# Quantification of diel vertical migration by micronektonic taxa in the northeast Atlantic

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## Abstract

Analyses of day/night changes in the bathymetric distribution of micronektonic biomass at 16 stations in the northeastern Atlantic, sampled between 1978 and 1994, provided quantitative estimates of the organic carbon fluxes associated with diel vertical migration of individual taxa of micronekton. Gelatinous taxa contributed 50–80% of the integrated standing crop by volume but, apart from tunicates, contributed relatively little to the active migratory fluxes when expressed in terms of carbon. Total micronektonic migratory fluxes into the upper 200 m ranged from 12.5 to 58 mgC per m$^2$. At 15 stations, fish and pteropods provided 50–80% of the fluxes into the upper 100, 200 and 400 m. At one station, tunicates (pyrosomes) contributed substantially. Wherever tunicates or the medusa *Pelagia* were swarming, migrations by other taxa appear to be suppressed. The mean proportions of the stock (in terms of biomass) of each of the dominant migratory taxa entering and leaving the upper 100 m were 23% for tunicates, 18% for fish, 22% for pteropods, 8% for decapod crustaceans and 23% for euphausiids. The maximum proportions for these five taxa were 90%, 60%, 75%, 25% and 75%, respectively. Similar estimates of the mean fluxes into and out of the upper 400 m were generally higher: 19% for tunicates, 39% for fish, 28% for pteropods, 49% for decapods and 55% for euphausiids; the respective maxima were 99%, 74%, 99%, 72% and 91%. It is estimated for fish that if these migrations occur throughout the year, they will result in an active carbon export (both POC and DOC) from the wind-mixed layer and immediate sub-thermocline depths of about 500% of the mean annual standing stock. If this estimate can be extended to other taxa, then the material fluxes resulting from these active migrations will be quantitatively similar to those resulting from the deposition of phytodetritus at temperate latitudes.

## Introduction

Diel vertical migration (DVM) is characteristic behaviour of many pelagic taxa (Longhurst, 1976). The usual diel migration pattern is for populations to occupy deeper strata during the day and to migrate up towards the surface at dusk as light levels begin to fall. The majority of individuals feed actively during the night but not during the day. Hence, they migrate down at dawn with full stomachs and return to near the surface at dusk with empty stomachs (e.g. Foxton & Roe, 1974; Atkinson et al., 1996; Hopkins et al., 1996). Generally, the stimulus for these migrations is considered to be rapid alterations in the rate of change of light intensity (Ringelberg, 1964; Longhurst, 1976) and their function to be a mechanism for minimising exposure to visual predation (Zaret & Suffern, 1976;

Iwasa, 1982; Vuorinen, 1987; Frost, 1988). In some freshwater plankton, it has been demonstrated experimentally that the migratory behaviour is triggered by chemical exudates from predators (Lampert, 1989; Ringelberg, 1991). In the North Sea, recent data imply that interannual variations in the intensity of diel vertical migration are correlated to fluctuations in stocks of planktivorous fish (Hays et al., 1996).

The range of the migrations, and the numbers and species composition of the migrators, must also influence ecological processes in the upper water column. The oscillations in the composition of the assemblages between day and night must be having substantial repercussions on grazing and predation pressure, and on intraspecific interactions. Those organisms, which have gut clearance rates slower than the duration of the migratory phase, will carry organic matter deep into

the water column (Vinogradov, 1968; Angel, 1985, 1989; Longhurst & Harrison, 1988, 1989). Such transport may account for sediment trap observations of flux maxima at midwater depths of around 500 m. In earlier studies, these maxima were considered to result either from lateral advection (Bishop et al., 1980) or to be an artifact resulting from the presence of 'swimmers' (Lee et al., 1988). Based on sediment trap data, and the observed changes in chemical composition of the sedimenting particles, Walsh et al. (1988) concluded that for bioactive transport – "packaging and transport of material by zooplankton and nekton is the most likely cause of the widely observed mid-water column flux maximum". It may also serve to account for the peak in fluxes of snow aggregates observed between 0800 and 1200h at subthermocline depths in the northeast Atlantic (Lampitt et al., 1993a).

The contribution by the migrants to particulate fluxes is supplemented further by fluxes of dissolved organic and nitrogenous materials released as a result of their metabolic activity (Small et al., 1983; Dam et al., 1995: Steinberg et al., 2000). Since both carbon and nitrogen are predominantly assimilated by the migrants during the shallow phase of their migration cycle, any subsequent excretion of respiratory carbon dioxide (Longhurst et al., 1990), and loss of dissolved organic matter (DOM) and dissolved nitrogenous organic matter (DON) during the day-time phase of their migration deep within the water column, will result in an export flux (Longhurst & Harrison, 1988; Longhurst et al., 1989). Likewise, the death of any migrant at deeper daytime depths as a result of predation, disease or senescence will also result in a net downward transfer of material. Quantitatively, the individual daily migratory fluxes may be relatively small, but when integrated over a full year, may make a significant contribution to carbon and nutrient budgets. Thus, if the migrants contribute only 2–3% of the export flux at the base of the thermocline, this would still be equivalent to the amount of organic carbon that reaches the sea-floor. There is also evidence for asynchronous migrations from passive traps (Harding et al., 1986), with the downward migrants having fuller guts than those migrating up. The fluxes resulting from these active migrations may make a substantial contribution to the material fluxes reaching the sea-floor, because the vertical velocity of the 'gut-flux' is much faster than the sedimentary flux. So the material is being transported rapidly out of the warm upper layers of the water column, where microbial metabolism is more active, into cooler waters where

*Table 1.* Station positions and dates, shown in the latitudinal order used in all the figures

| Station | Position | Date | Maximum sampling depth | |
|---|---|---|---|---|
| | | | By day | By night |
| 9791 | 50° N, 14° W | May, 1978 | 1000 m | 1000 m |
| 53304 | 49° 15′ N, 12° 50′ W | April, 1994 | 1000 m | 1000 m |
| 53305 | 49° 12′ N, 12° 17′ W | April, 1994 | 1000 m | 1000 m |
| 53318 | 49° 30′ N, 11° 30′ W | April, 1994 | 500 m | 500 m |
| 11794 | 47° N, 20° W | June/July, 1988 | 1000 m | 1000 m |
| 11056 | 46° N, 14° W | April, 1984 | 500 m | 800 m |
| 11040 | 39° N, 13° W | March/April, 1984 | 1000 m | 800 m |
| 9801 | 42° N, 17° W | May, 1978 | 1000 m | 1000 m |
| 10379 | 35° N, 33° W | June, 1981 | 1000 m | 1000 m |
| 10382 | 33° N, 32° W | June, 1981 | 1000 m | 1000 m |
| 10376 | 33° N, 33° W | May, 1981 | 1000 m | 1000 m |
| 10378 | 32° N, 34° W | June, 1981 | 1000 m | 1000 m |
| 10380 | 30° N, 34° W | June, 1981 | 1000 m | 1000 m |
| 10228 | 33° N, 32° W | November, 1980 | 1000 m | 1000 m |
| 10233 | 32° N, 32° W | November, 1980 | 1000 m | 1000 m |
| 10222 | 30° N, 30° W | October, 1980 | 800 m | 1000 m |

microbial degradation is likely to be slower. It is also 'packaged' into larger aggregates (faecal pellets) that will sink faster and have a shorter residence time in midwater, hence, it will be less likely to be intercepted by detrivores during its downward passage.

In this study, changes in biomass profiles between day and night have been used to derive quantitative estimates of the fluxes associated with the migrations (Allison & Wishner, 1986; Angel, 1989a; Roe et al., 1990; Angel & Hargreaves 1992). Longhurst (1976) estimated that up to 25% of zooplankton and micronekton biomass in the upper 1 km of an oceanic water column could be entering the epipelagic zone at night (i.e. the euphotic and seasonal thermocline zones). Around the Azores Front, Angel (1989b) showed that at some stations at night, the 50% level for the total micronektonic biomass in the upper 1000 m was shoaling by >350 m. Angel & Hargreaves (1992) compared changes in the total biovolumes in day and night samples from a series of stations along 20° W but made no distinction between gelatinous and non-gelatinous taxa. Here, night-time increases in the biomass (expressed in terms of carbon) of the main micronektonic taxa sampled at a series of stations occupied in the northeast Atlantic in 1978–1991 have been used quantitatively to estimate the vertical migrations.
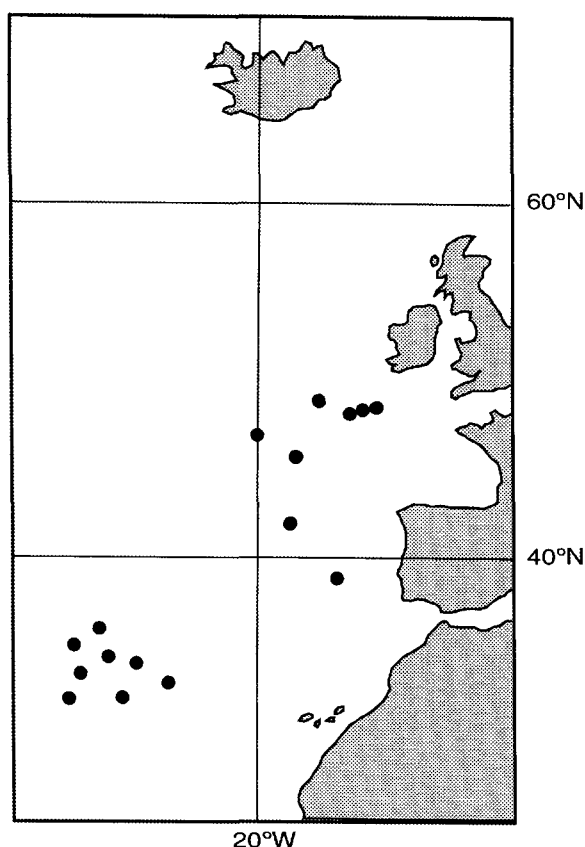
*Figure 1.* Map showing the locations of the stations analysed in this study.

## Materials and methods

The data are derived from 16 series of macroplankton and micronekton profiles observed during a series of sampling programmes conducted in the northeast Atlantic by the Institute of Oceanographic Sciences (now part of the Southampton Oceanography Centre) (Table 1, Fig. 1). The latitudes straddle the major faunistic boundary at around 40° N that marks the southern limit of deep-winter mixing and marked seasonality in the production cycle (see Campbell & Aarup, 1992; Longhurst, 1995). Most stations were occupied during spring or early summer, but three were conducted in late autumn as part of a major study of the Azores Front (Irwin et al., 1983; Gould, 1985; Fasham et al., 1985; Domanski, 1986; Angel, 1989b; Angel & Hargreaves, 1992); these provide limited information on seasonal variations in the migratory fluxes.

At each station, bathymetrically-stratified series of samples were collected by day and by night using an RMT(1+8)M sampler (Roe & Shale, 1979). Most series consisted of contiguous, but non-overlapping horizontal tows at 100 m depth intervals from the surface to depths of 1000 m. Some of the series were, however, curtailed by bad weather (see Table 1). One station (53 318) was situated over the continental slope where the sounding was only 600 m. The RMT(1+8)M is a multiple opening/closing Rectangular Midwater Trawl enabling collection of three sequential pairs of samples. Each pair consists of a macroplankton sample collected in a nominally 1 $m^2$ net (RMT1) which has a mesh size of 0.32 mm, and a micronekton sample in a nominally 8 $m^2$ net (RMT8) with a mesh size of 4.5 mm. The duration of each haul was usually 1 h, and the continuous read-out from a flow meter mounted on the net was used to keep *in situ* towing speeds as close as possible to 2 knots (ca. 1 $m.s^{-1}$). During a typical tow, about 2 650 $m^3$ of water were filtered by the RMT1 and about 30 500 $m^3$ by the RMT8, assuming 100% filtering efficiency.

The samples were fixed initially in 5% formalin seawater and, for each sample, the preservative was renewed after about 1 day, when routinely the biovolume of the total sample was measured. In the laboratory, the total displacement volume of each sample was re-measured prior to being sorted into the major taxonomic groups. The biovolume of each group sorted was then measured. The replicated measurements of displacement volumes of some of the samples showed measurement errors amounted to 5–10%. There were also inter-sample errors stemming from the varying amounts of interstitial water trapped within the sample. Although more of the interstitial water could have been removed, any marginal improvements in the precision of the biomass estimates would have been more than offset by the increased damage to the specimens. Differentiating between the contributions to the fluxes by gelatinous and non-gelatinous groups has proved to be important. The errors associated with the sampling and the subsequent measurements are large, but will generally lead to underestimates of the quantities involved in the migratory fluxes. For example, no allowance was made for the shrinkage of gelatinous organisms that occurs after preservation. All groups were not sorted for all the series, hence, in some cases, the total flux estimates are incomplete.

Two parameters have been used to quantify the migrations. Firstly, night/day differences in displacement volumes integrated over three ranges 0–100 m, 0–200 m and 0–400 m have been calculated for each station assuming that the quantitative estimates from the nets were not subject to sampling errors or variations res-

ulting from patchiness. Secondly, estimates of the carbon fluxes resulting from the migrations based on the integrated displacement volumes of each taxon were calculated, with a distinction being made between the contributions of gelatinous and non-gelatinous taxa.

The biovolume data for each haul were standardised to volume per 1000 m$^3$ of water filtered, and then converted into biovolume per m$^2$ within each sample range; these could then be summed to give the total volume from the surface to any selected depth within the sampling range. The daytime and night-time standing-crops were compared, assuming that the sources of error described above were small. However, in some cases, this was clearly not the case. For example, patchiness was probably the cause of the apparently large reverse migration by amphipods (the vast majority of which were *Themisto compressa*) at station 11794.

The data presented here are estimates of carbon (mgC m$^{-2}$) based on conversions of biovolume to organic carbon. For non-gelatinous plankton, the conversion used was that of Wiebe et al. (1975) and subsequently modified by Wiebe (1988):

$$\log_{10} V = 0.820 . \log_{10} C - 1.434,$$

where C is the biomass in terms of organic carbon per m$^3$ of water filtered and $V$ is the displacement volume (ml/m$^3$). For the gelatinous organisms, a displacement volume of 1 ml was assumed to contain 3.649 mgC; this value was derived by Pugh et al. (1997) from the data of Larson (1986). The taxa considered to be gelatinous were medusae, Siphonophora, Tunicata (thaliaceans and pyrosomes) and Chaetognatha. The taxa considered to be non-gelatinous were fish, Decapoda, Euphausiacea, Mysidacea, Amphipoda and Pteropoda.

## Results

Figure 2 shows histograms of micronekton (RMT 8 catches) integrated biomass in the total water column sampled (generally 900–1000 m, but see Table 1 for the exceptions) expressed as gC m$^{-2}$ by day and by night. At 5 of the 16 stations, the integrated catches were larger by day than by night. The five exceptional stations were: 1. At 47° N (station 11794) where the upper 200 m of the water column was dominated by a massive swarm of the hyperiid amphipod *Themisto compressa*. This amphipod appeared to be excluding (or consuming) other taxa from the upper water column. Patchy swarms of *T. compressa* are a regular seasonal feature of the temperate northeast Atlantic (e.g. Lampitt et al., 1993b). At night, there was a substantial reduction in the catches of this species integrated throughout the total water column. This was probably a result of patchiness but, in addition, if a large proportion of the population had migrated to within 5 m of the surface, it would not have been sampled by the nets, and hence the migratory flux would be grossly underestimated. 2. At 42° N, large numbers of salps were taken in the near-surface daytime catches, but very few were caught at night. Salps form dense, but highly heterogeneous swarms, so this was a patchiness problem. 3. At 35° N during summer and also at 33° N (4) and 30°N (5) in the winter in the vicinity of the Azores Front, large numbers of large *Pyrosoma* were caught by day at depths of 500–700 m. However, at night, when they could be seen in very large numbers at the surface (both in the lights of the ship and in the dark because of their intense bioluminescence), the near-surface nets collected relatively few. The trawl, as noted above, is ineffective in sampling the topmost 5 m of the water column in the wake of the ship.

The larger than usual disparities between day and night at the 46° N station resulted from less of the water column being sampled by day (to 500 m by day and 800 m at night, Table 1) as a result of bad weather. At 39° N, however, the daytime sampling extended down to 1000 m compared to only 800 m at night so the disparity is exacerbated. At least some of this disparity is explained by the exceedingly large swarms of pteropods in the upper 200 m at night that were largely absent from the daytime samples. At 49° N, the sounding at the shallowest slope station was only 600 m. Diel migrants appeared to have been migrating up from the benthopelagic zone where they are known to accumulate (Wishner, 1980; Hargreaves et al., 1984; Angel, 1990), which is likely to have greatly enhanced the night-time catches. The other highly disparate catch was at the 33° N station (10 376) which was targeted at the Azores Front itself; one series may have been more successful in sampling the frontal system than the other. What is clearly noticeable in Figure 1 is the quite sharp quantitative decline in total standing crop from ~100–150 mgC m$^{-2}$ to ~50 mgC m$^{-2}$ that occurred south of 39° N.

## Total micronekton biomass (mgC/m$^2$) in sampled water column
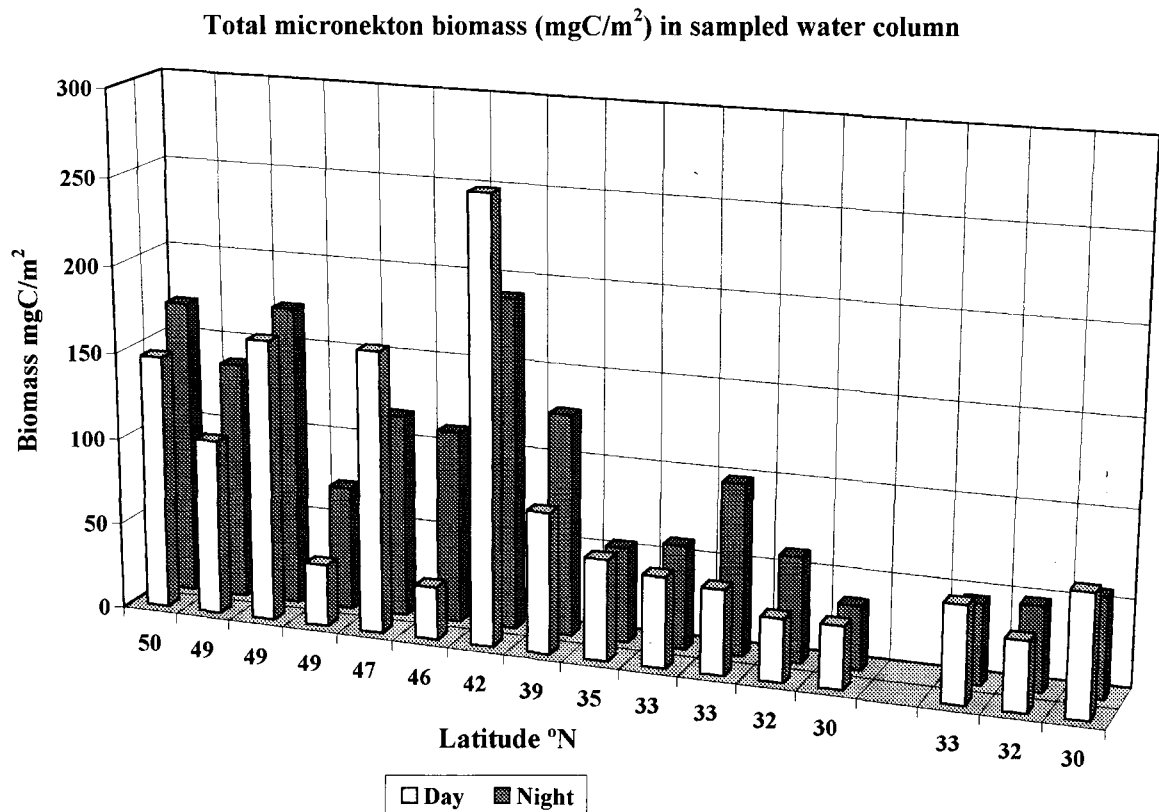


*Figure 2.* Day and night standing crops (mgC/m$^2$) of micronekton integrated over the total water column sampled (mostly 900 or 1000 m but see Table 1 for exceptions) in latitudinal order as shown in Table 1. The wintertime Azores Front station values are separated from the summertime values.

*Individual taxa*

*Amphipoda (Fig. 3)*

Figure 3 shows histograms of the night minus day standing crops (expressed in units of carbon) which are assumed to represent the carbon fluxes contributed by the diel vertical migrations of amphipods into the upper 100, 200 and 400 m of the water column. The backrow of histograms are plots of the integrated standing crop at each station (the largest value whether day or night is plotted). Generally, the standing crops of amphipods were quite small <6 mgC m$^{-2}$, but at 47° N and 42° N, the hyperiid *Themisto compressa* was the dominant component of micronekton biomass in the upper 200–300 m. It was also abundant at 39° N. At 47° N, there was a small positive flux (5% of the standing crop) into the upper 100 m, but the fluxes into the deeper two strata appeared to be negative. These negative fluxes, as discussed above, are mostly artifacts resulting from either patchiness, or the migration of a substantial proportion from daytime depths

of 200–400 m, into the upper 5 m at night where they would have been under-sampled. It is unlikely that *T. compressa* was undertaking a reverse migration (i.e. migrating down at night). The basis for this conclusion is that there was no evidence for this behaviour in the composition of the hauls. Moreover, sampling undertaken near 50° N in 1991 during the BOFS programme (Savidge et al., 1992) showed that *T. compressa* was undertaking diel migrations of the normal pattern. However, during a storm, the migrations were disrupted (Lampitt et al., 1993b). At both 39° N and 42° N, where there were high standing crops of *T. compressa* ~60% of its biomass was migrating into the top 200 m.

*Cephalopoda (not illustrated)*

The standing crop of Cephalopoda seldom exceeded 1 mgC m$^{-2}$, and at five stations too few specimens were caught for any analysis to be meaningful. At 47° N, where reasonable numbers were caught, the bulk of the population migrated up into the top 200 m, but
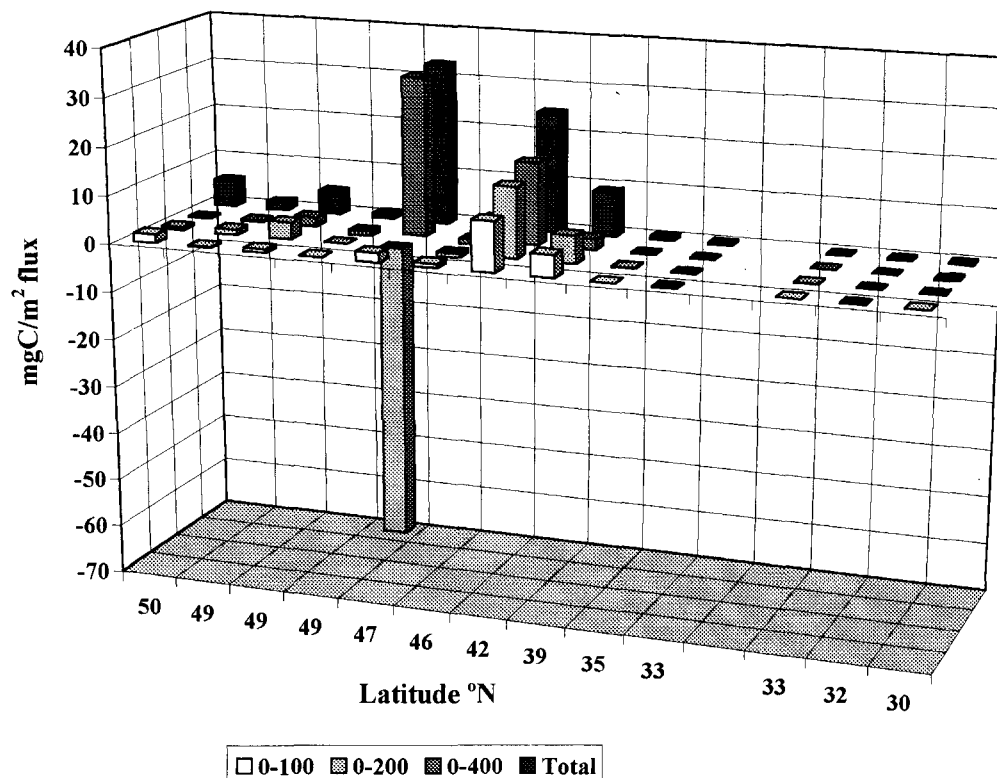
## Amphipoda: Fluxes (mgC/m$^2$) resulting from DVM



*Figure 3.* Amphipoda: migratory fluxes (mgC/m$^2$) into the upper 100, 200 and 400 m of the water column, together with the total night-time integrated standing crop in the water column sampled, in the same order as shown in Figure 2.

still generated a small carbon flux. While sampling at several of the stations at lower latitude, large numbers of ommastrephid squid were seen around the ship at night feeding on myctophid fish attracted in by the lights. Migratory fluxes by such large, actively swimming species remain undetected by samplers of the size used in this study. At those stations where there were adequate catches, mean fluxes increased from 17% of the total population sampled into the top 100 m to 55% into the top 400 m. However, none of the catches of this active group of animals was likely to be representative.

### Chaetognatha (Fig. 4)

At the majority of stations, the total water column standing crop of chaetognaths, in terms of carbon, was <6 mgC m$^{-2}$. However, at 50° N, large populations were sampled at depths of 100–400 m and 600–800 m, and the total standing crop attained was 45 mgC m$^{-2}$. At all stations, the diel migratory fluxes were <0.3 mgC m$^{-2}$. At seven stations, the fluxes were apparently negative and the possibility of some species undertaking reverse migrations cannot be ruled out. The maximum percentages of the standing crop moving up into the upper 100 m, 200 m and 400 m strata examined were 5, 13 and 22%, respectively.

### Ctenophora (not illustrated)

Only one species, *Beroë* sp., was sampled regularly. Since this species is a specialist predator of other ctenophores, its occurrence indicates that other species were present but not sampled. The great fragility of many ctenophores is well documented (Harbison et al., 1978), so the other species probably disintegrated in the net and were extruded. At only three stations were the numbers of *Beroë* worth analysing. It was undertaking vertical migrations at 42° N and 46° N, where its standing crop was high (7.5 and 1.7 mgC m$^{-2}$, respectively), but was mostly confined to depths >400 m. Thus, no estimate of the contribution by cten-
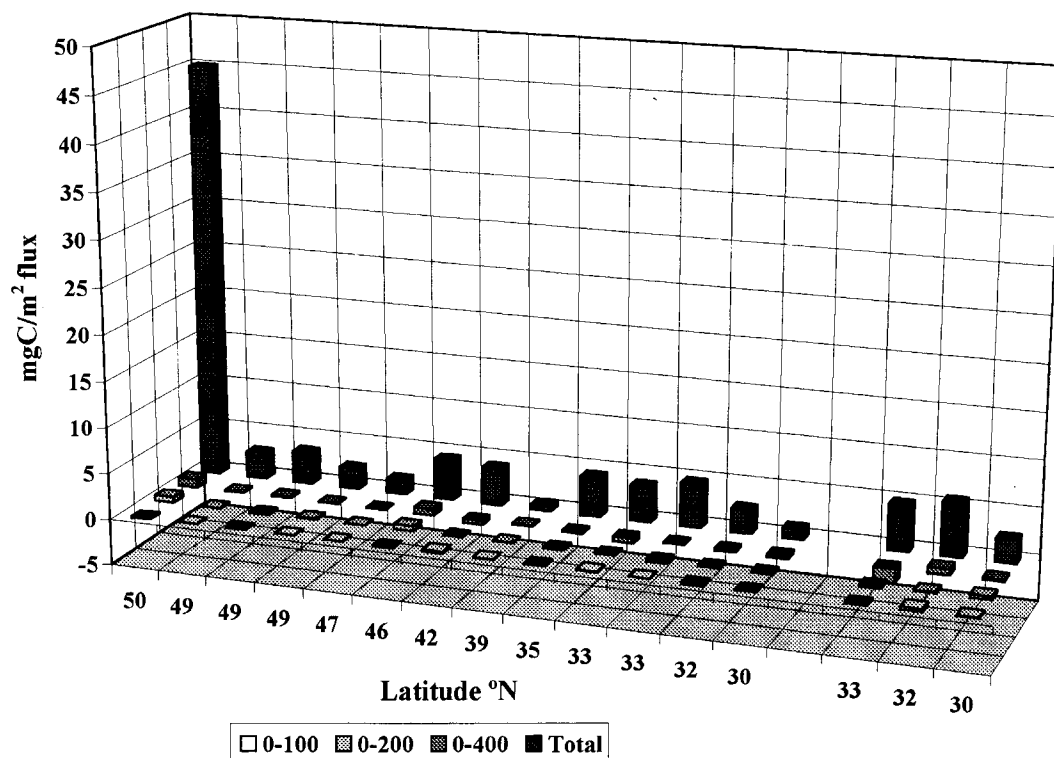
## Chaetognatha: Fluxes (mgC/m$^2$) resulting from DVM



*Figure 4.* Chaetognatha: migratory fluxes (mgC/m$^2$) into the upper 100, 200 and 400 m of the water column, together with the total nighttime integrated standing crop in the water column sampled, in the same order as shown in Figure 2.

ophores to migratory fluxes could be made on the basis of these data, but there was no indication that the ctenophores were a major contributor to migratory fluxes. However, there is no denying the potential importance of the group for other aspects of water column ecology.

### Decapoda (Fig. 5)

Total standing crop of decapods ranged only from 4.9 to 19.0 mgC m$^{-2}$. This group is one of the most conspicuous of the diel migrators. Their standing crops generally increased polewards but were particularly high in the vicinity of the Azores Front at 33° N (Domanski, 1986). Decapod biomass varied little between the late autumn and early summer in the vicinity of the Azores Front. At all stations, except the summer 30°N station in Western Atlantic Water near the Azores Front, there were detectable upward fluxes into the top 100 m at night, but only at five stations did these fluxes exceed 1 mgC m$^{-2}$; the highest being 3.6 mgC m$^{-2}$(ca.27% of the standing crop) at 42°

N. Upwards fluxes into the upper 200 m exceeded 2 mgC m$^{-2}$ at 10 stations; the maximum of 4.2 mgC m$^{-2}$ again being at 42° N. However, the migratory fluxes into the upper 400 m were much larger (2 – 7.8 mgC m$^{-2}$). A substantial proportion of the total decapod populations was involved in these migrations, the maximum being 71% at 35° N (where the upper 1000 m was sampled). Thus, diel vertical migration is an important element in decapod ecology. However, since most of the decapod migrants remained below the seasonal thermocline, they will contribute relatively little to export fluxes from the euphotic zone, but may be playing an important role in subthermocline fluxes. The mean percentage of the population migrating into the upper 100 m was 8% (maximum 27%), and into the upper 200 m and 400 m increased to 22% (44)% and 49% (71)%, respectively.

### Euphausiacea (Fig. 6)

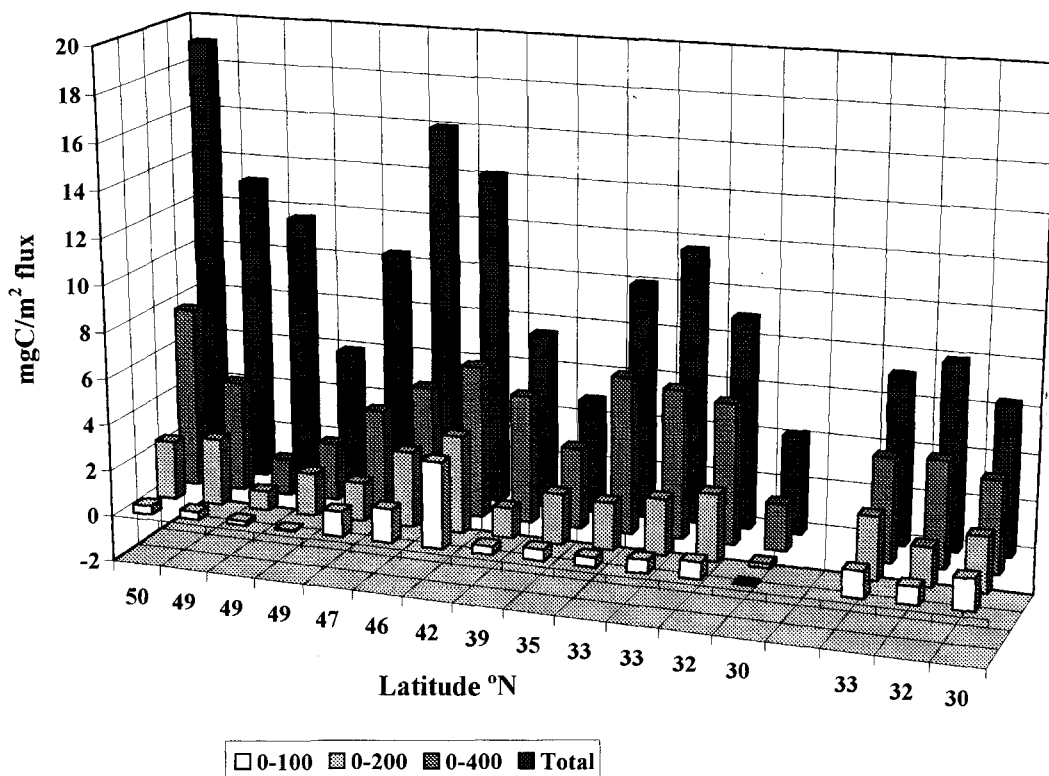Generally, euphausiid standing crops were relatively small, but ranged over more than an order of mag-

**Decapoda: Fluxes mgC/m$^2$) resulting from DVM**



*Figure 5.* Decapoda: migratory fluxes (mgC/m$^2$) into the upper 100, 200 and 400 m of the water column, together with the total nighttime integrated standing crop in the water column sampled, in the same order as shown in Figure 2.

nitude from 2.5 to 38.3 mgC m$^{-2}$. The highest biomasses (i.e. >7 mgC m$^{-2}$) were at middle latitude stations from 39° to 47° N. There seemed to be a positive correlation between the size of the standing crop and the percentage of the population undertaking diel migrations into the upper 100 m (>75% at 42° N). The maximum migration fluxes (>30 mgC m$^{-2}$) into the upper 200 and 400 m of the water column were observed at 39° N. At the three near-slope stations at 49° N, increasing proximity to the slope depressed both the percentage of the population migrating and the total flux. As for decapods, positive fluxes into the deeper strata were observed at all stations. Mean (maximum) percentages of the euphausiid population migrating into the upper 100, 200, and 400 m were 23 (64)%, 52 (88)% and 55 (92)%, respectively.

*Fish (Fig. 7)*

Standing crops of fish, like those of decapod crustaceans, varied over a limited range from 11.9 (at 46°

N) to 66.0 mgC m$^{-2}$ (at the Azores Front, 33° N). The highest fluxes, and the highest percentages of the total population migrating up into the upper 100 m at night, were at 42° N and at the Azores Front station at 33° N. The highest percentage of migrants was at the shallowest slope station at 49° N (sounding 600 m), but one of the lowest percentages was the next station on the cross slope transect where the sounding was 1000 m. This was a station at which Pteropoda occurred in very high abundances. One hypothesis to explain these sharp contrasts over such short distances is that the exceptional localised abundance of food deep within the water column may have reduced the need for the fish to migrate. At most stations, migration fluxes increased down to 400 m. The lowest percentage of migrants in the total fish assemblage was in Western Atlantic Water at 30° N, which coincided with the lowest observed standing crop. The mean (maximum) percentages of the total water column population migrating up into
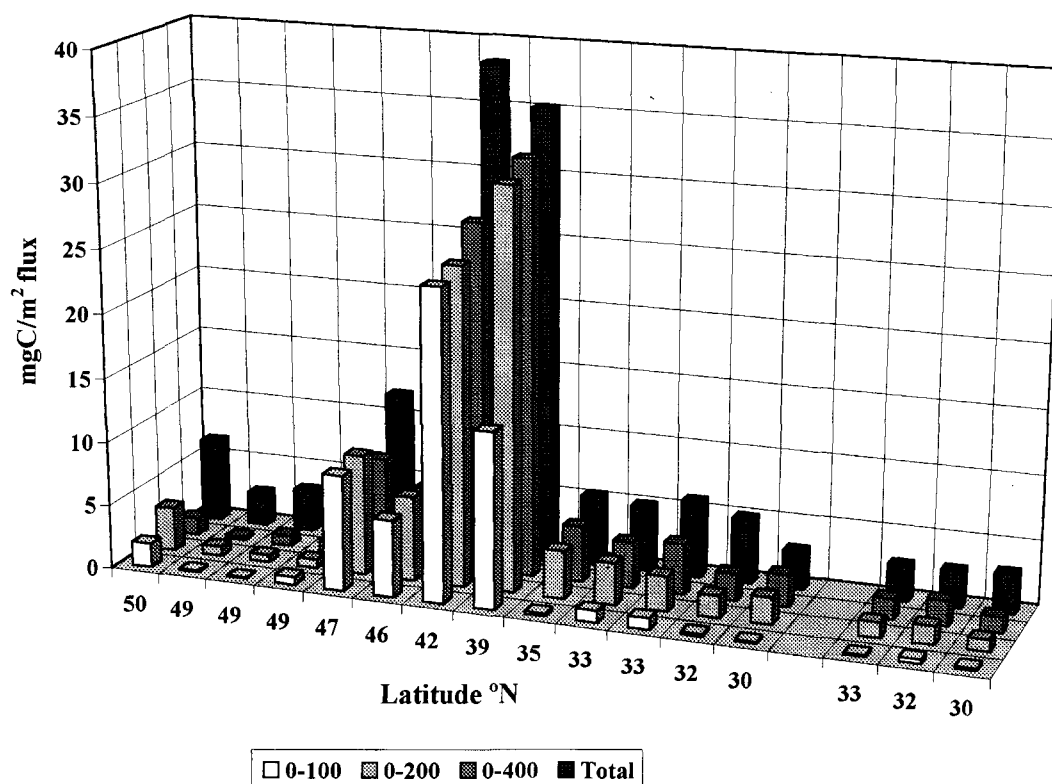
## Euphausiids: Fluxes (mgC/m$^2$) resulting from DVM



*Figure 6.* Euphausiiacea: migratory fluxes (mgC/m$^2$) into the upper 100, 200 and 400 m of the water column, together with the total nighttime integrated standing crop in the water column sampled, in the same order as shown in Figure 2.

the upper 100, 200 and 400 m, respectively, were 18(59)%, 29(71)% and 39(74)%.

### Medusae (not illustrated)

The standing crops and migrations of medusae were analysed at the seven more northerly stations only. Standing crops at two stations (50° N and 42° N) exceeded 10 mgC m$^{-2}$ and at each the medusae appeared to be undergoing reverse migrations. At 42° N, there was a large near-surface swarm of *Pelagia*, and such large swarms may inhibit upward migrations by other taxa. The mean percentages of the population migrating up did not exceed 2%, a value well within the range of likely observational error.

### Mysidacea (not illustrated)

The standing crops of mysids (predominantly a single species *Eucopia unguiculata*) ranged from 0.4 to 5.6 mgC m$^{-2}$ at northern stations (>39° N) and from 0.2 to 2.4 mgC m$^{-2}$ at southern stations. The species was

almost totally restricted to depths >400 m and so was not contributing to fluxes in the upper water column. However, data from repeated 48 h of sampling collected at 44° N, 13° W showed that *E. unguiculata* was undertaking diel migrations to at least 250 m during the spring bloom (Roe et al., 1984). Similarly, recent sampling in the vicinity of the Almeria-Oran Front in the Mediterranean in January (1997), showed that *E. unguiculata* species was a component of the population occupying daytime depths of <500 m and was undertaking diel migrations (Howell, pers. comm.). Hence, for most of the year, mysids make little or no contribution to migratory fluxes in the northeast Atlantic but may make a small contribution around the time of any seasonal bloom.

### Pteropoda (Fig. 8)

Seasonally, pteropods form dense swarms and their contribution to the standing crops in these samples was highly erratic. They made substantial (>15 mgC m$^{-2}$)
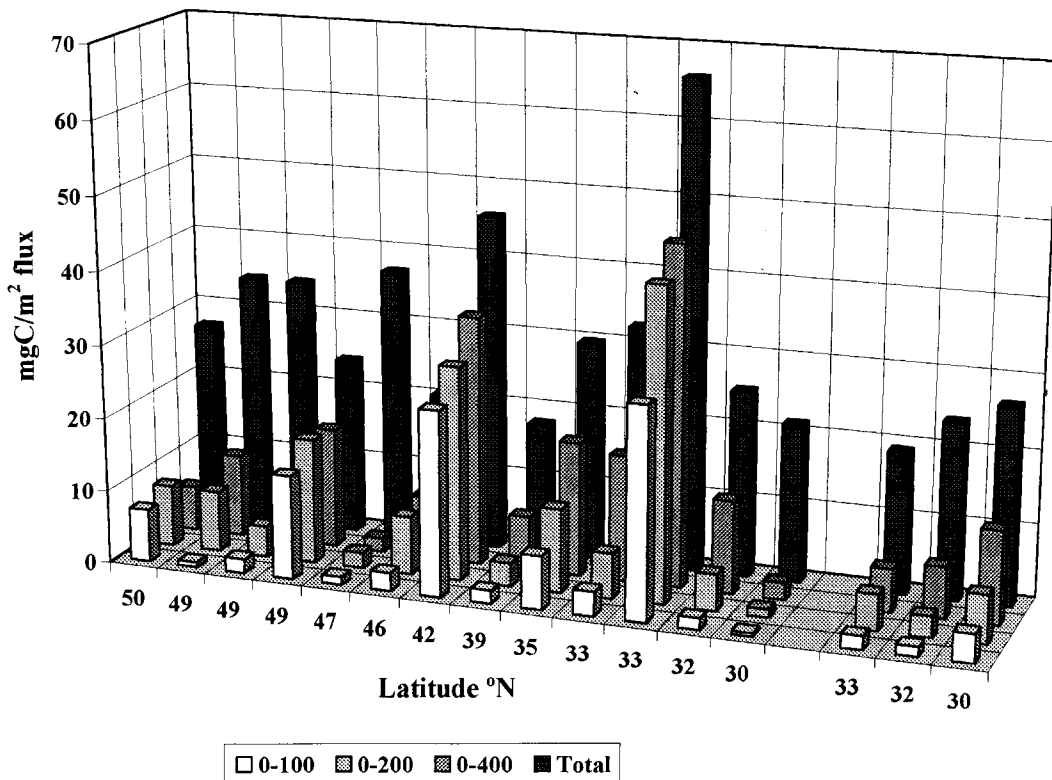
**Fish: Fluxes (mgC/m$^2$) resulting from DVM**



*Figure 7.* Fish: migratory fluxes (mgC/m$^2$) into the upper 100, 200 and 400 m of the water column, together with the total nighttime integrated standing crop in the water column sampled, in the same order as shown in Figure 2.

contributions to the total water column biomass at 39° N, 46° N and two of the near-slope stations at 49° N. In contrast, at all the more southerly stations (<39° N) their contributions were trivial. Whenever they were abundant, they made substantial contributions to the migratory fluxes. At 39° N and 46° N, their migratory fluxes into the upper 100 m amounted to 26 and 13 mgC m$^{-2}$, respectively. At the two outer slope stations at 49° N, their migratory fluxes into the upper 200 m were 28–38 mgC m$^{-2}$, but there was little migration into the upper 100 m. Ten days after the samples used in this analysis were collected at 39° N, the position was revisited. Already, the massive swarm of pteropods originally observed had disappeared, either because it had been advected out of the region or the population had collapsed. A similar situation prevailed at 42° N where a swarm of pteropods was sampled at 300–500 m by day, but only a relatively small biomass was taken at night mostly in the upper 100 m. This serves to highlight the high variability of the contri-

bution to migratory fluxes that may be made by such swarming species. The mean (maximum) percentages of the populations migrating up into the upper 100, 200 and 400 m, respectively, were 22(82)%, 31(98)% and 28(98)%.

*Tunicata (thaliaceans and pyrosomes) (Fig. 9)*

These gelatinous taxa often contributed substantially to total water column biovolumes but, in terms of carbon, their contributions to the total standing crop were quite small. At the southern stations in the vicinity of the Azores Front, the dominant species was *Pyrosoma atlantica*. In both seasons sampled, the whole of its population of large specimens was undertaking migrations from daytime depths of 500–700 m up into the upper 100 m at night. At the more northerly stations, *P. atlantica* was replaced by patchy swarms of the aggregate stages of *Salpa* and *Iasis* at some of the stations. These salps also undertook diel vertical migrations but not as extensive as the *P. atlantica* mi-

## Tunicata: Fluxes (mgC/m$^2$) resulting from DVM



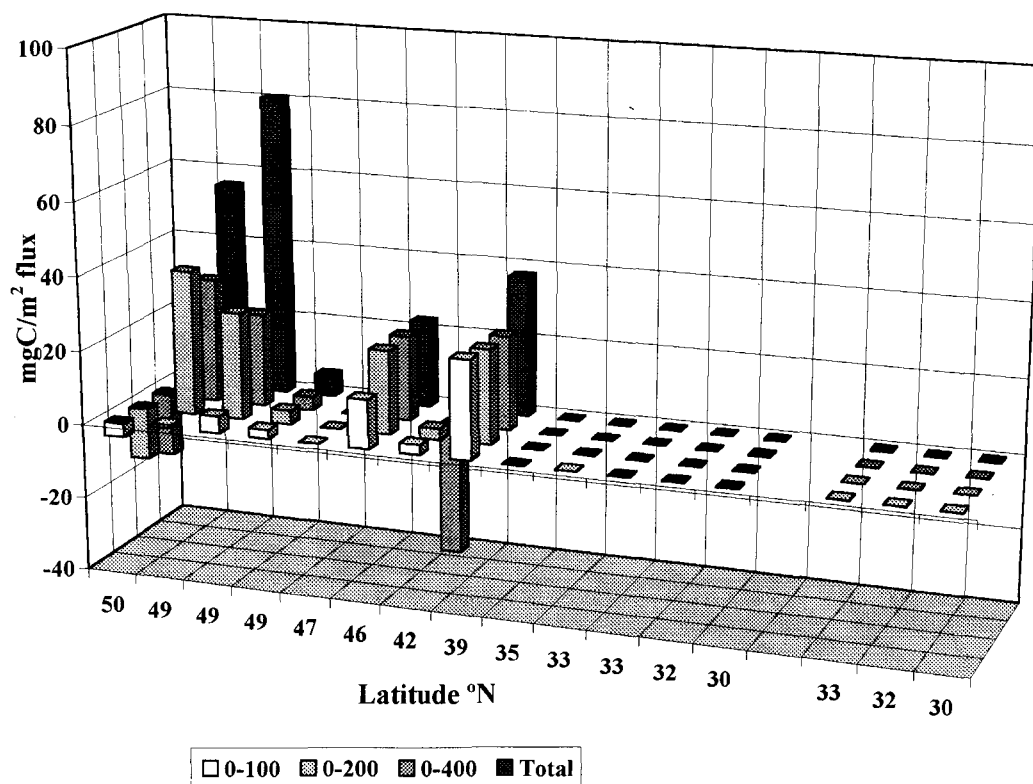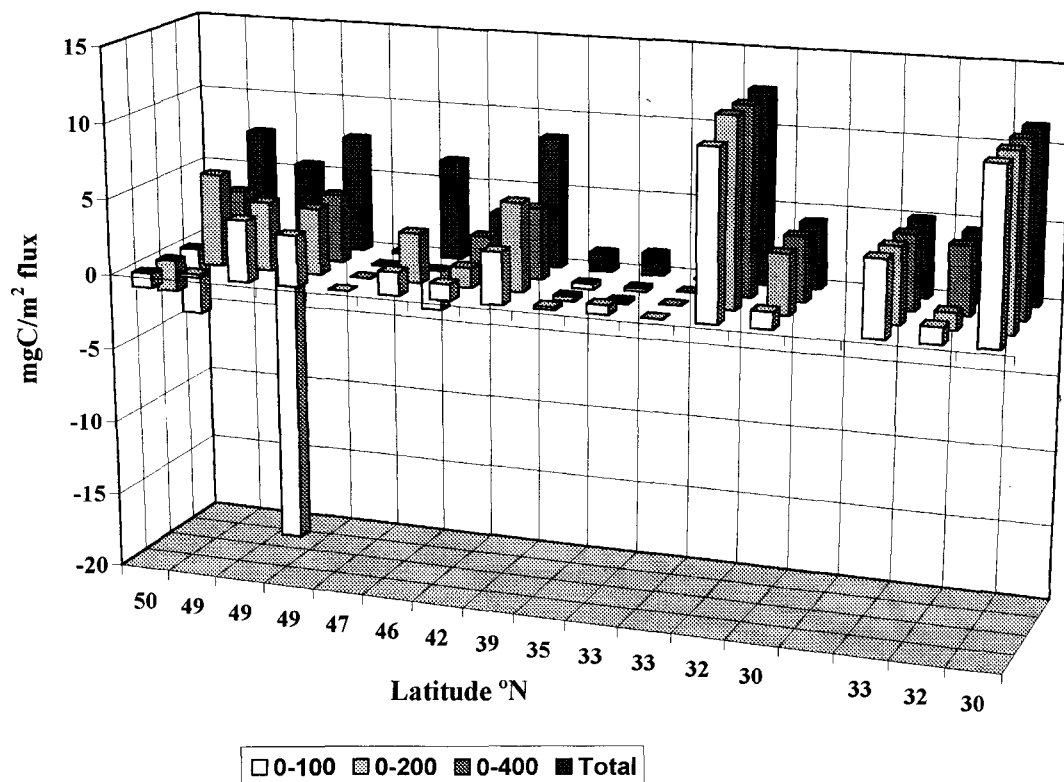*Figure 9.* Tunicata: migratory fluxes (mgC/m$^2$) into the upper 100, 200 and 400 m of the water column, together with the total nighttime integrated standing crop in the water column sampled, in the same order as shown in Figure 2.

through the meshes (e.g. Harbison et al., 1978; Pugh, 1989). Such extrusion effects will be unaffected by the day/night cycle. Secondly, avoidance of the nets by the organisms tends to be greater by day than by night. This contributes to the integrated biomass estimate for the daytime total water column sampled being lower and this will tend to result in migratory fluxes being over-estimated. The taxonomic groups that usually demonstrate the greatest day/night disparity are euphausiids (up to 40%), fish (10–20%) and decapod crustaceans (10–20%).

The third source of error arises if the vertical migrations are ranging to depths deeper than the lowest range of the sampling. Some species of fish and decapods are known to migrate from daytime depths of 1600–1700 m and 1200–1300 m, respectively, in the central oligotrophic gyre around the Azores Current region (Angel, 1989b; Domanski, 1986). However, in repeat samples from a depth of 1000 m in more productive temperate waters at 42° N, 17° W, Angel et al.

(1982) found that only one species of myctophid fish, *Notoscopelus elongatus kroyeri*, showed variations in abundance throughout 48 h of sequential sampling, and which were consistent with it undertaking diel vertical migrations from that depth synchronised with the light cycle. So at night, some of the shallow catches will have included some specimens, which may have migrated from depths deeper than the lower limit of daytime sampling. Over the slope, in particular, where the nets could not be fished very close to the sea-bed, the night-time catches may have been supplemented with diel migrants that are known to aggregate close to the sea-bed during the day (Wishner, 1980; Angel & Hargreaves, 1984; Angel, 1990). However, Pugh (unpublished data) has shown that several siphonophore species are unable to adapt their vertical ranges to shoaling or deepening bathymetry.

The fourth source of error is the high spatial heterogeneity shown by pelagic communities in general, which are known to show both passive and active re-
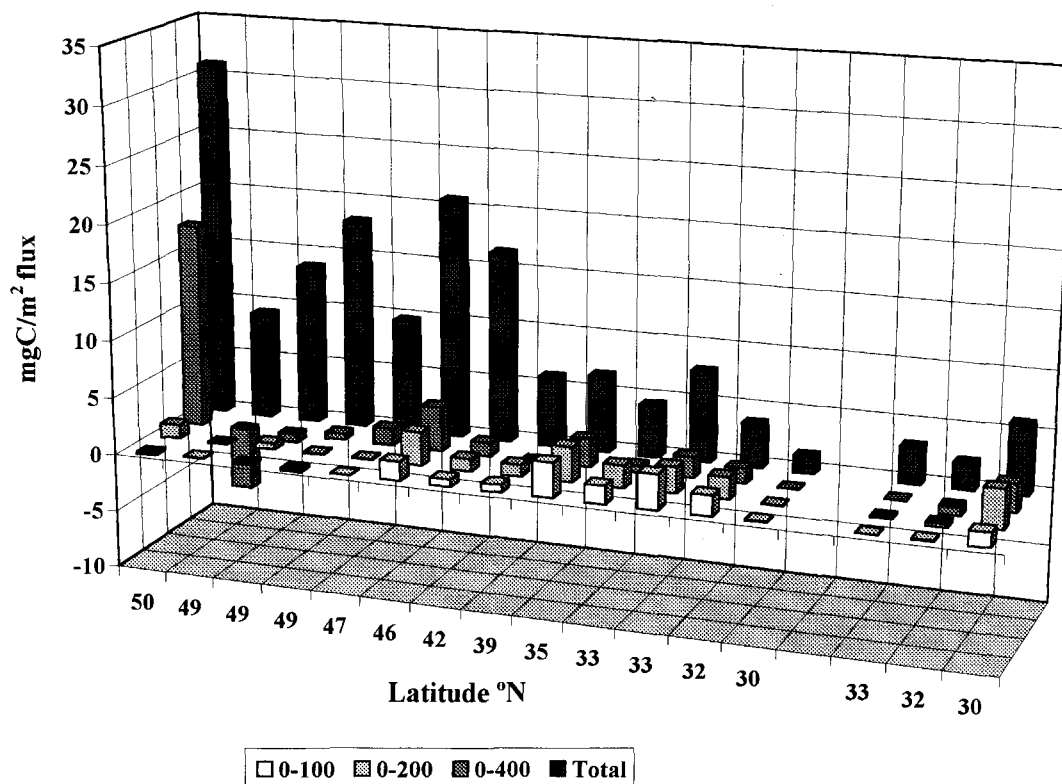
**Siphonophora: Fluxes (mgC/m$^2$) resulting from DVM**



*Figure 10.* Siphonophora: migratory fluxes (mgC/m$^2$) into the upper 100, 200 and 400 m of the water column, together with the total nighttime integrated standing crop in the water column sampled, in the same order as shown in Figure 2.

sponses to meso-scale eddies. Passive aggregation can occur at local convergences. But aggregation may be active, as postulated to explain the occurrence of much higher abundances of fish observed within the Azores Front than a few tens of kilometres on either side of it (Angel, 1989b). Aggregations can also build up as a result of very rapid reproduction and growth. Some taxa have exceptionally high potential rates of growth and reproduction. For example, Heron (1972) attributed the rapid build up (within a few days) of massive swarms of a *Thalia* species to its growth being more closely correlated to the second power of body length than to the usual third power. In other words, this species grows at a rate related to some function of area rather than body volume, and so it has the ability to respond exceptionally rapidly to localised enhancement of productivity. Swarming is a common phenomenon in several common pelagic taxa, notably thaliaceans, medusae and pteropods. Consequently, abundances of these groups may fluctuate by an order of magnitude

over quite small spatial scales and hence between successive samples. So by chance, a large swarm might have been sampled during the day but not by night (or vice versa); this will greatly distort our estimates of migratory fluxes.

Bearing these sources of error in mind, the data presented here are probably qualitatively reasonable but quantitatively questionable (may be accurate to within a factor of two or three), the consistency of many of the trends gives a measure of confidence. Until a technology capable of surveying large volumes of water is developed and validated (e.g. using bioacoustics), net-derived data remain the only basis on which the active migratory component of the biological pump can be assessed.

Biovolume, despite its widespread use in literature reports, is an unsatisfactory parameter for assessing the importance of these migratory fluxes. Gelatinous taxa in open ocean environments are often volumetrically dominant in the upper few hundred metres, but
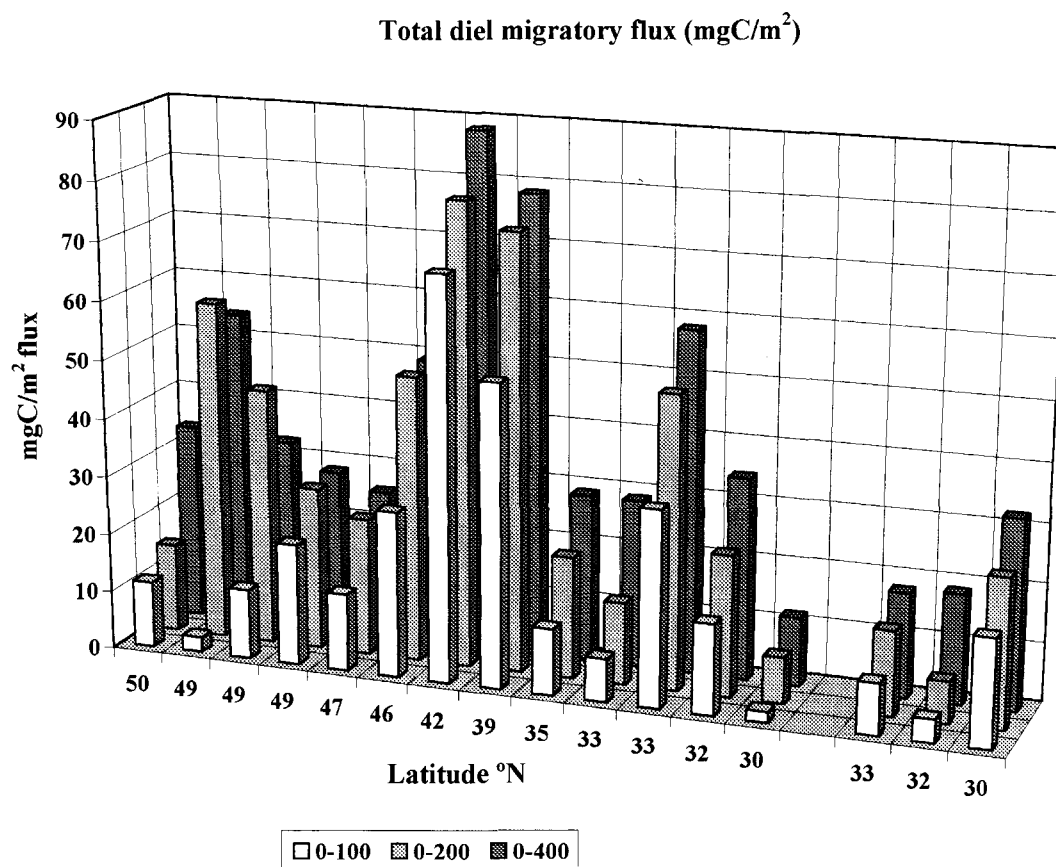
## Total diel migratory flux (mgC/m²)



*Figure 11.* Total micronektonic migratory nighttime fluxes (mgC/m²) into the upper 100, 200 and 400 m at all stations sampled. The fluxes values were calculated by summing the flux contributions by each of the dominant taxa.

in terms of organic carbon, their quantitative import-ance is lower. Since metabolic rates are more closely attuned to the organic content of the organisms rather than to their physical bulk, estimates based on carbon content are likely to provide a more precise estimate of the active fluxes resulting from the migrations. Even then, this assumes that all active fluxes are associ-ated with migrations that are synchronised with the light cycle. If non-synchronised movements are wide-spread (Pearre, 1979), the fluxes resulting from active transport may be even larger than estimated here. In addition, the intensity of acoustic back-scatter is better related to carbon content than biovolume.

The percentage of the total micronektonic biomass (in terms of carbon) involved in diel migrations into the upper 100 m ranged from 1.9% to 40.3%; from 8.8% to 58.0% into the upper 200 m; and from 19.7% to 61.4% into the upper 400 m. There appear to be systematic changes in these percentages related to lat-itude. The percentages migrating can be expected to

vary seasonally, particularly at the higher latitudes where many species undertake both ontogenetic and seasonal migrations, but the sampling coverage was inadequate to investigate such variations.

The fluxes into the upper 100 m integrated over all taxa at each station ranged from 1.8 to 68 mgC m$^{-2}$, and peaked at 39° and 42° N. The integrated flux at the Azores Front was high, but was low on either side of it but particularly on the western Atlantic Water side. There was also a low flux into the upper 100 m at the outermost slope station off the Goban Spur at 49° N, which was in marked contrast with the high flux into the upper 200 m at the same station. Integ-rated fluxes into the upper 200 m ranged from 7.8 to 78.5 mgC m$^{-2}$. Again, the maximum values were at middle latitudes at 39° and 42° N, closely followed by the high flux at the outermost station off the Goban Spur. Again, the lowest fluxes were associated with the waters either side of the Azores Front especially in winter; the flux at 50° N was also low. Integrated

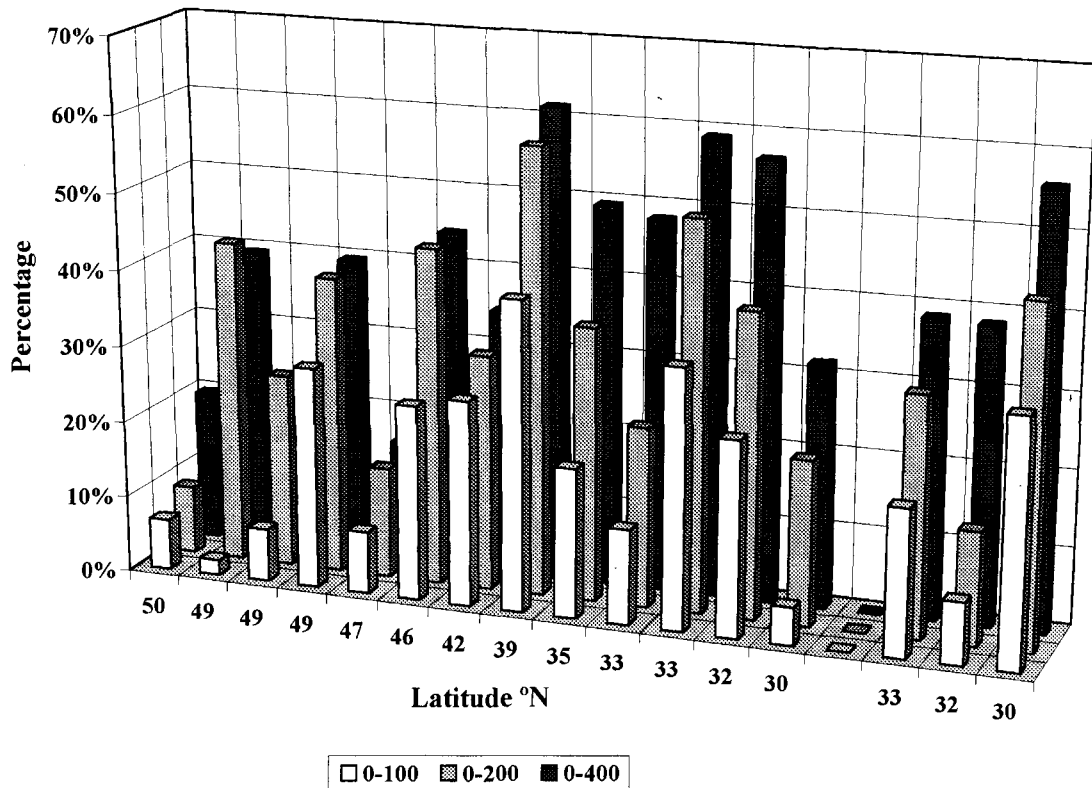## Percentage of the total micronektonic standing crop migrating



*Figure 12.* Percentages of the total micronekton standing crop engaged in vertical migration into the upper 100, 200 and 400 m.

fluxes into the upper 400 m ranged from 11.5 to 88 mgC m$^{-2}$ and were, with one exception, higher than those into the upper 200 m.

### Inter-taxa correlations in fluxes

A correlation analysis of the fluxes into the upper 100 m showed that the fluxes of amphipods, decapods, euphausiids, fish and pteropods were correlated positively at the 5% level with the total flux. However, there were few inter-taxa correlations. Flux estimates resulting from migrations by amphipods correlated positively with those generated by decapods and euphausiids, and those of decapods correlated with those of euphausiids and chaetognaths. Fluxes of euphausiids and pteropods into the upper 200 m were correlated positively with the total fluxes. However, the only significant correlation (at the 5% level) between individual taxa was a negative correlation between fluxes resulting from the migrations by amphipods and cephalopods, but this is almost certainly

an artifact resulting from the incomplete data set for the cephalopods. Generally, the number of correlations is small and within the number that statistically can happen by chance. In other words, these data provide no evidence for the migrations of the individual taxa being inter-related.

Fluxes up into the upper 400 m resulting from the migrations by decapods, euphausiids, fish and pteropods were correlated significantly with the total fluxes. However, the only positive correlation between pairs of taxa were between fish and amphipods, and pteropods and euphausiids; again there was a negative correlation between cephalopods and amphipods. These results suggest that the carbon fluxes associated with the migrations of the various taxa are independent of each other, the few positive correlations being no more than would be expected by chance.

*Taxa contributing most to active fluxes*

The taxa making the major contributions to the migratory fluxes varied with latitude. At seven stations, fish contributed the most to the fluxes into the upper 100 m; pteropods and tunicates were the major contributors at four stations, and euphausiids at one. Substantial contributions were made by fish at another two stations, euphausiids at a further three, tunicates at a further two. Generally, active carbon fluxes into the upper 100 m were dominated by four taxa: fish, pteropods, euphausiids and tunicates. Fluxes into the upper 200 m were dominated by these same taxa with very little change in their relative contribution. Fluxes into the upper 400 m were supplemented by decapod crustaceans whose fluxes ranging from 1.55 to 7.78 mgC $m^{-2}$, a relatively small range compared with most other taxa. At one station, they were the largest contributor and the second or third largest at eight other stations.

In previous sampling in the region and elsewhere, tunicates and pteropods have proved to be very patchily distributed in both time and space. Populations of both groups are highly responsive to the spring bloom in the north Atlantic (e.g. Vane & Colebrook, 1962; Hunt, 1968). Fish, on the other hand, are longer lived and less spatially patchy. Many fish species are migratory and many undertake ontogenetic migrations. So migratory fluxes can be expected to vary seasonally.

During May and June 1991, during a Lagrangian study centred at about 48° N, 17° 30′ W, the amphipod *Themisto compressa* was numerically the dominant component of the micronekton (Lampitt et al., 1993). At night, the ratios between the biomasses of fish:decapods:euphausiids:amphipods at 50–25 m were 1:10:100:450. Generally, during the day, populations of *T. compressa* were found at depths ranging from 100 to 400 m. However, one set of samples, collected immediately after a storm while wave conditions were still rough, showed that *T. compressa* had not migrated down and was still in very large numbers in the wind-mixed layer. Was this observation exceptional, or was it representative of a regular response by this (and maybe other species) to weather and rough seas? These amphipods were not only consuming marine snow but also producing faecal pellets, which resembled marine snow sampled deeper down (270 m) and contained viable cyanobacteria. Lampitt et al. (1993) estimated the gut flux at the time to be 0.43 mgC $m^{-2}$, which amounted to about 0.4% of the passive vertical flux of dry mass in floating sediment traps. Generally, in the stations reported here, amphipods were unlikely to be contributing more than a small percentage of the total active (migratory) flux.

*Estimates of diel migrants' contribution to export*

Longhurst & Harrison (1989) suggested that 20–50% of zooplankton vertically migrate, and Roman et al. (1993) reported that at night the zooplankton biomass nearly doubled in the upper 160 m of the water column near Bermuda. The possibility of diel vertical migration contributing to the transmission of food down through the water column was first postulated by Vinogradov (1968), who described the concept as "a ladder of migrations". Evidence for migrations contributing to the vertical fluxes of both organic and inorganic material has been reported subsequently in a number of publications (Angel, 1985, 1989; Longhurst & Harrison, 1988; Longhurst et al., 1990; Small & Ellis 1992; Dam et al., 1995; Steinberg et al., 2000). For gut fluxes to be substantial, feeding activity needs to be concentrated during the shallow phase of the migrations and gut clearance rates need to be long enough for the downward migrations to have been completed before evacuation occurs. This is well documented in indices of gut fullness in fishes (Merrett & Roe, 1974; Baird et al., 1975; Roe & Badcock, 1984; Gorelova & Kobylyansky, 1985; Hopkins et al., 1996).

Comparisons of the gut fullness of micronektonic and macroplanktonic species caught during the upward phase of migrations at dusk, and the downward phase at dawn (in Spring 1990; see Savidge et al., 1992), confirmed that, in most, their guts were full (Howell pers.com.). Similar observations of periodic feeding in mesoplankton have been published (e.g. Atkinson et al., 1996). However, reported gut clearance rates in copepods seem to be too rapid for them to be effective transporters of faecal material, even so they will still be contributing to active fluxes of carbon released either as respiratory carbon dioxide or as DOC – dissolved organic carbon (Dagg, 1976; Small et al., 1983). In *Calanus pacificus*, 17–19% of ingested carbon is released as DOC (Copping & Lorenzen, 1980). The migrants will also be exporting nitrogen from the euphotic zone, which is taken up during feeding near surface at night and then released by day at depth mostly as inorganic nitrogen (ammonia) but also as dissolved organic nitrogen (urea and amino acids) (e.g. Ikeda & Skoldal, 1989), and this probably makes a small, but still significant, contribution to the nutrient

fluxes (Longhurst & Harrison, 1988; Longhurst et al., 1989; Steinberg, et al., 2000).

It is worth attempting a tentative carbon export budget based on some of these estimates. In the Gulf of Mexico, Hopkins et al. (1996) estimated that the midwater standing stock of fishes of 133 kgC km$^{-2}$ (i.e. 133 mgC m$^{-2}$) produces 0.6–0.9 kgC km$^{-2}$ d$^{-1}$ of faeces. This represents a daily carbon transfer into faeces of 0.45–0.7% of the standing crop, which represents an annual transfer of about 150–250% of the fish standing crop. Since our data imply that 50% of the fish biomass is migrating, the fish gut flux is 75–125% of the mean standing crop of fish. Assuming that the daily ration of the fishes is 5% of the standing stock and that, like copepods, 20% of the carbon ingested is released as DOC. Then, a mean standing crop of fish of 100 mgC m$^{-2}$ produces an annual flux of DOC of 365 mgC m$^{-2}$, half of which will be released during the day at greater depths (i.e. 180%). Estimating mortality fluxes is even more problematical. But, if it is assumed that fish have annual life cycles, then the mean annual fish production will approximate the standing crop. So if half of the mortality occurs at the deeper daytime depths, then the annual mortality flux would be of the order of 50%. Thus, the total export flux will be equivalent to 100% (gut) plus 180% (DOC) and 50% (mortality) (i.e. of the order of 300% of the average standing crop). If other taxa contribute commensurately, then the export flux of migrating micronekton will be of the order of 300% of the total annual mean migrating population which, based on these samples, will be ~300–450 mgC m$^{-2}$ at latitudes >40° N and 150 mgC m$^{-2}$ at latitudes <40° N; this is comparable to the annual input of carbon of 70–390 mgC m$^{-2}$ estimated to be have reached an abyssal benthic community in the form of phytodetritus at 47° N, 20° W (Pfannkuche, 1993). While these estimates are highly speculative, and overlook seasonal variations in migration activity, they do serve to highlight the potential importance of these active fluxes, which so far with a few notable exceptions, has been ignored by those developing carbon and nutrient budgets for the deep ocean.

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