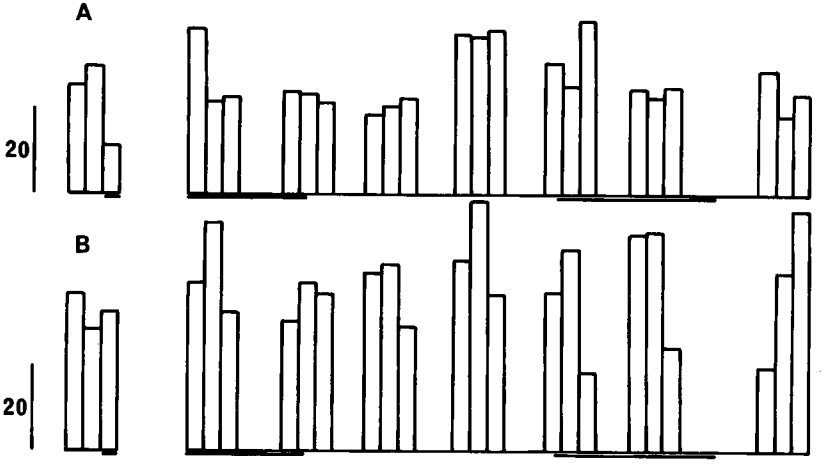

FIGURE 3. Histograms of the total sample displacement volumes in order of sampling expressed in mls per 1,000m^3 sampled of A. Micronekton (RMT 8 samples) and B. Plankton (RMT 1 samples). The double baseline indicates nighttime (sunset to sunrise), and each triad of samples represents a three-hour time scale.

plankton was 38.91 ± 10.72. A relatively low degree of variability is shown by the standard deviations, which imply that a single sample has a 95% probability of being within a factor of 2 of the mean. However, the coefficients of dispersion (C.D. = Variance/Mean) have values of 1.52 and 2.95, respectively, which indicate highly significant departures from a Poisson distribution toward a clumped distribution. Even so, the variability in biomass is lower than observed by McGowan (1976) for zooplankton in the highly advective environment of the California Current (where C.D. ranged from 16.3–1300.8) and the much more uniform environment of the North Pacific gyre (C.D. = 3.6). Factors possibly contributing to this low variability include the smaller range of fluctuations in the physical environment the organisms experience, a smoothing with depth of the fluctuations in food supply, and the large volumes of water filtered.

The ratio between the macroplankton and micronekton biomasses was examined to see if this too was consistent. However, the RMT 1: RMT 8 biomass ratios have a mean value of 1.47 ± 0.49 and so show a greater degree of variability. Cross-product correlation analysis be-

tween the biomass values for plankton and micronekton showed no significant correlation ($r = -0.023$).

In Table 1 the range and means of the concentrations of biomass (i.e., displacement volumes) of the dominant nektonic groups are listed together with the percentage contribution of each group of the total micronekton samples. The concentrations of displacement volume of each group are plotted in Figure 4. Salps, fish, ctenophores, and amphipods were very variable, their biomass distributions all had standard deviations >50% of the means, whereas the lowest variation was observed in the biomasses of mysids, chaetognaths, and decapods, for which the coefficients of variation ($s/\bar{x}$) were 23%, 29%, and 30%, respectively, implying their biomass was less variable in its distribution. However, comparison of the coefficients of dispersion (C.D. significance limits for 24 samples are 1 ± 0.295 for 5% level and 1 ± 0.59 for 1% level) show that the biomass of Ctenophora is clumped (p >99%), salps and doliolid and medusa biomass is randomly distributed, fish biomass is overdispersed (at 95% level), and all the other groups are very overdispersed (p >99%). A similar pattern was shown by the variability of each group's percentage contribution to the total biomass; the marked lowering of the coefficient of variation of the percentage contribution by ctenophores merely reflected the large contribution this group made to the total biomass estimation. One notable feature of the

Table 1.

Biomass parameters of the tem major micronektonic groups. Biomass is expressed as mls displacement volume per 1,000m^3 water filtered, coefficient of variation (CV) is the standard deviation expressed as a percentage of the mean, and coefficient of dispersion (CD) as the variance/mean. Limits of confidence for the coefficient of dispersion for small samples are given by the formula $1 \pm \sqrt{2(n-1)}^{-1}$ i.e., 1 ± 0.295 for 24 samples. Values > 1.295 indicated a clumped distribution; values < 0.705 an overdispersed distribution.

Group	*Displacement Volumes mls/1,000m^3*				*% Contribution to total sample biomass*		
	Range	*Mean*	*CD*	*CV*	*Range*	*Mean*	*CV*
1. Ctenophora	2.12-17.66	8.04±4.55	2.57	56	10.4-56.1	29.2±11.4	39
2. Medusae	1.51-12.51	7.40±2.82	1.07	38	12.1-49.0	28.0± 8.7	31
3. Mysids	1.28-3.44	2.03±0.48	0.11	23	5.1-14.8	8.2± 2.5	30
4. Siphonophora	0.62-3.24	2.01±0.79	0.31	39	3.2-14.4	7.8± 2.9	37
5. Decapoda	0.64-2.96	1.48±0.45	0.14	30	2.5-10.2	6.0± 2.0	33
6. Fish	0.48-3.84	1.40±0.91	0.59	65	1.7-17.7	5.6± 3.8	67
7. Chaetognaths	0.48-2.01	1.30±0.38	0.11	29	2.4-8.9	5.2± 1.8	34
8. Salps & Doliolids	0-3.76	0.75±0.90	1.08	120	0-15.8	3.5± 2.9	82
9. Amphipoda	0.06-0.85	0.47±0.24	0.12	51	0.2-3.4	1.8±0.9	50
10. Euphausiids	0.07-0.68	0.37±0.16	0.07	43	0.2-3.2	1.6±0.8	50

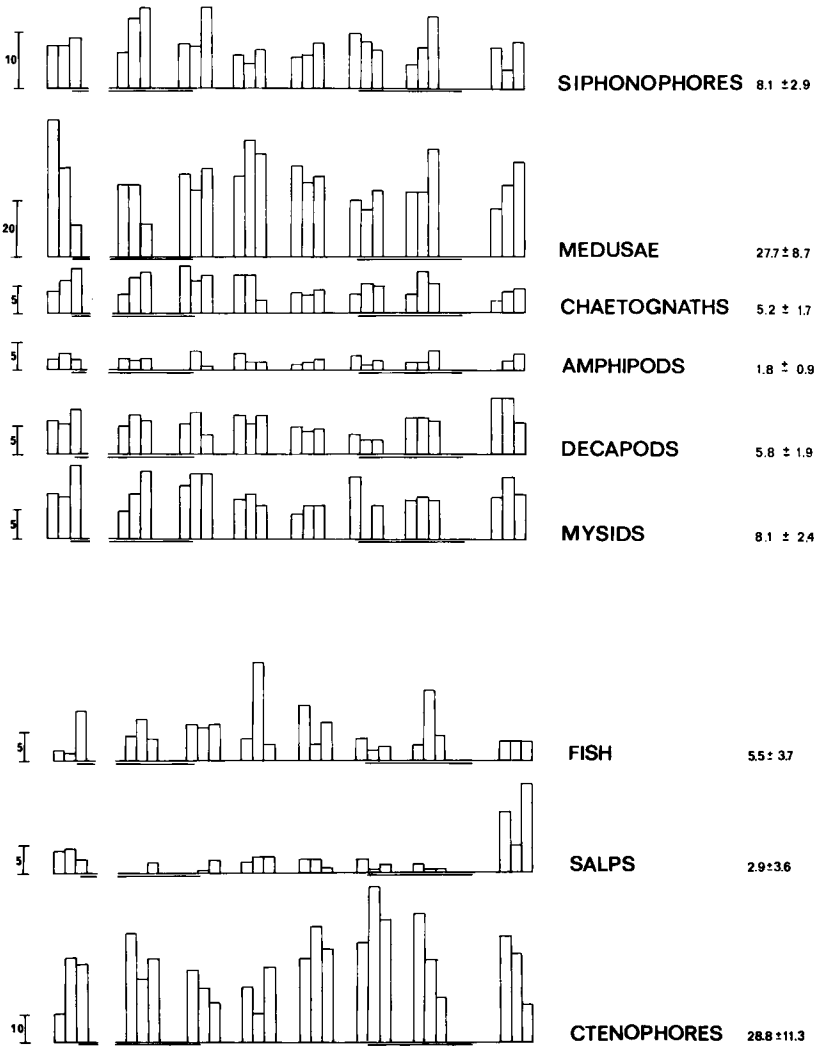

FIGURE 4. Histograms of the displacement volume of the main micronekton groups expressed as mls per 1,000m^3. The double baseline indicates nighttime. Each triad of samples represents a time scale of three hours.

data is the large contribution (68% on average) made to the total sample displacement volume of gelatinous organisms (i.e., siphonophores, medusae, ctenophores, and salps). Even this may be an underestimate, since *Beroe cucumis,* the only ctenophore in the samples, is reported to be a specialist feeder on other ctenophore species (Harbison et al., 1978). Madin and Harbison (1978) have observed, when SCUBA diving, many types of very fragile gelatinous forms that would either be mechanically fragmented by nets or disintegrate on preservation. So it seems probable that other ctenophores were present but not sampled, although no fragile ctenophores or salps were observed when the micronekton samples were examined before preservation.

The close ecological relationship between amphipods and gelatinous plankton (Thurston, 1977; Madin and Harbison, 1977; Harbison et al., 1977) suggested that there may be a close relationship between the standing crops of amphipods and those of siphonophores, medusae, and *Beroe*. Spearman rank tests were carried out comparing the rankings of the standing crops of all pairs of nektonic groups to look for evidence of any simple intergroup relationships, but there were no significant correlations, either positive or negative, between any of the pairs. So if there is a relationship between amphipod standing crop and the gelatinous organisms, either the scale or the mode of sampling was inadequate to detect it.

Specific Composition

A total of 194 species were identified from the samples. In each group for which specific identifications were made the species:specimen ratio is as follows: ctenophores (1:704), medusae (21:10,021), mysids (8:13,532), siphonophores (38:12,330 + 1,431 physonect fragments), decapod crustaceans (18:2,309), fish (56:2,084), and euphausiids (13:2,052). The only planktonic group studied was the Ostracoda, for which the ratio was 40:50,795. A full listing of the species and counts is available from the IOS Biological Data Base. Forty-nine species occurred in every sample. Thirty-five occurred only in single samples; these included not only contaminants from shallow depths, but also some species that were truly rare at the sampling depth and position. The haul counts for each of the 194 species (i.e., the number of hauls in which a species occurred) were used as the basis for the species-haul

frequency curve plotted in Figure 5. The occurrence of vertical migrants present in only day or only night samples would be expected to produce a maximum in the curve at around 8 to 12 hauls. The curve shown in Figure 5 suggests that diel migrants were not numerous at the sampling depth.

Data are presented only for micronektonic species occurring either at mean frequencies of >2½ or in more than 19 hauls, and in the planktonic ostracods in more than 19 hauls. These criteria exclude less than 5% of specimens and does not exclude any species with cyclic variability likely to have been produced by diel migration. In Table 2 the species are listed together with the number of specimens taken of each

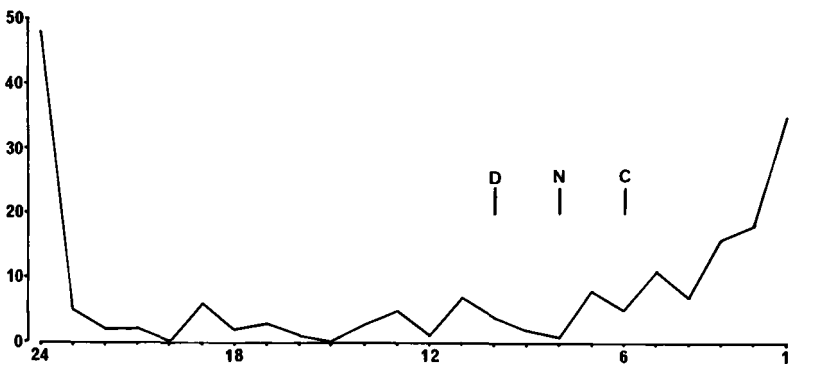

FIGURE 5. Species-haul frequency distribution for all 194 species in the 24 repeated samples. The numbers of daytime (D), nighttime (N), and crepuscular (C) hauls are indicated. Hauls were considered crepuscular if sampling occurred within an hour of sunrise or sunset.

Table 2.

List of the 55 most abundant species with the number of specimens taken and their CD values. $\underset{\sim}{O}$ = very overdispersed (1%), O = overdispersed (5%), r = random, C = clumped (5%), $\underset{\sim}{C}$ = very clumped (1%).

Fish (Figure 6)			
Cyclothone microdon (Günther, 1878)	1,352	0.81	r
Poromitra crassiceps (Günther, 1878)	136	0.74	r
Notoscopelus elongatus (Malm, 1861)	150	5.43	$\underset{\sim}{C}$

Table 2, *Cont.*

Decapod crustaceans (Figure 7)			
Gennadas elegans (Smith, 1882)	1,274	1.74	C
Acanthephyra pelagica (Risso, 1816)	575	1.17	r
Parapasiphaea sulcatifrons Smith, 1884	221	0.30	O
Mysids (Figure 8)			
Eucopia unguilculata (W.-Suhm, 1875)	9,118	2.37	C
Boreomysis microps Sars, 1883	795	1.78	C
Eucopia sculpticauda Faxon, 1893	384	1.04	r
Eucopia grimaldi Nouvel, 1942	420	3.11	C
Euphausiids (Figure 9)			
Nematobrachion boopis (Calman, 1905)	1,028	0.88	r
Bentheuphausia ambylops Sars, 1885	359	1.91	C
Thysanopoda acutifrons Holt & Tattersall, 1905	204	0.64	O
Euphausia krohnii (Brandt, 1851)	70	1.08	r
Meganyctiphanes norvegica	151	0.94	r
Medusae (Figure 10)	56	3.24	C
Aeginura grimaldi Maas, 1904	1,659		C
Pontachogon haeckeli Maas, 1893	818	2.44	C
Atolla parva Russell, 1958	612	2.24	r
Haliscera bigelowi Kramp, 1947	151	1.11	r
Aegina citrea Eschscholz, 1829	123	0.86	O
Atolla wyvillei Haeckel, 1880	131	0.56	O
Halicreas minimum Fewkes, 1882	175	0.45	O
Aglantha digitale O. F. Müller, 1776	3,585	0.41	
		43.54	C

Table 2, *Cont.*

Siphonophores (Figure 11)			
Lensia conoidea (Kefferstein & Ehlers, 1860)	4,719	51.94	C
Lensia multicrista (Moser, 1925)	1,059	1.41	C
Lensia lelouveteau Totton, 1941	102	0.10	O
Dimophyes arctica (Chun, 1897)	1,606	3.53	C
Chelphyes appendiculata (Eschscholtz, 1829)	125	0.98	r
Bassia bassensis (Quoy & Gaimard, 1934)	267	4.20	C
Clausophyes ovata (Kefferstein & Ehlers, 1860)	2,564	4.20	C
Chuniphyes multidentata Lens & van Riemsdijk	1,656	6.18	C
Ctenophore (Figure 11)			
Beroe cucumis	704	3.30	C
Ostracods (Figure 12)			
Gigantocypris muelleri Skogsberg, 1920 (RMT 8)	431	0.61	O
G. muelleri (RMT 1)	66	4.31	C
Conchoecia stigmatica Muller, 1906	20,039	32.79	C
C. daphnoides (Claus, 1890)	11,502	269.12	C
C. discoveryi Gooday, 1981	2,906	3.20	C
C. elegans Sars, 1866	2,163	5.28	C
C. lophura Muller, 1906	1,795	1.15	r
C. hyalophyllum Claus, 1890	1,727	7.91	C
C. ametra Muller, 1906	1,704	1.74	C
C. kampta Muller, 1906	1,641	3.87	C
Archiconchoecia cucullata (Brady, 1902)	1,493	6.66	C

Table 2, *Cont.*

Conchoecia pusilla Muller, 1906	653	2.08	C
C. brachyaskos Muller, 1906	687	3.08	C
C. borealis Sars, 1866	422	2.43	C
C. haddoni Brady & Norman, 1896	400	0.65	O
C. fowleri Gooday, 1981	398	1.97	C
C. curta Lubbock, 1860	386	1.25	r
C. magna Claus, 1874	308	0.50	O
C. loricata (Claus, 1894)	229	1.82	C
C. dorsotuberculata Muller, 1906	103	0.69	O
Halocypria globosa Claus, 1874	44	0.73	O
Conchoecia procera Muller, 1894	21	0.37	O
C. rhynchena Muller, 1906	48	1.37	C

species and its coefficient of dispersion. In Figures 6–12 the abundan... (in number per 10,000m^3 for the nekton and per 1,000m^3 for the ostracods) of these species are plotted against time of sampling. The standard deviations for most species were 25–50% of the means, but even so the coefficients of dispersion for all the more abundant species show they had very significantly clumped distributions. An interesting contrast is seen in the data from the two nets for the ostracod *Gigantocypris muelleri*. The RMT 1 data were highly significantly clumped, whereas the RMT 8 data were overdispersed. This may be either the result of the larger volume of water filtered by the RMT 8, or that the early juvenile stages taken by the RMT 1, but which will have passed through the meshes of the RMT 8, were clumped, whereas the adults were overdispersed. In all, 17 of the nektonic species were clumped, 10 were random, and 7 were overdispersed. For the planktonic ostracods the parallel figures were 15, 2, and 6, respectively. In both nekton and plankton the less abundant species tended to be those with random or overdispersed distributions; the notable exceptions were *Cyclothone microdon, Nematobranchion boopis,* and *Conchoecia lophura*. One of

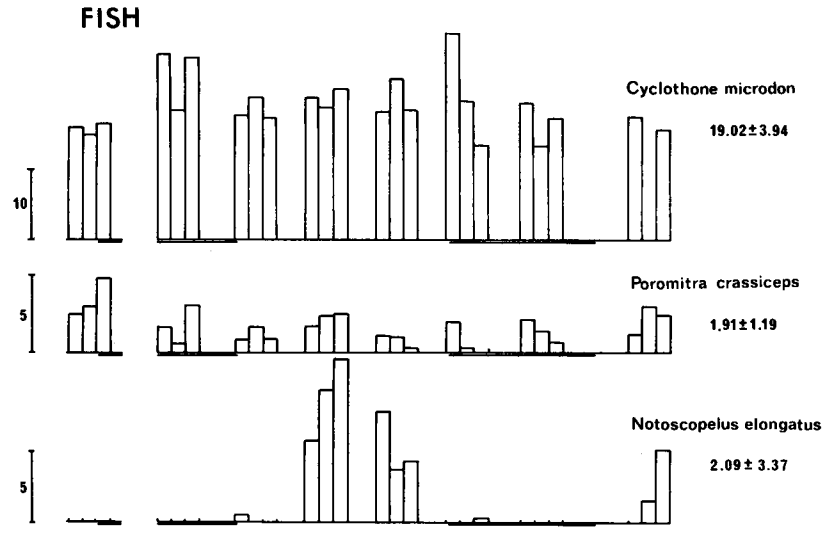

FIGURE 6. Histograms of the numerical abundance per 10,000m^3 of three fish species, together with their mean abundances. The double baseline indicates nighttime, spanning the time between sunset and sunrise.

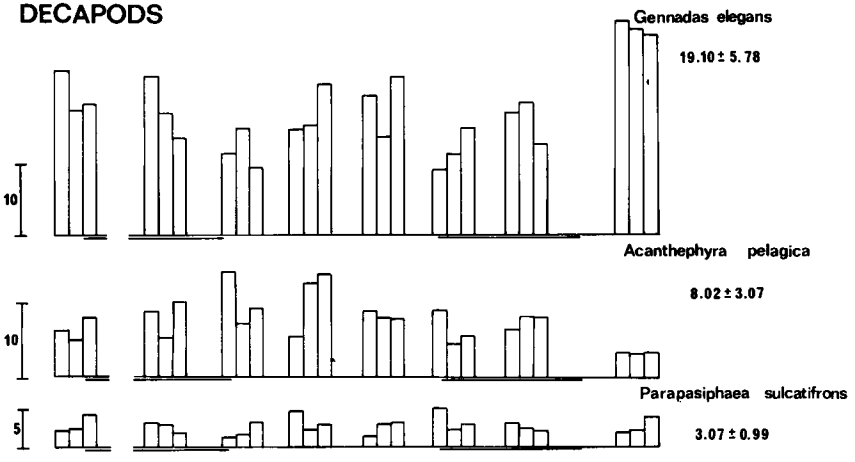

FIGURE 7. Histograms of the numerical abundance per 10,000m^3 of three decapod species, together with their mean abundances. The double baseline indicates nighttime.

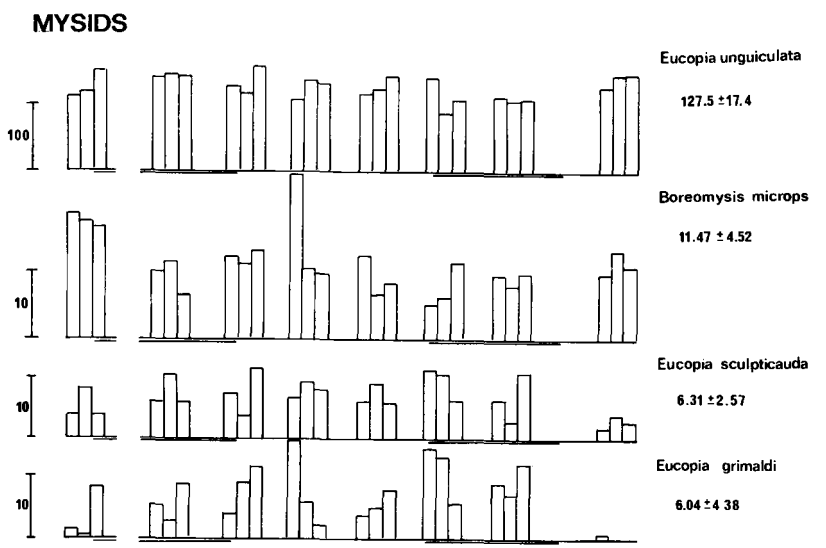

FIGURE 8. Histograms of the numerical abundance per 10,000m³ of four mysid species, together with their mean abundances. The double baseline indicates nighttime.

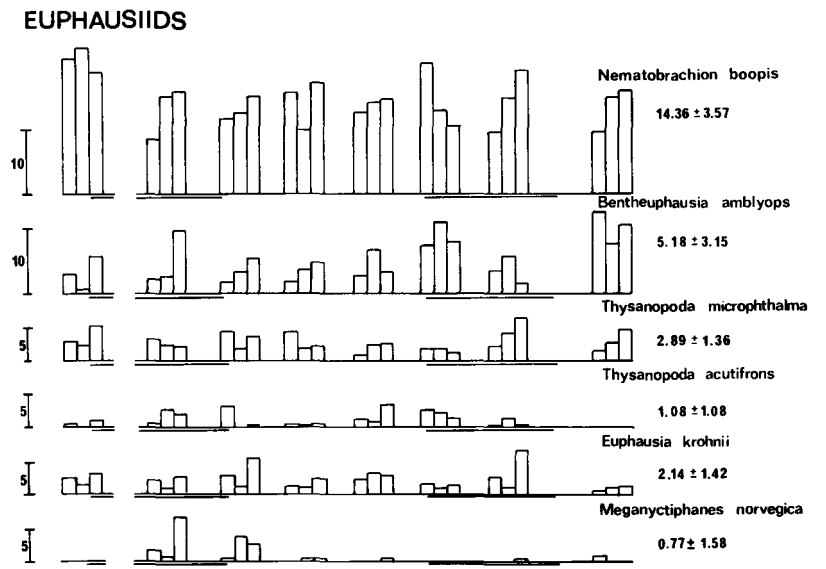

FIGURE 9. Histogram of the numerical abundance per 10,000m³ of six euphausiid species, together with their mean abundances. The double baseline indicates nighttime.

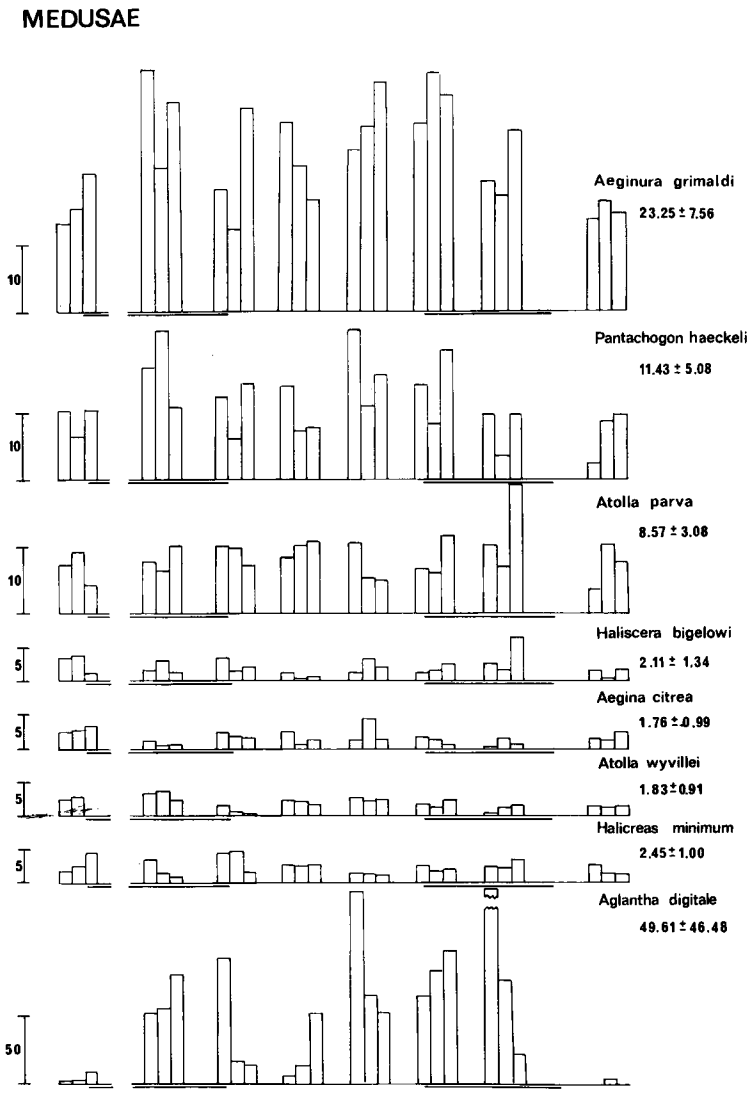

FIGURE 10. Histograms of the numerical abundance per 10,000m^3 of eight medusae species, together with their mean abundances. The double baseline indicates nighttime.

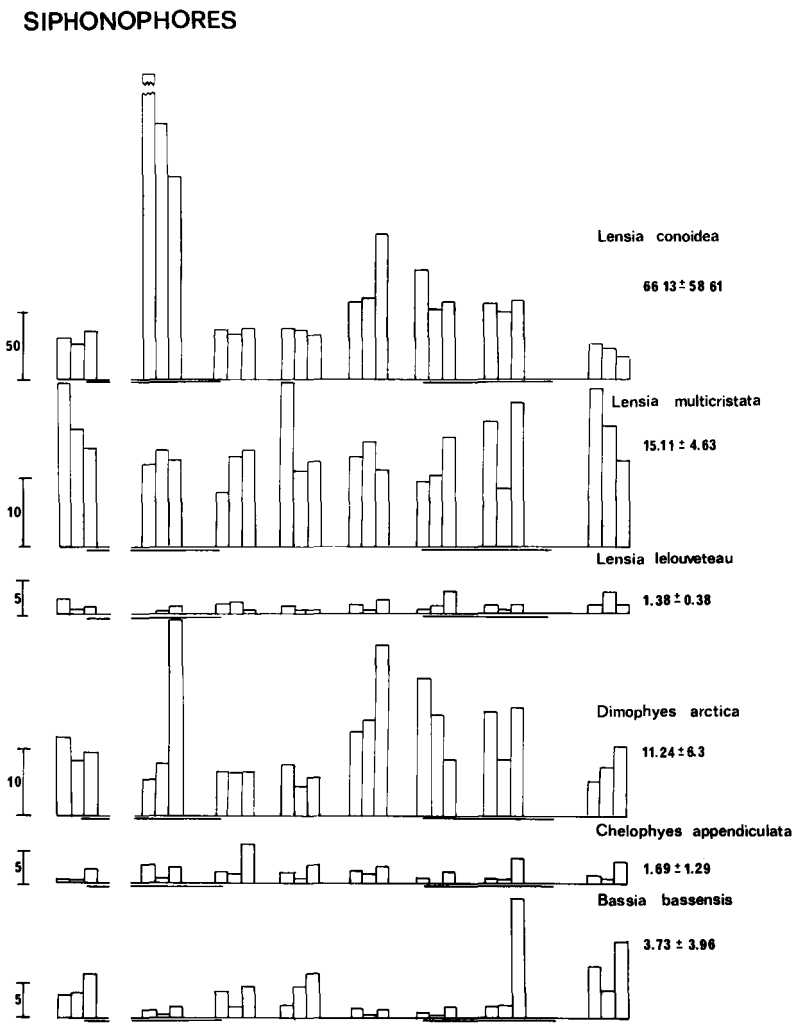

FIGURE 11. A, B. Histograms of the numerical abundance per 10,000m^3 of eight siphonophores and one ctenophore, together with their mean abundances. The double baseline indicates nighttime.

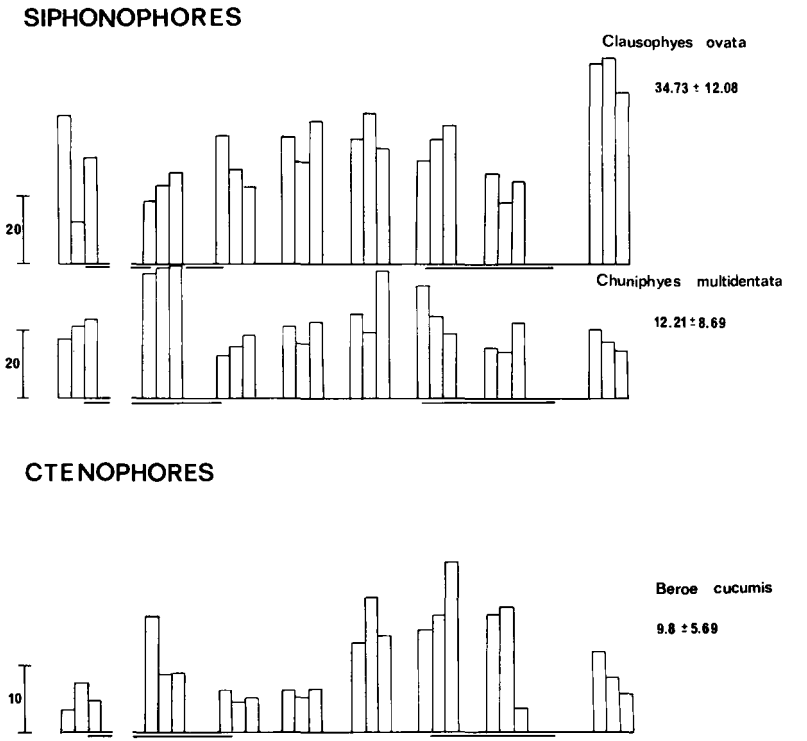

FIGURE 11.B.

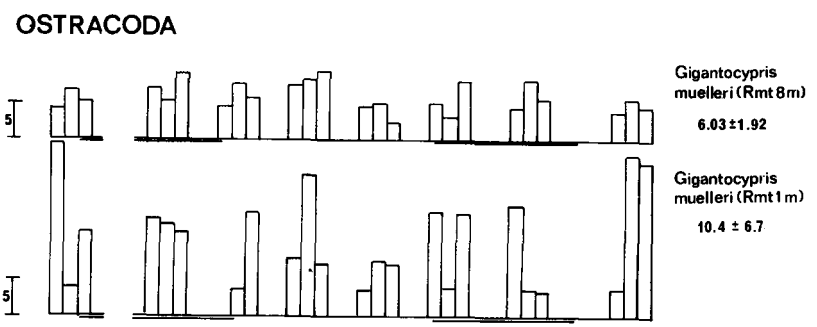

FIGURE 12. A, B, C. Histograms of the numerical abundance per 10,000m^3 of 22 species of planktonic ostracods, together with their mean abundances. The double baseline indicates nighttime. Both RMT 1 and RMT 8 data are presented for *Gigantocypris muelleri*.

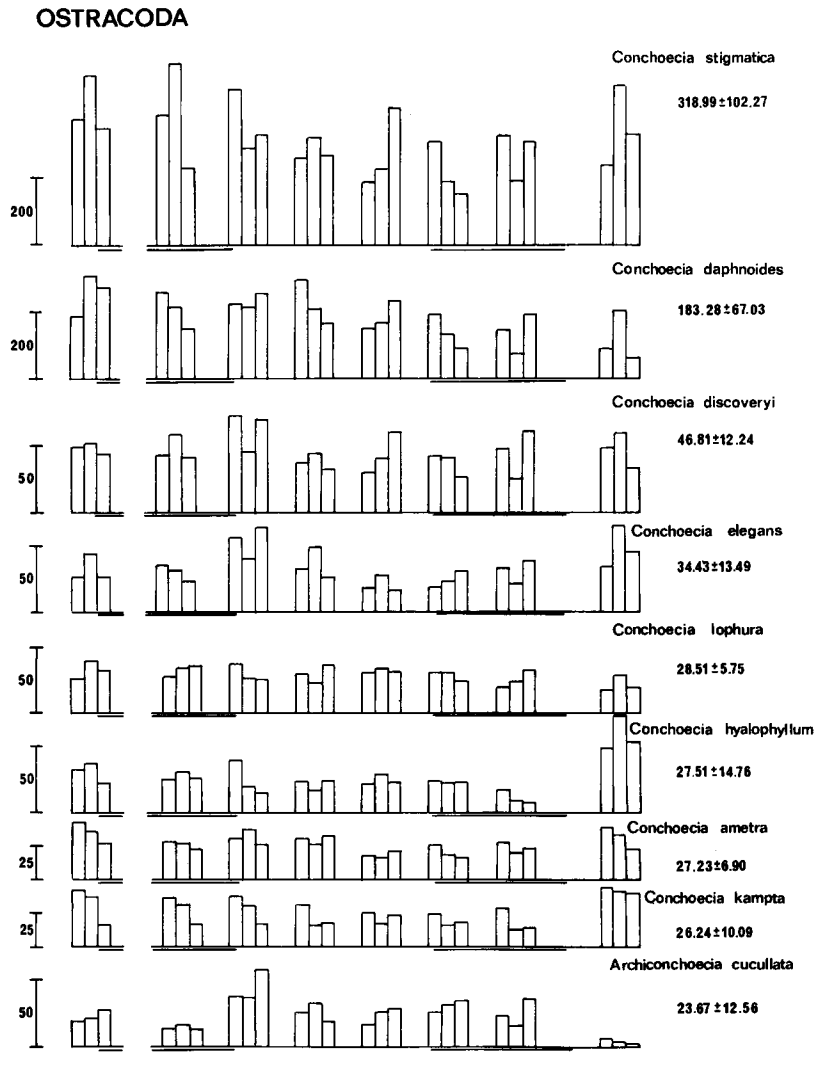
OSTRACODA
Conchoecia stigmatica
318.99±102.27
200
Conchoecia daphnoides
183.28±67.03
200
Conchoecia discoveryi
46.81±12.24
50
Conchoecia elegans
34.43±13.49
50
Conchoecia lophura
28.51±5.75
50
Conchoecia hyalophyllum
27.51±14.76
50
Conchoecia ametra
27.23±6.90
25
Conchoecia kampta
26.24±10.09
25
Archiconchoecia cucullata
23.67±12.56
50

FIGURE 12-B.

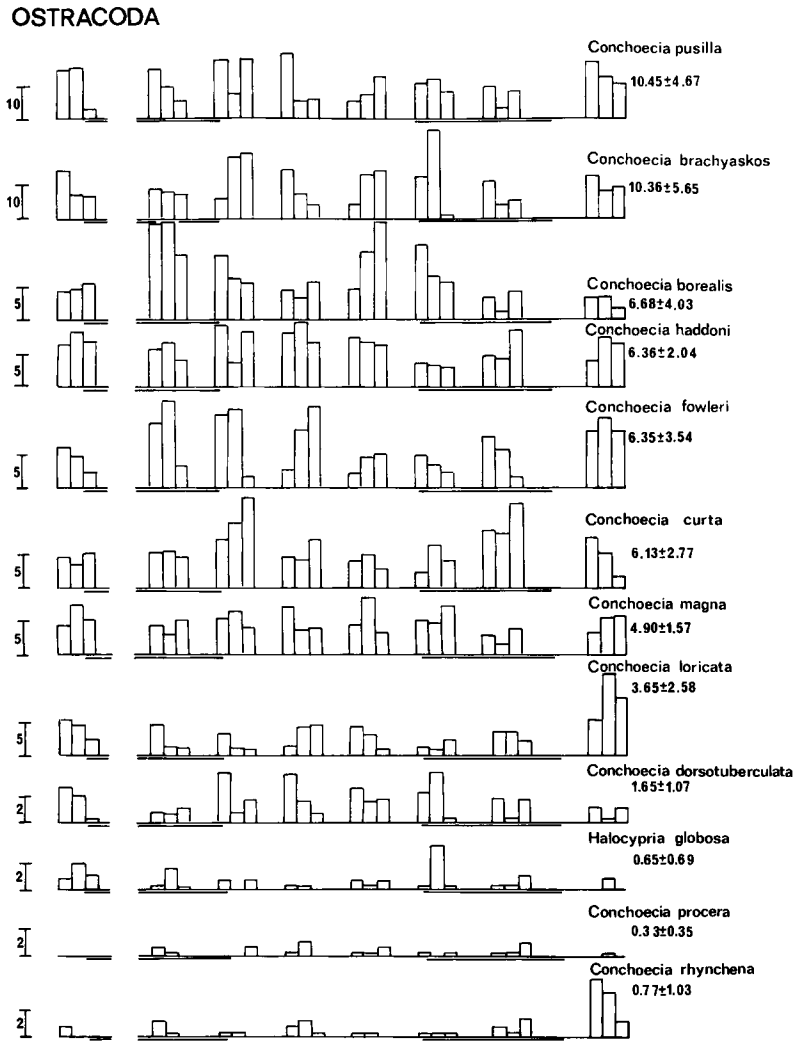
OSTRACODA
Conchoecia pusilla
10.45±4.67
Conchoecia brachyaskos
10.36±5.65
Conchoecia borealis
6.68±4.03
Conchoecia haddoni
6.36±2.04
Conchoecia fowleri
6.35±3.54
Conchoecia curta
6.13±2.77
Conchoecia magna
4.90±1.57
Conchoecia loricata
3.65±2.58
Conchoecia dorsotuberculata
1.65±1.07
Halocypria globosa
0.65±0.69
Conchoecia procera
0.33±0.35
Conchoecia rhynchena
0.77±1.03

FIGURE 12-C.

the least abundant species to show a highly significant clumping was the fish *Notoscopelus elongatus kroyeri*. It was one of only three species in which the mean abundance was exceeded by the standard deviation, and was the only species in which there was a clear and repeated day/night cycle of abundance. *Notoscopelus* started to appear in the samples about 3½h after sunset, reached its maximum abundance around midday, and then dwindled in abundance until it finally disappeared from the samples about 2–3h before sunset. This species, like many of its congeners, is known to migrate up into the upper 100m at night (Nafpaktitis et al., 1977; Badcock, personal communication).

One further possibility was investigated, that although the total abundance of a species may not have changed in a noticeably cyclic pattern, the population structure may have been changing. The size-frequency distributions of the fish *Cyclothone microdon* and of all the mysid species were measured. The ratios of adults to the various juvenile instars of all the planktonic ostracods were examined. The data for *C. microdon* are presented in Figure 13, and like the data for all the other species examined show no evidence of cyclic changes in population structure.

The data for *Parapasiphaea sulcatifrons* (Figure 7) is of particular interest because this was one of the species that Waterman et al. (1939) concluded was an active diel migrant at depths of 1,000m. Fasham and Foxton (1979) showed that the other abundant decapod species caught in these samples, *Acanthephyra pelagica* and *Gennadas valens*, are extensive vertical migrants higher in the water column. However, none of these species showed a cyclic pattern of variability at 1,000m that suggested they were performing diel migrations. The possibility that in the absence of regular cues from the light cycle the deep part of the population is vertically migrating asynchronously cannot be ruled out.

Discussion

The geographical position of the station was close to where there may be a wintertime front of considerable biological significance (Pollard, personal communication; Angel, 1979). To the north there is considerable deep mixing of the surface layers during the winter months, whereas to the south there is a permanent shallow thermocline. This is most clearly seen in Robinson et al., (1979), who give figures showing the

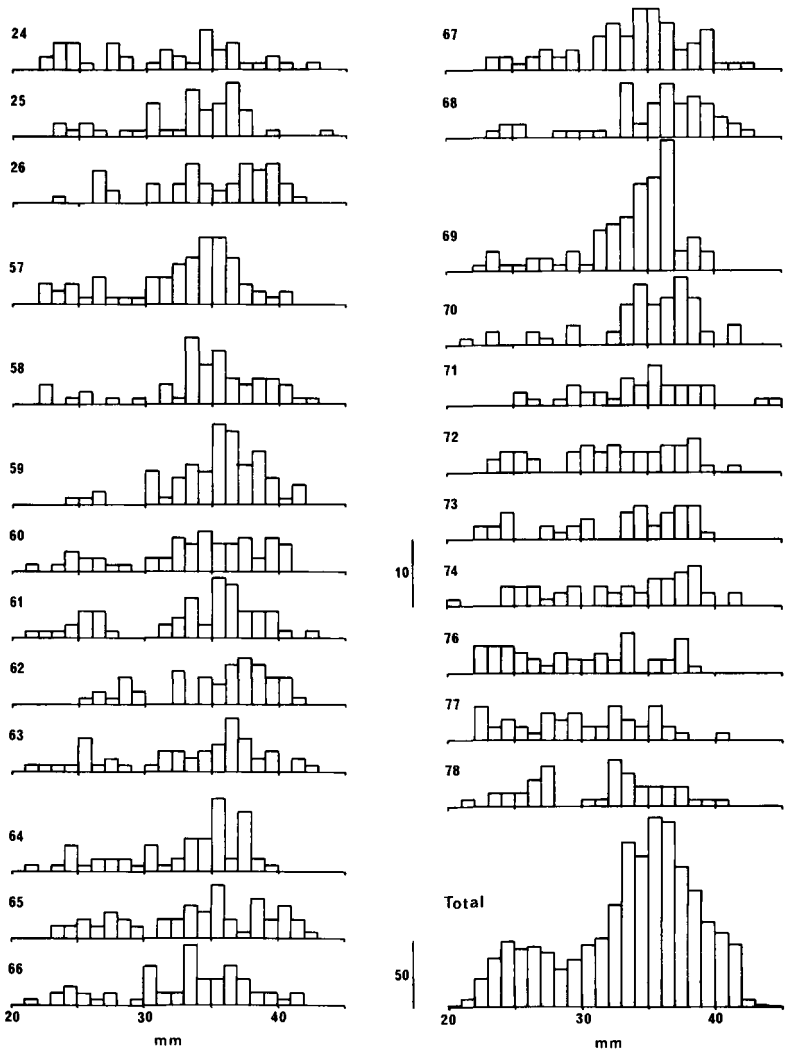

FIGURE 13. Size-frequency distribution of standard length (mm) of *Cyclothone microdon* in the 24 repeat samples together with the total size frequency distribution. The vertical scales are the same for all the individual samples (designated by haul numbers), but the scale for the pooled total data is smaller by a factor of five.

mean depths to the top of the thermocline in February and March (their Figures 28 and 42, respectively). This front may have an influence on the deep-living communities via its effect on the surface standing crop of phytoplankton, and hence the transparency of the surface layers. The sampling was carried out near the core of the lower salinity maximum associated with Gulf of Gibraltar Water which, from the T-S profiles (Figure 2), was rather "noisy." It seemed possible that this noise could be related to some of the variability of some species like the medusa *Aglantha digitale* (Figure 10).

In order to investigate whether there was any regular pattern of association between species, or if there was any pattern to the relationships between samples in their specific composition and community structure, K means cluster analyses were carried out on the data for all species that occurred in 22 or more samples. Analyses were carried out on relative abundance data, assuming the number of clusters ranged from 2 to 8. The range of correlations between hauls was so tight that it was soon clear from the analyses that the clustering was forcing pattern on the data; furthermore, the analyses failed to segregate the day and night samples. Multidimensional scaling (Fasham, 1977) of the correlation matrices both between hauls and between species failed to produce any clear pattern of species associations. Therefore, it is concluded that all the samples came from one community, and that within the community the patchiness of each constituent species was independent of the patchiness of any other and so generally unrelated to any 24h cycle. In Figure 14 the two-dimensional plot from the multidimensional scaling of the rotated species cross-product correlation matrix shows a cloud of points with a very faint hint of a linear trend. However, projection of the points in one dimension gave no sensible relationship to time of day, in situ water temperature, or geographical position.

A further check on the homogeneity of the data is by examination of species accumulation curves for the various taxonomic groups. If the species frequency distribution is log normal, a plot of the accumulated species number against the log of the accumulated number of specimens will give a straight line, the slope of which will provide an estimate of species diversity. Any community heterogeneity at the length/time scales of the samples will result in a slope change. The accumulation curves for five of the groups have been plotted in Figure 15. For three groups (decapods, siphonophores, and mysids) the plots approximate to

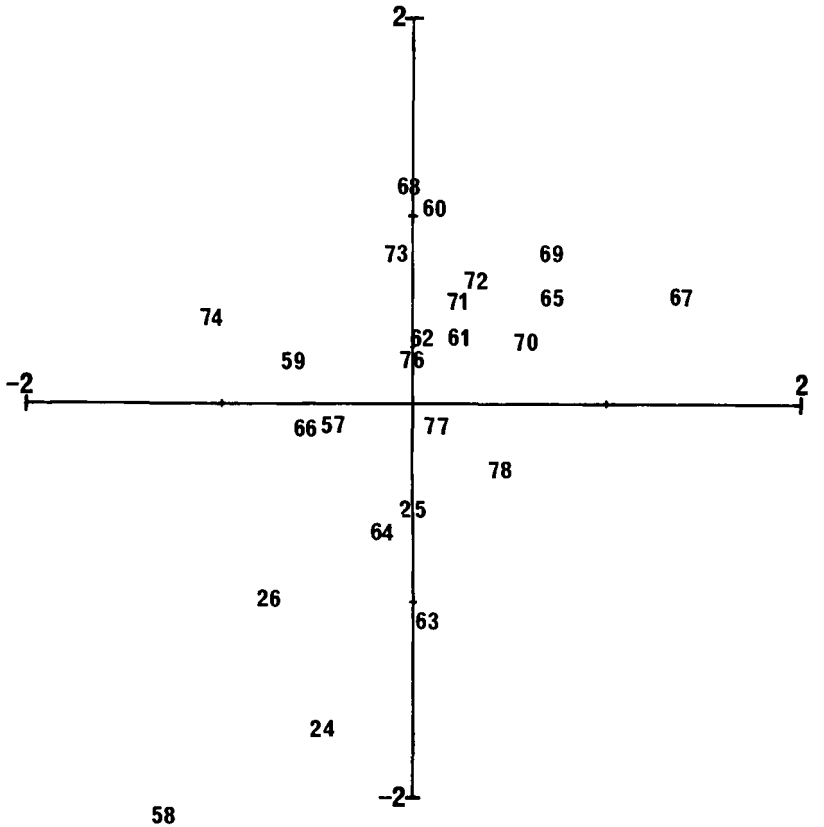

FIGURE 14. Two-dimensional configurations of the hauls resulting from the multidimensional scaling of the cross-product correlation matrix. The scales of the two axes are in arbitrary units.

straight lines in which there are no clear changes in slope related to time of day. The ostracod data suggest that once around 12,000 individuals had been sampled, the full compliment of species living in the community had been recorded. If this conclusion is correct and the community structures of mysids and siphonophores (exclusive of the physonect data) are similar,then the number of species caught probably represent the total present in the community. Physonect data were excluded from the analysis of the siphonores, because the individuals fragment into multiple replicate pieces, making it impossible to decide how many individuals were originally taken.

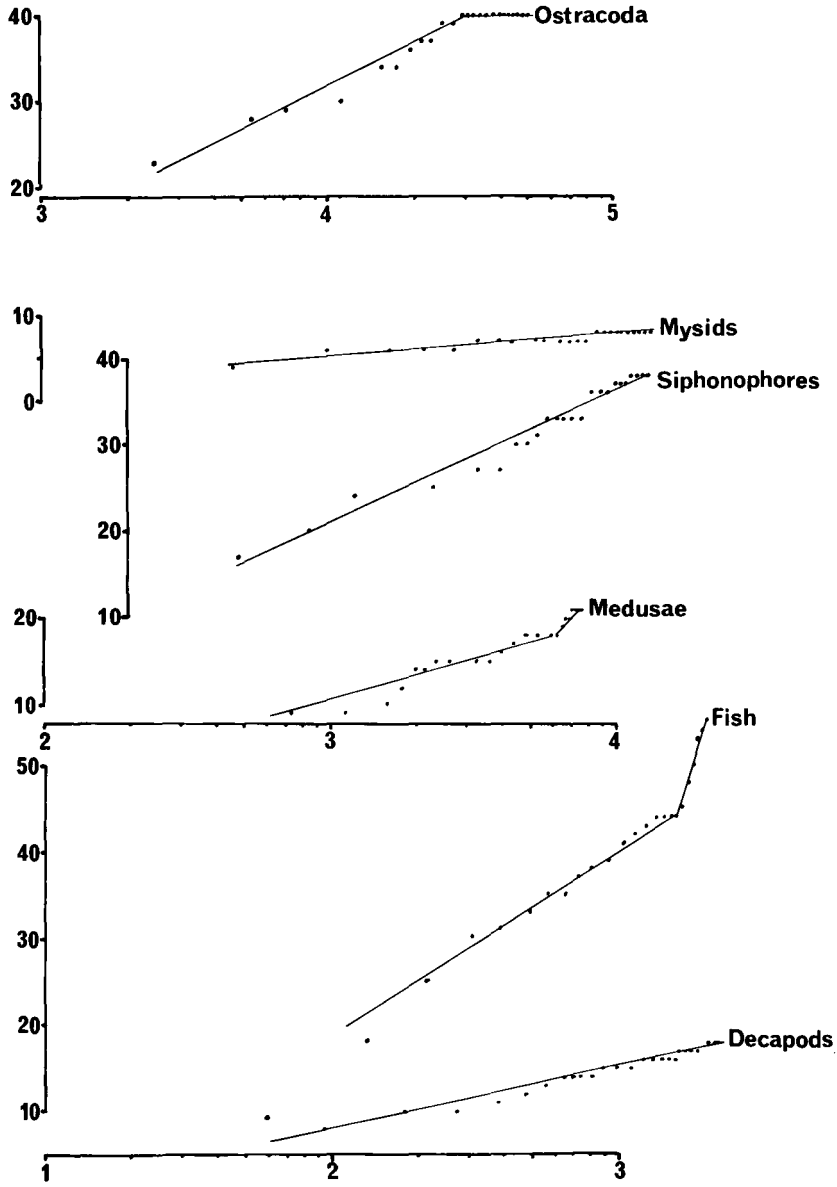

FIGURE 15. The species accumulation curves for the six taxonomic groups studied. Vertical scales are numbers of species. The horizontal scales are logarithms of accumulative sample sizes to the base of 10. The lines have been fitted by eye.

The accumulation line for the medusae oscillates quite markedly about a general trend, implying there is a poor fit to a log-normal distribution. The oscillations, however, do not have a 24h periodicity. The data fit a straight line better if it is assumed there is a slope change after the nineteenth data point, i.e., between hauls 72 and 73. A slope change after the nineteenth data point is much more clearly seen in the fish data. The change occurred between two samples of the same triad, which were collected during the middle of the night. Subjective examination of the data suggests that the change is the result of the incidence of a number of rare species in the final few samples. However, the statistical analyses show that there was no change in the community structure evident in the data for the abundant species. The average number of fish species taken per haul was 13.4, and the total species count was 56. This, together with the accumulation curve, implies that not only is a single RMT 8 sample about an order of magnitude too small to give an estimate of the species richness of the community, but also that the total water filtered ($716.10^3 m^3$) in the program was insufficient to estimate the simplest population parameters of any but the most abundant species.

Replicate sampling has been used extensively for studying sampling variability, whatever its underlying causes. Considerable effort has been expended on assessing the effects of patchiness in space on sampling error and in attempting to understand the causal factors determining spatial pattern (e.g., Cassie, 1963; Wiebe and Holland, 1968; Wiebe 1971; Fasham et al., 1974; McGowan and Hayward, 1978). These and similar studies, in which the sampling has been carried out in the top 600m of the water column, have all emphasized the clumped nature of the spatial pattern shown both at the community and at the specific level. Roe (1974) demonstrated how replicate sampling at single depths can provide useful insight into the timings of vertical migrations, and this approach has been extended by Roe et al. (in press) and Angel (in press). In the latter paper it is shown that in replicate samples from depths of 450m and 600m taken over 48h periods, the standard deviations of the abundance data for nonmigrant species or instars were less than half the means, whereas for diel migrants they were approximately equal or exceeded the means.

The scale of spatial pattern has been shown to have time characteristics similar to those of the dominant physical processes affecting the pattern (Angel, 1976; Haury et al., 1978). In these data the maximum

horizontal separation between the start and finish positions of samples was around 70km, and the minimum sampling discrimination was 3–4km (Appendix 1); the similar ranges in time scale were 1–88h. Haury et al. (1978) apportioned the amount of variability of a biological parameter, such as biomass, into the appropriate regions of space and time in the form of a Stommel Diagram. They considered that within the space/time scales of this sampling program (their coarse scale) the two major contributors to variability are diel vertical migration and swarms. In the absence of well-developed synchronized diel migratory behavior at a 1,000m, the major cause of both direct and interactive variability (e.g., patchiness produced by predation) is removed. Critical reexamination of reports by Waterman and Berry (1967) and Waterman (1974) suggests that their data, far from proving the existence of diel vertical migration at such depths, keep within the factor of 2 variability that appears to be the level of the background "noise." However, in the central gyre conditions of the central North Atlantic at latitudes of around 30°N to the southwest of the Azores, recent Discovery cruises have provided vertical profile samples that indicate that in that region diel vertical migratory activity probably extends well below 1,000m. Therefore, the possibility that the range of diel migration extends deeper in other seasons at higher latitudes also needs to be investigated.

The delimitation of the ranges of diel migration is important in the understanding and quantification of organic fluxes into the deep ocean. Diel migrants will have a potential influence on these fluxes one or two orders of magnitude larger than migrants of similar standing crop that undergo low frequency migrations with periodicities of months related to seasonal or ontogenetic movements. Thus, although the fish *Notoscopelus elongatus* only constituted about 1% of the total micronekton biomass at 1,000m by day, its influence on organic fluxes may be equivalent to or even exceed the influence of the rest of the micronekton, particularly if its gut retention time is long enough to ensure that food eaten in the relatively rich surface zone is passed out of the gut at their maximum daytime depth.

If the sampling depth of 1,000m was close to the lower limit of diel migration at this latitude, at greater depth the main source of input of organic material must be via sedimentation (Eppley and Peterson, 1979). Sediment trap experiments have suggested that the main flux of labile organic material is via faecal pellets of copepod size (Honjo and Roman, 1978; Hinga et al., 1979; Honjo, 1980). This flux is equivalent

to 1% of surface primary productivity and is sufficient to satisfy the demands of benthic respiration (Hinga et al., 1979). Angel and Baker (in press) show that, at three stations in the Northeast Atlantic, the total integrated standing crop of sampled nektonic biomass is about one third that of the plankton. In this data the nektonic standing crop is two thirds the size of the planktonic standing crop. Assuming that the physiological rates in the nektonic organisms are equivalent to the rates in planktonic organisms, then the faecal production will be proportional to the standing crop. (Heyraud (1979) showed that for large *Meganyctiphanes norvegica* the rates were lower than for small specimens, so this assumption may be wrong by a factor of 2 or 3.) The faecal pellets produced by the nekton will be much larger and rarer (by 2 to 3 orders of magnitude on the basis of the numbers of organisms producing them). They will probably sink faster (e.g., Honjo and Roman, 1978) and so have a shorter residence time in the water. This will mean there will be less time for bacterial degradation to reduce the labile organic content of the pellets or to disrupt any enclosing membrane that would be followed by the distintegration of the pellets. These pellets, like their producers, would probably be patchily distributed so that sediment traps and pump samplers, which process relatively small volumes of water, will tend to underestimate their importance. Sampling large, rare, fast-falling pellets that are patchily distributed presents a difficult sampling problem.

The deep-living populations, which rely on the detrital fall as their main source of energy, act as an inefficient sieve by catching and utilizing the rain of pellets. This sieve becomes progressively less efficient with increasing depth as the population density declines (Vinogradov, 1968; Angel and Baker, in press). Consequently, the bigger the pellet and the deeper it is produced, the greater its chance of reaching the seabed without being intercepted by a detritivore. These factors point to the potential importance of the pellet flux from nekton in the supply of organic material to the deep benthic communities. The absence of diel vertical migration at depths below 1,000m will simplify the problem of trying to model organic fluxes to the deep ocean.

Acknowledgments

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