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Life in the Benthic Boundary Layer: Connections to the Mid-Water and Sea Floor [and Discussion]

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Life in the benthic boundary layer: connections to the mid-water and sea floor

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The abyssal benthopelagic zone is enriched in biomass and numbers of species, relative to the overlying water column. It is inhabited by (i) pelagic species whose ranges are truncated by the sea bed, (ii) normally benthic species who use the zone as a refuge, for dispersal or for locating their food, (iii) a specialized fauna, which includes many novel species with primitive characteristics. The increase in the standing-crop in the zone is related to the greater availability of organic material on the sea bed, and the extent of its resuspension and diffusion from off the bottom. Several species are known to be capable of responding to both predictable and erratic pulses of input, but otherwise their physiologies seem to differ little from other pelagic and benthic species. These communities contribute a small but significant percentage of the benthic recycling.

Introduction

The general exponential decline in pelagic biomass with depth is a well-known phenomenon (Vinogradov 1972; Angel & Baker 1982), see figure 1. There are now data showing that this is also true for benthic communities (see, for example, Lampitt *et al.* 1986). This phenomenon is associated with the increasing separation of the communities from their primary source of production in the euphotic zone. Less expected is the tendency for the slope of this decline to be consistent with latitude. The mean size of the populations generating the flux increases polewards so pure stokesian sinking cannot control the fluxes to the sea bed.

The organisms inhabiting the benthic boundary layer (BBL) are termed benthopelagic, defined by Marshall (1965) as referring to those organisms 'that swim freely near the ocean floor'. Marshall & Merrett (1977) discussing the significance of the benthopelagic fish faunas, wrote 'apart from the copepods, we have no knowledge of the special zooplankton at benthopelagic levels'. Earlier submersible observations had indicated a near sea-bed enrichment: Wolff (1971) described 'an incredible number of isopods and amphipods swimming close to the bottom' at a depth of 4160 m off Madeira from the bathyscape *Archimede*. Wishner (1980*a*) first published qualitative data on benthopelagic plankton derived from nets mounted on Deep-Tow. She showed that within 100 m of the sea bed there was a sharp increase in pelagic biomass. This paper summarizes the extensive literature that has built up since then, and explores the possible reasons for this increase and their implications.

Food supply to the benthopelagic zone

The dominant source of organic material to deep abyssal environments is primary production sedimenting from the overlying euphotic zone (Angel 1984; Fowler & Knauer

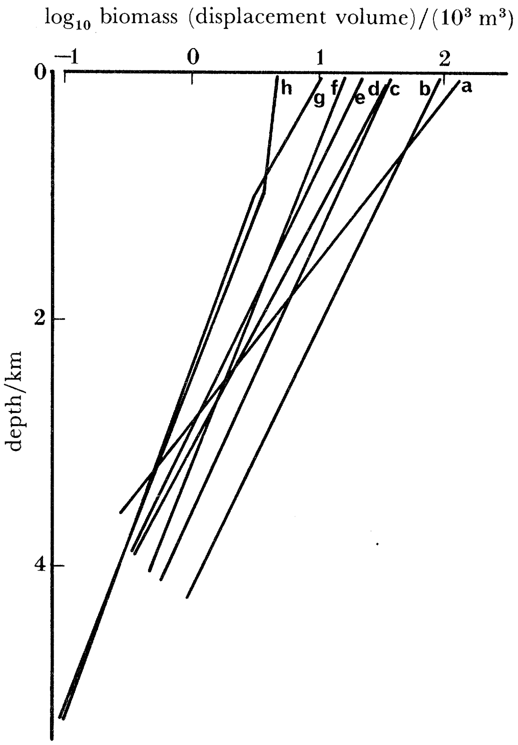

FIGURE 1. Regressions of $\log_{10}$ biomass (displacement volume) per 1000 m^3 against depth at locations in the northeast Atlantic for plankton and micronekton. a, plankton at 49° 40′ N, 13° W; b, plankton at 20° N, 21° W; c, plankton at 42° N, 17° W; d, micronekton at 42° N, 17° W; e, micronekton at 49° 40′ N, 13° W; f, plankton in the northeast Atlantic from Wishner (1980*a*); g, micronekton at 31° 20′ N, 25° 20′ W; h, micronekton at 31° 20′ N, 25° 20′ W.

1986). About 10 % of the surface production sinks from the euphotic zone as sediment (see, for example, Walsh *et al.* 1988). In addition, the diel migrations by plankton and micronekton may actively transport material either in the form of gut contents or as a result of predation (Angel 1989; Longhurst & Harrison 1989). Another export is in the form of very large carcasses; globally this input is thought to be trivial (Stockton & Delaca 1982), but locally it may be able to support up to 11 % of benthic respiration (Smith 1985). This organic input reaches abyssopelagic depths in three categories of particles: fine, medium and large.

The fine particles (less than 10 μm) sink very slowly. Those that are detrital contain mainly refractory organic compounds, but freely suspended bacteria may play a major role in determining the fluxes of organic carbon within the water column (Cho & Azam 1988). Aggregation, by incorporating fine material into marine snow (Alldredge & Silver 1986), accelerates it towards the sea bed. Even so, nepheloid layers generated in slope regions and advected over deep water (Dickson & McCave 1986) tend to be conservative features.

The medium-sized particles (10–500 μm) consisting mainly of aggregates, and faecal pellets provide the main flux of material (see, for example, Fowler & Knauer 1986). They sink fast enough to reach the bottom before all their organic content is microbially degraded, but slowly enough to be intercepted, fed upon and repackaged by the deep-living pelagic fauna, and are the main source of input for these communities. These fluxes are seasonally variable (see, for example, Deuser 1986; Billett *et al.* 1983; Lampitt 1985; Wefer *et al.* 1988), but their variability at other space and timescales is yet to be adequately described.

The larger food falls range in size from clumps of *Sargassum* and sea-grasses to whale carcasses. They occur unpredictably and are difficult to estimate qualitatively. Their occurrence will be relatively frequent in certain regions, for example beneath the migration routes of whales. The large populations of benthic scavengers (see, for example, Isaacs & Schwartzlose 1975) imply that generally these inputs are important. Rowe & Staresinic (1979) have estimated that sinking *Sargassum* weed provides up to 10% of the total input to the Sargasso Sea benthos. Salp corpses have been photographed in profusion on the sea-floor, where they influence the settlement of benthic larvae (Grassle & Morse-Porteous 1987). In some regions scavenging amphipods are so abundant that they appear to exclude all other fauna (Isaacs & Schwartzlose 1975). A corpse of a whale may overwhelm the ability of the local necrophages to consume it, and may persist for very many years (C. R. Smith, personal communication), no doubt continually leaking organic carbon in particulate (POC) and dissolved (DOC) form into the BBL. There is substantial qualitative difference between the bioavailability of the animal and plant material which reaches the bottom. Lignin and cellulose are far less labile than most animal tissues, so specialized faunas are associated with sea-grass debris (Wolff 1976) and wood (Turner 1981; Maddocks & Steineck 1987). The richness of these communities and the speed with which the material is colonized on the bottom has been a surprise.

Much of the plant debris is part of an off-shelf flux of organic material, which Walsh (1983) postulated provides a major sink for global carbon in slope 'depots'. However, along the American east coast this export is limited to less than 10% of the annual shelf primary production (Biscaye *et al.* 1988), but intense down-slope flows of turbid waters occur seasonally. On a geological scale, turbidity flows and slumps probably contribute substantially to sources of organic material at abyssal depths, but these major events are too erratic and unpredictable for biological systems to have become adapted to them.

Recently the existence of chemosynthetic activity has been recognized at hydrothermal vents (see, for example, Jannasch & Wirsen 1985), cold saline seeps (see, for example, Sibuet *et al.* 1988) and hydrocarbon seeps (see, for example, Kennicutt *et al.* 1985). These chemosynthetic sources seems to be trivial in global terms, but locally their effects can be dramatic. Methane, hydrocarbons and other DOC emitted from these point sources as plumes may prove important in enriching extensive volumes of benthic boundary water, and hence the benthopelagic communities.

The benthic interface acts as a sediment trap, accumulating all the material that sinks on to the bottom. Organic concentrations are enhanced at the interface, creating concentration gradients. The slopes of these gradients are influenced by physical processes (diffusion, turbulent mixing, plume injection and sedimentation) and biological activity (suspension-feeding, active dispersion, reproduction, etc.), and determine the characteristics of the benthopelagic fauna. Thus, species inhabiting the few tens of metres above the sea bed can exploit either the material sedimenting onto the sea-bed, or that on the interface, or that resuspended from the interface in either particulate or dissolved form.

RESUSPENSION

Resuspension processes are clearly of considerable importance to the ecology of the benthopelagic communities, as was illustrated by some of the first sediment trap data. Spencer *et al.* (1978) analysed the chemical fluxes from a trap used by Honjo (1978) at 114 metres above bed (m AB) in a sounding of 5367 m in the Sargasso Sea. 60% of the total mass flux was resuspended material; mostly in the form of faecal pellets, which contained 80% red clay. GEOSECS chemical data show clear perturbations in trace element profiles extending 1000–2000 m AB in the Sargasso Sea, probably as a result of benthic storms associated with the intense eddy activity in the region. Resuspension may result from currents, tidal oscillations (Lampitt 1985) and benthic storms (see, for example, Hollister & McCave 1984; Weatherley & Kelley 1985), or from biological activity (see, for example, Jumars & Nowell 1984). In most cases the resuspended material, being denser than the ambient seawater, will eventually resediment back on to the sea bed creating an exponential decay in available organic material above the well-mixed benthic boundary layer, and possibly within the boundary layer. However, upward fluxes occur; Smith *et al.* (1989), using inverted sediment traps at two abyssal stations in the Pacific, observed upward fluxes of buoyant particles and lipid-rich eggs and larvae, which at times were equivalent to two-thirds of the concurrently measured downwards flux. This was an attempt to validate the hypothesis first put forward by Yayanos & Nevenzel (1978) that lipids released during feeding and in the form of reproductive products, may provide a significant upward flux. Robison & Lancraft (1984) had demonstrated that the eggs of certain near-bottom, slope-dwelling fishes are buoyant, and the larvae of some abyssal, benthic molluscs are known to float up into the surface waters (see, for example, Bouchet & Waren 1985). Not all the fluxes observed by Smith *et al.* (1989) will have originated on the sea bed, for example, many pelagic euphausiids are known to lay heavy eggs that sink into deep water. After hatching, the non-feeding larval stages undertake a developmental rise (Mauchline & Fisher 1969). Intuitively it seems unlikely that any such upward flux will be *in toto* more than a small percentage of the downward flux, unless far more chemosynthetically derived organic matter is available than expected. However, these data suggest that seasonal pulses of upward flux could be unexpectedly important especially where there is seasonal reproduction (Tyler 1988).

Resuspension is not a simple function of the current régime. Time-lapse sequences have revealed a time lag between the arrival of phytodetritus on the sea bed at a depth of 4000 m in the Porcupine Seabight following the Spring bloom, and increases in turbidity associated with its resuspension resulting from tidal oscillations (Lampitt 1985). Long-term variations in nephelometer records at 2100 m depth on the continental slope in the Bay of Biscay (Vangriesheim & Khripounoff 1990), showed that the minimum light-scattering in the BBL during summer was followed by a sharp increase in late-summer–early-autumn, well after the seasonal pulse in sedimentation. Thus freshly settled aggregates appear to be resistant to resuspension, but become more susceptible on ageing.

Resuspension and sedimentation in regions where there are relatively constant currents can lead to the formation of major sedimentary features such as the mud waves described by Flood & Shor (1988) in the Argentine Basin. Benthic storm activity is expected to be most intense in those regions where mesoscale eddy activity is high, such as along the boundary zones of strong surface currents (Hollister & McCave 1984). However, in the Argentine Basin the major sedimentary drifts and mud waves occur outside the region where the strongest and most intense benthic storm activity is predicted to occur. Hollister & McCave (1984) produced a qualitative scale of erosion–deposition sea-bed features relating to intensity of the bottom current environment. Lebenspurren (the tracks and trails of benthic organisms) persist only in the more tranquil regions, where current velocities remain less than 5–10 cm s^{-1}. They defined benthic storms as periods of persistantly high currents (greater than 20 cm s^{-1}). These storms may inject nepheloid layers high into the water column, hence the relatively high suspended loads that occur at mid-depths (greater than 2000 m AB) in the northwest Atlantic. This resuspended sediment may carry with it meiofaunal species (Thistle 1988). The high numbers of harpacticoid copepods observed by Wiebe *et al.* (1988) in the vicinity of hydrothermal plumes in the Guyamas Basin may have been suspended. In regions subject to strong benthic storm activity, the meiofaunal harpacticoids, in contrast to their shallow-water counterparts, may tolerate being suspended. There have been no studies yet that attempt to quantify the importance of passive dispersion in the ecology of benthic communities.

BIOMASS PROFILES

Wishner (1980*a*) first described the increases in planktonic biomass that occur within about 100 m of the abyssal sea-bed. Similar increases in planktonic biomass have been reported at bathyal depths (Smith 1982; Ellis 1985; Wishner & Gowling 1987; Childress *et al.* 1989), at abyssal depths (Angel & Baker 1982; Smith *et al.* 1986), and associated with hydrothermal vents (Berg & Van Dover 1987; Wiebe *et al.* 1988). For nektonic biomass, increases have been recorded at bathyal depths (Hargreaves 1984, 1985) and abyssal depths (Angel & Baker 1982; Roe *et al.* 1989). The apparent absence of an increase in planktonic standing-crop at abyssal depths of 5540 m over the Madeiran Abyssal Plain in the North Atlantic (figure 2; Roe *et al.* 1989) was because beneath this highly oligotrophic region the standing crop was too tiny to distinguish clearly any doubling from the background variability. Intercomparisons of these data are difficult because of the differences in sampling methodology. Towing nets from surface vessels close to the bottom is hazardous to the gear, hence Wiebe *et al.* (1988) in a region of rugged terrain, did not dare to fish their MOCNESS closer than 80 m AB. The near-bottom echo-sounding device (Roe & Darlington 1985) used on the RMT1+8M by Roe *et al.* (1989) allowed the RMT8 to be fished within 5 m of the sea bed in an abyssal plain region with the

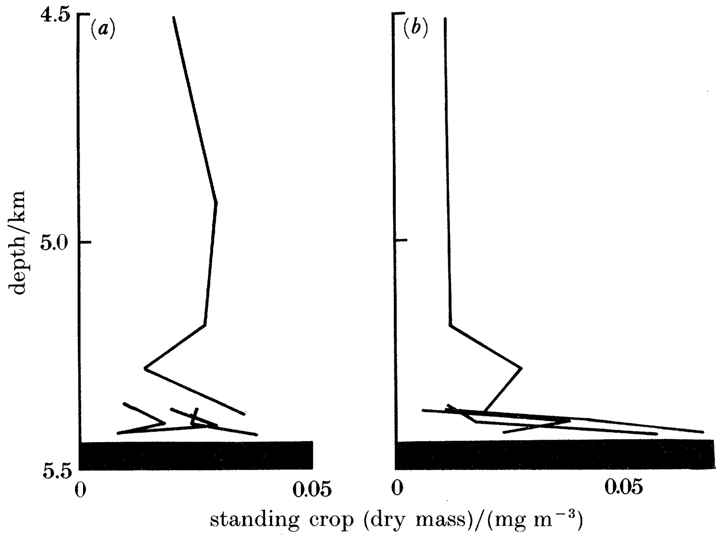

FIGURE 2. Near sea-bed profile of standing-crop mg (dry mass) m^{-3} for (*a*) plankton, and (*b*) micronekton at 31° 20′ N, 25° 20′ W on the Madeiran Abyssal Plain at a sounding of 5540 m.

macroplankton net (RMT1) about 5 m above that. Nets towed from the surface are well calibrated, filter large volumes of water, and can be towed fast enough to minimize avoidance. The nets used by Wishner (1980*a*) and by Berg & Van Dover (1987) were mounted on submersibles and could be fished with precision relative to the sea bed. However, they were of smaller mouth area, finer mesh, and were fished much more slowly. Smith *et al.* (1986) utilized yet another approach, which was to filter pumped water.

In the North Atlantic, Angel & Baker (1982) showed how both macroplankton and micronekton biomasses decline by an order of magnitude between the surface and depths of 2000 m and by a further order of magnitude by 4000 m depth. Roe *et al.* (1989) observed exactly the same change in a highly oligotrophic region (figure 1). The macroplanktonic standing crop usually exceeds that of the micronekton 5–10 fold in the top 200 m, but at depths greater than 1000 m they are generally within a factor of 2. Moreover, micronekton biomass may become the larger especially at high latitudes. It is upon this pattern that the near-bottom enhancement is superimposed, and is generally first detectable about 100 m AB and increases by a factor of 2 at 10 m AB. Smith *et al.* (1986) observed a further enhancement at 1 m AB at 1300 m depth in the Santa Catalina Basin. The plumes from hydrothermal vents may extend 100–200 m up into the water column, so Wiebe *et al.* (1988), whose sampling got no closer than 80 m AB because of the rugged terrain, were able to detect the influence of the bottom and the vent plume. The difficulties of sampling over rough terrain have prevented much being learnt about the pelagic fauna of such regions. The observations by Childress *et al.* (1989) of a marked zonation and by Wishner (1980*c*) of the heterogeneity in the distribution of acoustic scatterers, suggests that at least in some regions the profiles may provide a very simplified impression of the BBL communities.

Community composition

Table 1 shows a summary of selected data from four studies on the composition of the macroplankton at group level. Columns A, B and C were all sampled in the vicinity of hydrothermal vents. A and B were both from the Guyamas Basin, with A being sampled by MOCNESS and B by a submersible mounted net; these data highlight the difficulty of trying

Table 1. Percentage composition of near-bottom plankton

(At A, Guyamas Basin (sample 4 of Wiebe *et al.* 1988); B, Guyamas Basin (Berg & Van Dover 1987); C, east Pacific Rise (Berg & Van Dover 1987); D, Ecuador Trough (Wishner 1980*a*); E, Maury Channel (Wishner 1980*a*); F, San Diego Basin (Wishner 1980*a*); G, Madeiran Abyssal Plain (Roe *et al.* 1989).)

	A	B	C	D	E	F	G
Copepods	74.3	73.9	51.6	85.5	79.2	85.9	91.0
Ostracods	13.6	12.1	—	1.2	10.0	6.1	2.9
Chaetognaths	5.3	2.2	4.8	5.5	3.3	1.6	0.7
Polychaetes	2.7	—	0.5	0.9	1.7	1.0	0.4
Siphonophores	2.0	—	—	—	—	1.3	3.6
Medusae	0.9	—	—	—	—	—	—
Decapods	0.8	—	—	0.9	0.4	1.9	0.2
Amphipods	0.5	1.4	0.5	0.5	1.3	0.6	0.3
Isopods	—	3.4	0.2	3.2	2.5	1.2	0.5
'larvae'	—	5.0	0.2	2.3	0.4	1.0	—
molluscs	—	2.0	15.7	—	—	—	—
Larvacae	—	—	24.9	—	—	—	—
Euphausiids	—	—	—	—	—	—	0.4
fish	—	—	—	—	—	—	0.2

to compare the results obtained using different methods. There are striking similarities, the dominance of copepods, the subdominance of the ostracods, and the consistency of chaetognaths, polychaetes, amphipods and isopods. The extreme fragility of some groups in addition to the gelatinous groups, can cause sampling problems. Even species of normally robust taxa such as decapods and mysids (not featured in the table) are often extremely delicate from these depths.

Another notable feature of planktonic samples from great depths is the very high proportion of half-degraded corpses and exoskeletons of copepods that occur. Wishner (1980*b*) recorded 60–88 % of the copepods in her samples were probably dead before collection. Wiebe *et al.* (1988) only found 10–31 % were corpses and suggested that Wishner's data were the result of net damage. There was a similar high proportion of corpses in the Discovery material from the Madeiran Abyssal Plain. In the sample quoted in table 2, there were 494 carcasses of copepods compared with 94 that were clearly live when sampled, a ratio of 5.3:1, dead to live. H. S. J. Roe (personal communication) kept some deep-living copepods unpreserved in the laboratory at room temperature and it was at least five days before the specimens looked as decomposed as the carcasses taken at depth. Even in midwater there have been reports of large numbers of carcasses, and it seems unlikely they can all be attributed to net damage.

These benthopelagic communities are very rich in species, although only few are usually dominant (Wiebe *et al.* 1988). Wishner (1980*b*) recorded 117 species from three widely separated geographical locations (San Diego Trough, Ecuador Trench region and the northeastern Atlantic). These included representatives of 17 families and 35 genera. However, 50 of the species were represented by single specimens. Wiebe *et al.* (1988) also recorded a very high species richness in the Guyamas Basin. Half of the 67 species that they collected were previously unknown, but only five or six exceeded abundances of 100 per 1000 m^3.

Boxshall (1983), when describing four new genera of misiophorioid copepods taken in a benthopelagic sample from a depth of 3000 m near the Azores, pointed out that the species and genera demonstrate many plesiomorphic characters and strongly resembled the hypothetical ancestral type of copepod. This trend is also seen in other groups such as the chaetognaths (Casanova 1986); the primitive genus *Heterokrohnia* is proving to be diverse in abyssal benthopelagic samples from Discovery Collections (see, for example, Casanova & Chidgey 1987).

Angel (1983*b*) noted that the total fauna of pelagic ostracods taken 10 m AB at a depth of 4000 m at 20° N 21° W were then novel; a sample taken at 3000 m contained 12 species, but the BBL samples from 1000 m deeper contained 25. Several of these species occurred within the water column, and so could be regarded as abyssopelagic species. However, at least 15 only occurred within the BBL. One genus in particular, *Bathyconchoecia*, is strongly associated with this zone (Ellis 1989), and has several primitive features.

Numerical dominance does not always mean gravimetric dominance. Wiebe *et al.* (1988) found that, whereas copepods were dominant both numerically and in terms of biomass, medusae and decapod crustaceans contributed relatively large percentages of the standing-crop, although being few in number. Table 2 shows the comparison between the catches of samplers with different mesh sizes (320 μm and 4.5 mm) and mouth areas (1 and 8 m^2) fished simultaneously at 11–31 m AB over the Madeiran Abyssal Plain at a sounding of 5540 m. The fauna caught with the larger sampler with bigger mesh size, which are the larger more mobile species – decapod crustaceans, fish, medusae and amphipods – have a total biomass higher than that of the total planktonic biomass (figure 2).

Table 2. Comparison of abundances (numbers 1000 m^{-3}) of macroplankton and micronekton groups sampled simultaneously at 11–31 m ab over a sounding of 5540 m on the Madeiran Abyssal Plain (Roe *et al.* 1987)

(Discovery station 11261 no. 65)

	macroplankton	micronekton
Copepods	133.8	—
Ostracods	4.2	—
Chaetognaths	1.0	0.07
Polychaetes	0.6	—
Siphonophores	5.3	0.22
Medusae	—	0.07
Decapods	0.2	0.09
Amphipods	0.4	0.05
Isopods	0.8	—
Euphausiids	0.6	—
fish	0.2	0.09

MADEIRAN ABYSSAL PLAIN DATA

The full results for the Madeiran Abyssal Plain study are only available in a report. Roe *et al.* (1990) have presented the major findings of more general interest, so here just some of the data of the nektonic groups pertaining to the benthopelagic samples will be considered. Three sets of samples were taken each sub-dividing the 100 m ab zone approximately into three horizons: 100–50, 50–25 and 25–10 m ab.

Twelve species of amphipods were taken in the deep midwater, benthopelagic and benthic samples. Three of these were eusiroid species belonging to genera (*Cleonardo* sp., *Eusirus* sp., *Rhachotropis* sp.), which are ubiquitous in the deep ocean, usually as long-legged epibenthic fauna. All the other nine species were lysianassoids; most are necrophages, *Eurythenes gryllus*, *Orchomene gerulicorbis*, *Paralicella caparesca* and *P. tenuipes*. These amphipods rapidly appear at baited cameras (Shulenberger & Hessler 1974; Hessler *et al.* 1978; Thurston 1979). They are most abundant in the bottom mixed layer (Ingram & Hessler 1983), but some take extensive excursions up into the overlying water column (see, for example, Smith & Baldwin 1984; Thurston 1990), and even turn up in seabird stomach contents (Barnard & Ingram 1986).

Decapod crustaceans are frequently seen in the bbl from submersibles and in photographic transects. Q. Huggett (personal communication) has recorded one large decapod per 1900 m^2 in a survey covering over 90000 m^2 in the Meteor Abyssal Plain region and one per 2500 m^2 in a 80000 m^2 survey in the Kings Trough region (cf. figure 3). They are seldom taken in large numbers either in plankton nets or benthic samplers, because of their ability to avoid and their sparse abundances (usually 1–2 per 1000 m^3). Domanski (1986) described a four-fold increase in decapod abundance within 100 m ab at a depth of 4040 m in the Kings Trough region (41° 30′ N, 30° W) (figure 3), as did Hargreaves at bathyal depths southwest of Ireland. However, there were faunistic differences: the decapods Hargreaves recorded were all normally mesopelagic species (one had extended its vertical range significantly deeper in the region of the slope), whereas Domanski found several which are predominantly benthopelagic. At both the Kings Trough site and over the Madeiran Abyssal Plain, the carids *Hymenodora glacialis* and *H. acanthitelsonis* were taken in both the deep pelagic and benthopelagic tows. Their gut contents were devoid of sediment, so Domanski concluded that they are truely pelagic

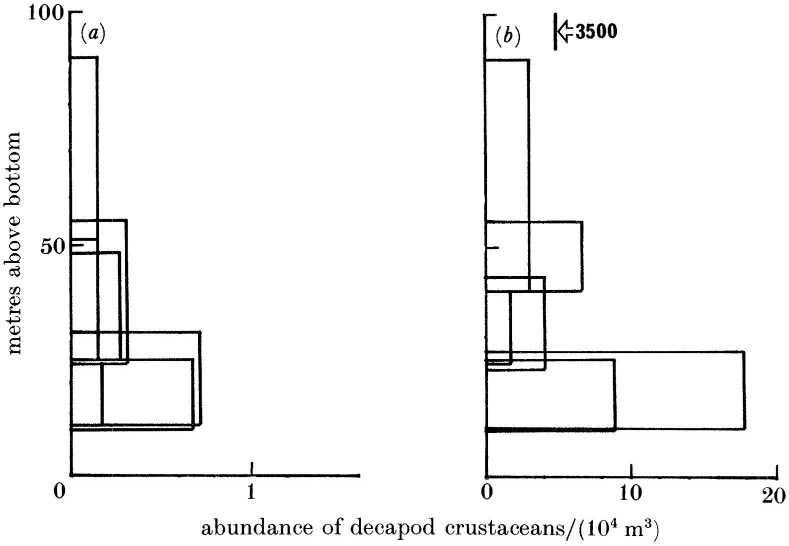

FIGURE 3. Abundances of decapod crustaceans (numbers per 10^4 m^3) in the benthic boundary layer at (*a*) Madeiran Abyssal Plain (31° 20′ N, 25° 20′ W; sounding 5540 m) and (*b*) Kings Trough region (41° 30′ N, 30° W; sounding 4040 m) with the mean abundance from 15 repeated tows at 3500 m (Domanski 1986).

species whose ranges were truncated by the sea-bed. Specimens of *Acanthephyra microphthalma*, which were taken both in pelagic and benthic samples, had sediment in their guts and so were facultative benthopelagic species. Two of the four penaeids species taken over the Madeiran Abyssal Plain were caught only in benthic gear. The other two, both of which were *Benthesicymus* species, were also taken benthopelagically.

All the fishes taken near and on the bottom were predominantly benthic in habit. In midwater below a depth of 2700 m, the fish fauna was limited to just two pelagic species, *Monognathus* sp. and *Neocyema erythrosoma*. However, in the benthic samples (five trawls and four sledges) there were 188 specimens of 18 species. 78% of the specimens belonged to just three species, *Bathymicrops regis*, *Bathypterois longipes* and *Echinomacrurus mollis*, all bottom feeders. So in this highly oligotrophic region there were few if any necrophagous fishes in contrast to slope regions where demersal fishes feed, either exclusively in the overlying water column (these tend to have anterior mouths) or both on the bottom and in the water column (these tend to have inferior mouths) (Marshall & Merrett 1977). Analysis of the stomach contents of such bathyal species show that mesopelagic prey is extensively taken. Rat-tailed fishes such as *Coryphaenoides rupestris* have been caught 270–1440 m AB feeding in midwater (Haedrich 1974). Normally benthic fishes do occasionally get caught high up in the water column; for example, Angel (1983*a*) reported a juvenile *Bathypterois* at a depth of 100 m over a sounding of 3300 m. These upward migrations must be infrequent, as Forster (1971) when long-lining rarely caught squaloids and teleosts more than a few tens of metres above the bottom. This relatively high concentration of predators within the BBL may result in the overlying water column being used as a refuge.

There are several other taxonomic groups that have species which seem to be specialized to the benthopelagic environment. Pugh (1983) described the rhodalid siphonophores, which occur within the BBL both in the vicinity of vents and in slope regions. The appearance of cirrate octopods in sea-bed photographs (Roper & Brundage 1972) shows that they live in very close proximity to the sea bed. Childress *et al.* (1990) describe two large mysids (*Boreomysis scyphops* and *Gnathophausia* nov.sp.) as occurring only in the BBL of the Californian Basins. The advent of submersible observations provided the first evidence of how important pelagic holothurians are in certain regions, which has subsequently been confirmed by more classical sampling techniques (Barnes *et al.* 1976; Billett *et al.* 1983; Childress *et al.* 1990). However, the relation between these organisms and the sediment interface may vary, *Enypniastes* feeds extensively on the interface, whereas *Scotoanassa* despite inhabiting the 20 m AB zone never seems to come in contact with the sediment, a behaviour that might not be possible to maintain in a region with high currents.

METABOLIC ACTIVITY IN THE BBL

Williams *et al.* (1980) described increases of 20% in dissolved organic carbon (DOC) and 10% in dissolved organic nitrogen (DON) within 20 m AB at depths greater than 5680 m in the Pacific, but found no changes in adenosine triphosphate (ATP) or dissolved organic phosphate (DOP). Bacterial counts showed no change from the concentrations of $10^7\ \mathrm{dm}^{-3}$, which prevailed throughout the water column below depths of 1000 m. Consequently, they considered the increases described by Holm-Hansen *et al.* (1966) to have resulted from contamination. They interpreted the lack of any increase in bacterial abundance corresponding with the increases in DOC and DON as indicating that dissolved organic material (DOM) was being released from the old organic material in the sediments. A finding which is not in accord with the interpretation of ^{14}C data by Williams *et al.* (1987). Karl *et al.* (1976) were able to demonstrate an enrichment of ATP in the BBL – an indicator of microbial biomass – confirming that at least at bathyal depths there are increases in microbial concentrations in the BBL.

Direct measurements of planktonic and microbial BBL respiration have been conducted by Smith (1982) and Smith *et al.* (1986) using a slurp gun respirometer mounted on a submersible. In the first study at bathyal depths (1300 m) in the Santa Catalina Basin, where surface productivity was around 140 mg (C) $\mathrm{m}^{-2}\ \mathrm{a}^{-1}$, there was a 4–5 fold increase in macroplankton biomass between 50 and 1 m AB. The weight specific oxygen consumption of 1.44–2.19 μl (O_2) mg (dry mass) d^{-1} (plus one anomalous result of 3.16) showed no change across the BBL. However, nitrogen excretion in a very limited data set showed a five-fold increase between 50 and 1 m AB, to a maximum of 35.9 nM (NH_4) mg^{-1} (dry mass) d^{-1}. Smith (1982) estimated that the integrated respiration of the BBL was about 1500 μl (O_2) $\mathrm{m}^{-2}\ \mathrm{d}^{-1}$, which was equivalent to about 3% of the sediment respiration and 0.24% of the surface productivity.

In the later study in the Panama Basin (Smith *et al.* 1986) the BBL planktonic respiration at a depth of 3850 m was estimated to be 11 μl (O_2) $\mathrm{m}^{-2}\ \mathrm{d}^{-1}$ h, equivalent to 0.05 mg (C) $\mathrm{m}^{-2}\ \mathrm{d}^{-1}$. They also measured the respiration of the suspended bacteria to be equivalent to 0.30 mg (C) $\mathrm{m}^{-2}\ \mathrm{d}^{-1}$, accounting for 3% of the POC flux. When they added, in their estimate for the carbon utilization rate of the bacteria, the total combined utilization by the planktonic and microbial communities accounted for 11% of the POC flux.

Childress *et al.* (1989) have recently presented further data on biomass profiles and oxygen consumption in the Californian Basins. They found that the BBL was dominated by gelatinous organisms and that there was a striking zonation. Closest to the sea bed but apparently never feeding on the interface were dense concentrations of the pelagic holothurian *Scotoanassa*, which

1 m AB sometimes reached densities equivalent to greater than 500 mg (wet mass) m^{-3}. Its zone of abundance extended to 20 m AB. At 50–100 m AB there was a zone dominated by the narcomedusan *Solmaris* sp., which at 50 m AB reached densities of greater than 250 mg (wet mass) m^{-3}. The other pelagic groups totalled only 2.1–7.9 mg (wet mass) m^{-3} and showed a minimum in the zone where the narcomedusan was most abundant. In terms of carbon, however, the gelatinous and other plankton were similar in standing-crop. *Scotoanassa* had a remarkably low weight specific oxygen consumption of 0.0009 μl O_2 mg^{-1} (wet mass) h^{-1}, whereas the crustaceans showed similar oxygen consumption rates to other bathypelagic species: the large species used 0.024–0.029 μl (O_2) mg^{-1} (wet mass) h^{-1}, but the equivalent rate for copepods was 0.067. Childress *et al.* (1990) suggest that *Scotoanassa* is adapted to being an opportunist species able to respond to seasonal and other major oceanographic events. They found large differences between the pelagic communities of the different basins making generalizations difficult.

Wishner & Gowing (1987) have attempted to measure *in situ* rates of filtration and ingestion of BBL zooplankton, again at 1300 m AB in the Santa Catalina Basin, using a short-term radioisotope incorporation technique. The median rate for weight-specific filtration was 12.4 ml mg^{-1} (dry mass) h^{-1}. These were similar to rates for wintertime plankton in shallow water in Narragansett Bay and for bathypelagic plankton from depths of 2175 m in the North Atlantic. Gowing & Wishner (1986) had already shown that the copepods that were dominant in the communities, were predominantly detritivores ingesting suspended particles, large faecal pellets, particles from off the sediment–water interface and phaeodia of certain radiolarians. They found no evidence of the copepods having attached enteric bacteria, but they did find evidence of the presence of metal-precipitating bacteria in some species. The ingestion rates ranged very widely from 0–61.7 μg (C) mg^{-1} (wet mass) h^{-1}, which the authors interpreted as indicating the ability of copepods to switch activity on and off: a useful adaptation in an environment in which the food supply is to patchy in both time and space (Wishner & Meise-Munns 1984).

Feeding rates can also be extremely high in necrophagous amphipods. Hargrave (1985) used photographic sequences to measure the rate of disappearance of 100 g baits deployed at depths of 5840 m on the Nares Abyssal Plain. The average residence time of the amphipods on the bait was 30 ± 10 minutes, during which each amphipod ate at a rate of 1.8 g h^{-1}. At each visit an animal would ingest about 30–60 % of its body weight before moving away. A single such feed would support each animal's basic metabolism for 3–5 months, but they must feed more frequently than this if they are to breed and to locate further food-falls. Smith (1985) described how gorged amphipods will 'roost' away from food-falls and then return to feed again after some time. Laver *et al.* (1985) have shown that the swimming rates of the amphipods is 7.3 ± 3.7 m^{-1}, when they are in the vicinity of baits. Relating such swimming speeds to currents near the sea bed, there must be an optimum current speed which enables the amphipods to scan the maximum area of sea-floor for food-falls. If the currents are lower, then the search may be too efficient, but if the velocity exceeds the swimming ability of the animals they will not be able to reach food up current. Hence, it is not surprising that Lampitt *et al.* (1983) found that the arrival of small amphipods (*Paralicella* sp. and *Orchomene* sp.) on baits was related to the tidal cycle when current velocities were 4–5 cm s^{-1}. The larger species (*Eurythenes gryllus*) did not show arrival times related to the cycle of tidal currents possibly because the maximum current recorded was 6 cm s^{-1} within the swimming capability of these larger animals. They also found that a fish (*Paraliparis bathybius*), which fed specifically on amphipods, attended when both the tidal currents were at their maximum and the numbers of amphipods on the bait were at their highest. Such observations together with those of Childress *et al.* (1990) suggest that behavioural responses of the organisms in the BBL play an important role in the way the communities function.

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Discussion

G. A. Boxshall (*British Museum* (*Natural History*), *U.K.*). At slope depths of 1–2 km the fauna of the benthic bottom layer has a large component of mesopelagic species, whereas the fauna at abyssal depths has a high proportion of novel forms. Can Dr Angel suggest at what depth the transition between the two takes place and what factors determine this depth?

M. V. Angel. Sampling in the northeastern Atlantic suggests that the benthopelagic fauna is 'well known' at 1650 m, but largely 'novel' at 4000 m. To some extent this is a function of the discrepancy in sampling effort expended, but it probably also reflects an ecological reality. Rex (1983) showed that, for a wide variety of benthic taxa, the maximum species richness occurs at 2000–3000 m, depths where Lampitt *et al.* (1986) showed that the standing crop has declined to less than 10% of that occurring at the shelf-break. Empirically, species richness is correlated positively with long-term environmental stability and predictability, productivity, trophic level, abundance and ecosystem area and complexity (see, for example, Pimm 1984). In benthopelagic environments, most of these factors are positively correlated with increasing depth, but availability of food in particular decreases with increasing depth. In shelf seas there is an intimate relation between the benthic and the pelagic communities, but with increasing depth down the slope the influence of benthic processes on the surface pelagic system becomes progressively more tenuous. I suggest that it is when this influence becomes insignificant that the maximum faunistic change in the benthopelagic communities will occur. I also expect that the depth at which this occurs will show extensive variation geographically.

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