# Oceanic pelagic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region

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ABSTRACT: The availability of oceanic plankton and micronekton to the benthopelagic fish assemblages on the slopes of the Rockall Trough, a marginal region of the northeast Atlantic deep-sea environment, is examined. The vertical distribution of pelagic species predated by the fish was determined in the off-slope water column, as were the depths at which they are predated by the fish in the benthic boundary layer of the slope. The benthopelagic fish predated pelagic species at depths on the slope corresponding to the daytime depths of the pelagic prey. The occurrence of these pelagic species at the benthic boundary layer is primarily through truncation of their pelagic vertical distributions rather than horizontal impingement, although this does occur: this applies not only to epi- and mesopelagic but also to the bathypelagic species which can even reach abyssal sediments. Diel vertical migration of the pelagic species did not make them available to slope fishes in shallower depths presumably because vertical migration is strictly upwards within the pelagic water column and not up the contours of the slope sediment.

## INTRODUCTION

The associations of organisms living immediately above the sea bed are referred to as suprabenthic (Brunel 1979, Kaartvedt 1989), hyperbenthic (Anger & Valentin 1976, Hesthagen & Gjermundsen 1978), or hypoplanktonic (Mauchline 1972) in coastal and shelf regions. These associations contain endemic species resident in the near-bottom environment, species derived from downward extensions, often seasonal in nature, of pelagic planktonic populations, as well as infaunal species emerging into the water column, often on diel cycles. The top-level predators in these systems are, of course, the demersal fish associations.

Analogous associations are now known to inhabit the near-bottom environment of the deep-sea where they are usually referred to as the benthopelagic fauna (Marshall & Merrett 1977). Wishner and her colleagues have examined this fauna in some detail (Wishner 1980a, b, c, Wishner & Meise-Munns 1984, Gowing & Wishner 1986, Wishner & Gowing 1987). They refer to this environment as the benthopelagic or benthic boundary layer, as do Childress et al. (1989). It has its own endemic fauna, phylogenetic aspects of which have been partially examined (Grice & Hulsemann

1970, Grice 1972, Wishner 1980c, Hargreaves 1984, 1985, Hargreaves et al. 1984, Domanski 1986, Gowing & Wishner 1986, Childress et al. 1989). These studies are linked to those of benthopelagic coupling reviewed by Angel (1984, 1990), Deuser (1986) and Fowler & Knauer (1986). Rapid sedimentation of phytoplankton to the ocean bottom has been recently documented by Rice et al. (1986), Hecker (1990) and Thiel et al. (1990) and evidence of its direct utilization by component species of the benthos obtained (Gooday & Lambshead 1989, Graf 1989). Some attention has centred on the episodic descent of large lumps of organic matter as instanced by nectonic carcases (Stockton & DeLaca 1982, Smith 1985). Little attention, however, has been paid to impingement horizontally on to the slope, in marginal oceanic regions, of species of plankton and micronekton, nor of the downward extensions of pelagic populations making them directly available to predators such as the benthopelagic fish. Merrett (1986) reviewed the occurrence of micronektonic fish in the stomachs of demersal fish, noting records of 24 species representing 10 families of meso- and bathy-pelagic fishes.

Fraser (1961, 1968, 1969) and Hopkins et al. (1981) examined the on-shelf or landward distribution of

oceanic plankton and micronekton, while Hargreaves (1984, 1985) and Hargreaves et al. (1984) described the occurrence of species of micronekton in the vertical water column and in the near-bottom environment of an adjacent slope region by using conventional multiple Rectangular Midwater Trawls. The present investigation supplements the current information on constitution and occurrence of the benthopelagic fauna. It examines the occurrence of micronektonic and planktonic species in the stomach contents of demersal fish in different bathymetric horizons between 400 and 3000 m depth on the slope of the Rockall Trough relative to their bathymetric occurrence in the oceanic water column adjacent to the slope.

## MATERIALS AND METHODS

A vertical series of samples was collected at Stn 10105 at 54°30' N, 13° W in August/September 1979 using a multiple Rectangular Midwater Trawl (RMT 8 + 1) (Roe & Shale 1979, Roe et at. 1980). Samples were collected from 100 m depth strata between the surface and 900 m depth by both day and night to determine the extent of any diel migration of species. The influence of downwelling daylight was assumed to be absent at depths greater than 900 m where there would then be no significant diel vertical migration of species (Angel et al. 1982). Deeper samples were, therefore, collected at 200 m depth intervals between 900 and 1900 m irrespective of day or night. A full description of the sampling procedure at this station is given by Hargreaves et al. (1984). A comparison of the sampling efficiencies of the RMT 1 and 8 nets showed that the RMT 1 was more efficient for organisms of body volume less than 0.12 ml (Mauchline 1989). This was true for all euphausiids, mysids except *Gnathophausia zoea*, and the small decapods *Gen-*

*nadas elegans*, *Sergestes arcticus* and *Hymenodora glacialis*. The data used in this paper are from the RMT 1 samples.

The demersal fish were collected from the Hebridean Terrace and floor of the Rockall Trough in the area of 55 to 57° N, 9 to 12° W at depths between 400 and 3000 m. The discrete depth zones sampled are shown in Table 1 along with the numbers of species that consumed pelagic prey species and the corresponding numbers of their stomachs that contained food. The number of species without pelagic prey in their stomachs is given. Full descriptions of the trawls and fishing methods used are given by Gordon & Duncan (1985, 1987) and Gordon (1986). The contents of each stomach were identified individually (Mauchline & Gordon 1985, 1986, Gordon & Mauchline 1990).

The bathymetric incidence of individual pelagic prey species has been examined in the following manner. The numbers of individuals of each pelagic prey species occurring in the stomachs of each predatory species of fish in each bathymetric horizon were listed. Each pelagic prey species was then examined separately and the numbers of stomachs, with food present, of its predatory species of fish were listed for each bathymetric horizon irrespective of whether the predatory species consumed that pelagic species in every horizon in which it occurred. The numbers of the pelagic species that occurred per 100 stomachs with food in each horizon were determined.

## RESULTS

The prey species have been grouped according to their bathymetric occurrence in the pelagic water column and whether or not they perform a diel vertical migration. Epipelagic and mesopelagic vertical migrators are shown in Fig. 1. These species perform a diel

Table 1. Abundance of fish species predating pelagic organisms. Numbers of species and individuals with pelagic food present in the different benthopelagic depth horizons are given along with the corresponding numbers of species that did not consume pelagic prey

| Depth horizons (m) | No. of species consuming pelagic prey | No. of stomachs with food | No. of species not consuming pelagic prey |
|---|---|---|---|
| 415–575 | 12 | 482 | 29 |
| 595–860 | 25 | 1680 | 14 |
| 816–1083 | 30 | 1830 | 3 |
| 1185–1296 | 26 | 427 | 5 |
| 1420–1536 | 16 | 230 | 18 |
| 1725–1890 | 11 | 160 | 16 |
| 1940–2045 | 12 | 109 | 1 |
| 2170–2300 | 12 | 197 | 4 |
| 2400–2565 | 12 | 142 | 6 |
| 2880–2975 | 7 | 151 | 2 |

vertical migration at night, the epipelagic species entering the extreme surface layers from a daytime depth range of ca 100 to 500 m. Mesopelagic species rarely enter the surface 100 m of the water column from a daytime depth of about 300 to 800 m. All species in Fig. 1 are predated from their daytime modal depths.

The species in Fig. 2 are characterized by their exploitation at depths on the slope deeper than their modal depths in the oceanic water column. The data for salps are not explicit in Fig. 2. Salps could not be counted in RMT 1 or 8 samples because they were so badly damaged (Hargreaves et al. 1984); hence the data on their vertical distribution in the water column is
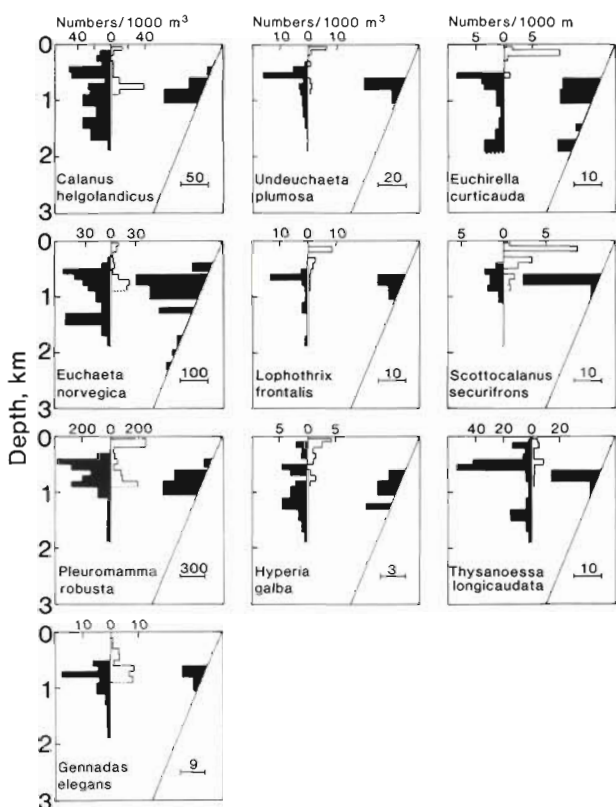


Fig. 1. Epipelagic and mesopelagic migrators: their vertical distribution in the oceanic water column (left) and their exploitation by the fish assemblages on the slope of the Rockall Trough (right). Their vertical distribution in the water column was determined from RMT 1 samples collected at 100 m depth intervals by day (shaded bars) and night (open bars) in the upper 900 m of the water column, and at 200 m depth intervals below 900 m (shaded) irrespective of day or night, at Stn 10105 in the Rockall Trough. Their incidence, number per 100 fish stomachs with food (denoted by the bar to the lower right of each figure), was determined for each bathymetric horizon of the slope as described in the text. Species are the calanoid copepods Calanus helgolandicus through to Pleuromamma robusta, the hyperiid amphipod Hyperia galba, the euphausiid Thysanoessa longicaudata and the decapod Gennadas elegans. The incidence of species in the water column is given as number per 1000 m³ of water filtered
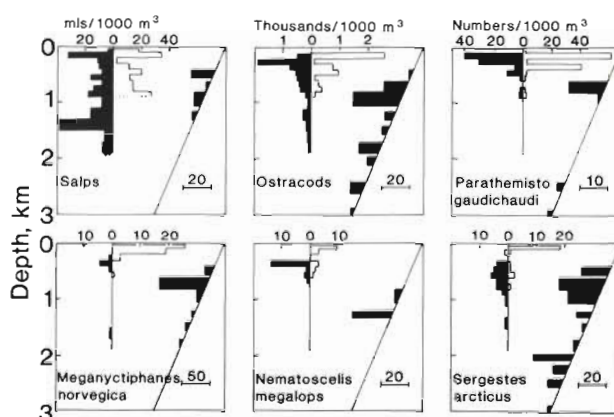


Fig. 2. Additional epipelagic and mesopelagic migrators: their vertical distribution in the oceanic water column (left) and their exploitation by the fish assemblages on the slope of the Rockall Trough (right) as defined in the legend to Fig. 1. Salps and ostracods were not identified to species. The other graphs are for the hyperiid amphipod Parathemisto gaudichaudi, the euphausiids Meganyctiphanes norvegica and Nematoscelis megalops, and the decapod Sergestes arcticus. With the exception of the 2 top left figures, all others are presented as number per 1000 m³ water filtered

presented as a volume measurement (Fig. 2). There is also considerable difficulty in positively identifying their remains in fish stomachs. Gordon & Mauchline (1990) conclude that it is quite probable that much of the unidentified component of the diets of fish in the 800 to 1900 m depth horizons consists of coelenterates, salps and ctenophores. Swarms of salps have been reported in the Rockall Trough (Bathmann 1988) and would be expected to deposit on the sea bed, so becoming available to the slope fishes.

The conchoecid ostracods exploited below 1700 m depth probably reflect their pelagic occurrence below the maximum sampling depth of 1900 m of the vertical series. The amphipod Parathemisto gaudichaudi may be scavenged by the fish at 2500 m and deeper. The euphausiids Meganyctiphanes norvegica and Nematoscelis megalops and the decapod Sergestes arcticus appear, on impingement on the slope, to extend their lower vertical depth range and so be available to predatory fish at depths below 1000 m.

Mesopelagic non-migrators (Fig. 3) occur in fish stomachs at depths corresponding to their vertical distribution in the oceanic water column. The distribution in the water column was determined from analysis of the RMT 1 samples but in the corresponding RMT 8 samples Boreomysis microps occurred to 1900 m while Meterythrops picta was caught in the 1300 to 1500 m sample (Hargreaves 1985). The euphausiid Thysanopoda acutifrons occurred in the deepest sample of the vertical series and its distribution therefore probably extends below 1900 m as also implied by the data of

James (1987). Thus, there is no evidence of an extension of the lower vertical depth range of these species on impingement on the slope.

The vertical distributions of the bathypelagic species, which perform no diel vertical migration, extend below the lower sampling limit of the vertical series at 1900 m (Fig. 4). The only apparent exception is the mysid *Gnathophausia zoea* whose large size and relative rarity in the water column caused it to be inadequately sampled by the RMT nets. It occurs in epibenthic trawl samples from the Rockall Trough indicating its occurrence in the benthopelagic zone in significant numbers, as the data of Hargreaves (1985) also imply. The decapod *Hymenodora glacialis* rarely occurs above 1500 m in the pelagic water column and was found by Domanski (1986) to be the most abundant shrimp species within 10 to 25 m of the sea bed at depths of 4000 m south of Kings Trough centred at 41° 30′ N, 30° W. Its exploitation by the fish at 3000 m depth in the Rockall Trough must result from a similar vertical distribution to that found by Domanski.

## DISCUSSION

The pelagic prey species occurring in the stomachs of the benthopelagic fish assemblages are not necessarily the commonest or dominant species in the oceanic water column. Many of the epipelagic species live at depths that are too shallow to make them available to these fish. The prey must also be a certain minimum size and this precludes common crustacean plankton such as the cyclopoid copepods which only occurred in the diets of the smaller sized *Alepocephalus bairdii* and *Coryphaenoides rupestris* in small numbers (Mauchline & Gordon 1983, 1984a).

What are the mechanisms that make these pelagic organisms available to the benthopelagic fish assemblages? Populations of epi- and mesopelagic species can extend vertically to the sediment surface, where their vertical distribution tends to become truncated, if the sediment is within the vertical range of the species. Consequently, the predation of fish of pelagic species in the benthopelagic regime at the daytime depths of the pelagic prey in the water column (Figs. 1 & 3) does not necessarily involve horizontal impingement of these species on the slope. Their normal vertical distribution in the water column would make them available to the fish.

The same is true of bathypelagic species (Fig. 4). Domanski (1986) demonstrated an increase in abundance of decapod crustaceans in the benthopelagic layer within 100 m of the ocean bottom at depths of 4000 to 5500 m. This undoubtedly reflects, as it does in coastal and shelf waters, a general increase in biomass
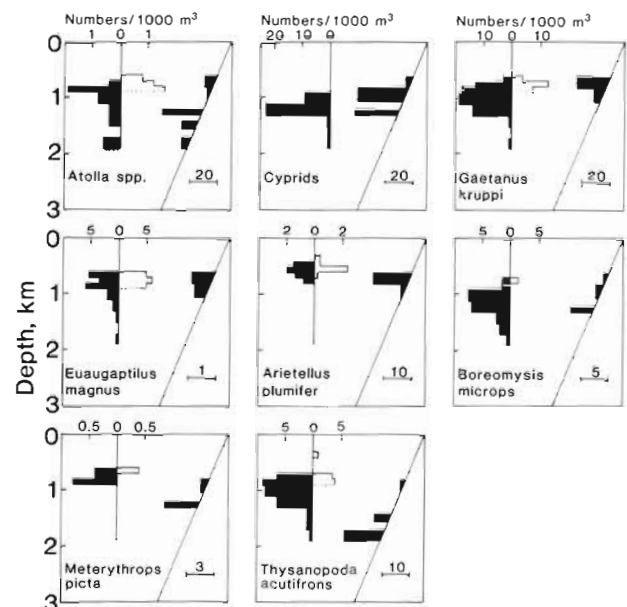


Fig. 3. Mesopelagic non-migrators: their vertical distribution in the oceanic water column (left) and their exploitation by the fish assemblages on the slope of the Rockall Trough (right) as defined in the legend to Fig. 1. The 3 scyphomedusan species of the genus *Atolla* (see Mauchline & Harvey 1983) were not separated. Cyprid larvae of barnacles were not identified. The other graphs are for the calanoid copepods *Gaetanus kruppi*, *Euaugaptilus magnus* and *Arietellus plumifer*, the mysids *Boreomysis microps* and *Meterythrops picta*, and the euphausiid *Thysanopoda acutifrons*

at this boundary layer relative to the water column immediately above it, as Wishner (1980a) found. Populations of many pelagic copepods, mysids, euphausiids and decapods have their lower vertical limits at the sediment surface in coastal, shelf and slope environments. The abyssal sediments are within range of the bathypelagic populations such as those of the decapod *Hymenodora glacialis* as demonstrated by Domanski (1986) and confirmed here.

There is, however, evidence of impingement through horizontal movement from the pelagic to benthopelagic environments in a few species (Fig. 2) These are the 2 euphausiids *Meganyctiphanes norvegica* and *Nematoscelis megalops* and the decapod *Sergestes arcticus*. Hargreaves (1984), sampling the benthopelagic slope environment with closing nets, found this downward extension of the distribution of *S. arcticus* in Porcupine Seabight immediately south of the Rockall Trough. *M. norvegica* is known to feed on the surface layers of the sediment in coastal environments (Mauchline & Fisher 1969), as do presumably these other 2 species, but that does not explain the downward extension of the distribution below about 1500 m.

Some species among the benthopelagic fish assemblages scavenge dead organisms that have sunk to the
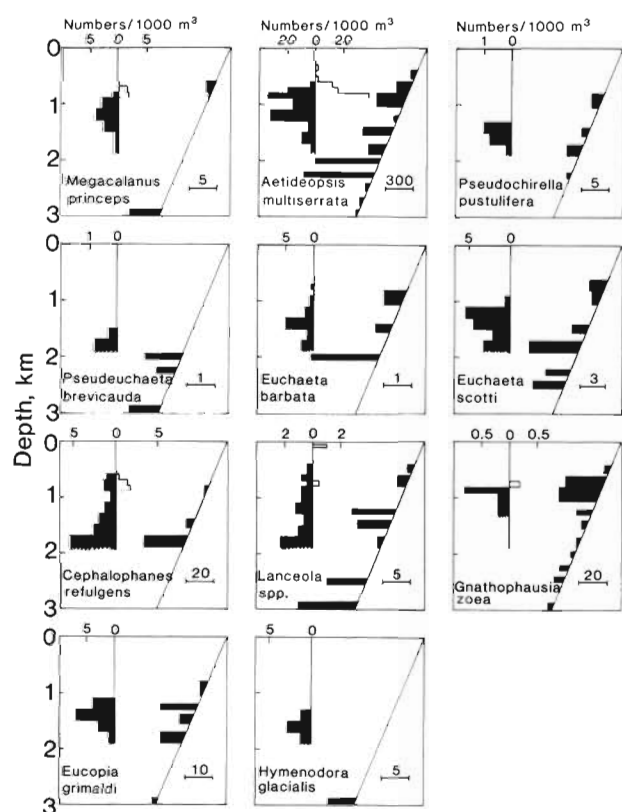
Fig. 4. Bathypelagic non-migrators: their vertical distribution in the oceanic water column (left) and their exploitation by the fish assemblages on the slope of the Rockall Trough (right) as defined in the legend to Fig. 1 The species are the calanoid copepods *Megacalanus princeps* through to *Cephalophanes refulgens*, unidentified amphipod species of the genus *Lanceola*, the mysids *Gnathopausia zoea* and *Eucopia grimaldi*, and the decapod *Hymenodora glacialis*

surface of the sediment. The blue whiting *Micromesistius poutassou* spawns in the surface 400 m of the Rockall Trough and occurred in the stomachs of *Synaphobranchus kaupi*, *Histiobranchus bathybius*, *Nematonurus armatus* and *Antimora rostata* at depths of 2200 to 2900 m in April in each of the 3 years in which samples were collected (Mauchline & Gordon 1984b). The *Parathemisto gaudichaudi* and *Sergestes arcticus* recorded in fish stomachs at 2500 to 3000 m depth (Fig. 2) may have been scavenged. Both these pelagic species occurred in the stomachs of *Nematonurus armatus*. The *S. arcticus* recorded at 1700 to 2200 m had been eaten by *S. kaupi* in a strict seasonal window between the end of July and mid-September. Those occurring in the deeper *N. armatus*, at 2500 m depth, were present in the period mid-August to mid-October. The breeding season of *S. arcticus* probably extends to July or August in the Rockall Trough and a natural post-breeding mortality could be expected. It is the second most abundant decapod in the water column of the Trough, occurring in aggregations. Conse-

quently, scavenging of these pelagic species may have given rise to their occurrence at these excessive depths.

Pelagic species are eaten by benthopelagic fish at depths corresponding to their daytime vertical distribution in the oceanic water column, or, in the case of a few species, at greater depths. Diel vertical migration into shallower regimes at night does not make them available to shallower assemblages of demersal fish presumably because such vertical migration is strictly into the pelagic domain and not up the contours of the slope sediment. The slope current travelling parallel to the shelf edge (Ellett et al. 1986) at depths down to about 800 m may restrict slopeward movement of the pelagic fauna and its subsequent transport on to the shelf. Fraser (1961, 1968, 1969) records the occurrence of oceanic epipelagic species on the Scottish continental shelf but found that meso- and bathypelagic species occurred rarely. Hopkins et al. (1981) similarly found virtually no on-shelf transport of mesopelagic species in the west Florida region of the Gulf of Mexico, nor did Pearcy (1964) in the case of mesopelagic fish off the Oregon shelf. They suggested that even if these species migrated into the epipelagic and penetrated the on-shelf waters, their survival there, through either predation or the lack of a vertical water column of sufficient depth to enable their lower daytime depth distribution, must be limited. This is also presumably true of impingement from their night-time depth on to the slope: predation and lack of depth in the water column will preclude colonisation in any numbers, or such that would register in fish diets.

Benthopelagic fish may migrate vertically into the water column to predate pelagic species. Haedrich (1974) caught 49 *Coryphaenoides rupestris* in mid-water in the Denmark Strait: 37 of them were at least 250 to 500 m above the sea bed, a further 11 at least 660 to 710 m above, and one individual at least 1440 m above the bottom. These observations have never been repeated. Merrett et al. (1986) recorded *C. rupestris*, *Halargyreus johnsonii* and *Synaphobranchus kaupi* between 3 and 60 m above the bottom in the Rockall Trough but in small numbers. It is not known how frequently such pelagic excursions occur, nor whether they are short-term events, nor whether individual fish live in the water column for periods. The lack of data suggests that such excursions are rare or on a short-time scale.

Demersal fish biomass is greatest between 800 and 1550 m depth, with a pronounced maximum at 1200 to 1300 m depth, on the slope of the Rockall Trough (Gordon & Mauchline 1990). This corresponds to the depth range of greatest potential vertical and horizontal impingement of the epi- and mesopelagic fauna on the slope. The vertical impingement through the truncation of the vertical distribution of the species in the

water column is probably the major factor involved in making this fauna available to benthopelagic fish assemblages in marginal oceanic regions and confirms the situation reported by Marshall & Merrett (1977). The net northeastward flow of the water masses of the Trough in a shallowing environment (Mauchline 1990) must ensure that horizontal impingement of the fauna on the sides of the Trough is also active, probably most so at the northeastern, geographical limits of the Trough, south of the Wyville Thomson Ridge, an area that has not been sampled in this investigation.

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