



Large-scale patterns of diel vertical migration in the North Atlantic

G. C. HAYS*

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Abstract—Samples historically collected and analysed by the Continuous Plankton Recorder (CPR) survey in the North Atlantic were used to examine large-scale spatial patterns in both the normal diel vertical migration (normal DVM) behaviour and the mean body size within epi-pelagic copepod communities. Normal DVM was most marked in the northwest Atlantic and less marked in the northeast Atlantic and in shallow coastal areas such as around the U.K. and on the Grand Banks of Newfoundland. These patterns of normal DVM were strongly correlated with patterns of mean body size, with normal DVM being more marked in those areas where larger species predominated. In both the northwest and northeast Atlantic, marked seasonal changes occurred in the migrating biomass. In the northwest Atlantic, *Euchaeta norvegica* and *Calanus finmarchicus* were the most important contributors to the total migrating biomass, while in the northeast Atlantic the most important contributors were *E. norvegica*, *Metridia lucens* and *Pleuromamma robusta*. Copyright © 1996 Elsevier Science Ltd

INTRODUCTION

It has been known for many years that a diverse range of zooplankton regularly undertake daily vertical movements through the water column, a behaviour generally termed diel vertical migration (DVM) (Clarke, 1930; Hardy, 1936). The normal pattern (normal DVM) is for populations to occupy greater depths during the day and shallower depths at night, with the amplitude of vertical movement (i.e. the difference between the mean day and mean night depths) varying between species from a few metres to tens or even hundreds of metres (Longhurst, 1985).

Due to the widespread occurrence of normal DVM there has been much debate over the function of this behaviour, with the strongest evidence suggesting that normal DVM serves principally to reduce the risk of mortality from visually orientating predators such as fish (for review see Lampert, 1989). According to this “predator-evasion” hypothesis, zooplankton use deep waters as a dark daytime refuge where their probability of being perceived, and hence consumed, is lower than if they remained in the more well-lit near-surface waters. The evidence in support of the predator-evasion hypothesis comes from a variety of sources. For example, in experimental enclosures, normal DVM may be induced in previously non-migratory populations by the introduction of planktivorous fish (Bollens and Frost, 1989); in natural populations long-term decadal changes in the intensity of normal DVM may be highly correlated with changes in the abundance of planktivorous fish (Hays, 1995); seasonal variations in the timing of vertical migration occur so that populations tend to occur near the surface mainly at night (Hays *et al.*, 1995); and normal

* School of Biological Sciences, University of Wales, Singleton Park, Swansea SA2 8PP, U.K.

DVM tends to occur most strongly in large or heavily pigmented species, i.e. those species that are most susceptible to visual predators (Hays *et al.*, 1994).

While an understanding of the ultimate cause of normal DVM is of intrinsic biological importance, normal DVM is also of topical interest in the context of its biogeochemical impacts. These impacts have been considered in general terms for many years (cf. Vinogradov, 1968) but have recently been more rigorously quantified (Longhurst and Harrison, 1988, 1989; Longhurst *et al.*, 1989). For example, by feeding predominantly above the thermocline at night and then residing below the thermocline during the day, where they feed little but continue to excrete and respire, migrating zooplankton may cause the removal of elements such as nitrogen and carbon from the surface mixed layer at rates approaching or even exceeding those mediated through the passive sinking of particulate material (Longhurst and Harrison, 1988). As the rate of nitrogen removal from the surface mixed layer is typically an integral component in ecosystem models of plankton dynamics (e.g. Taylor *et al.*, 1993), accurate parameterisation of this rate of removal is important. To date, however, efforts to quantify the vertical elemental flux caused by normal DVM have been restricted to a small number of sites (Longhurst and Harrison, 1988) and, consequently, an assessment of the extent of DVM on more spatially extended scales is an important goal for biological oceanography.

In this paper I therefore examine the large-scale spatial patterns of normal DVM for epipelagic copepod communities in the North Atlantic and adjacent seas. To do this, the data-set historically collected by the Continuous Plankton Recorder (CPR) survey is used (Warner and Hays, 1994). The data from the CPR survey have traditionally been used to examine spatio-temporal patterns and long-term trends in the abundance of zooplankton but more recently have been used to examine intra- and inter-specific patterns of normal DVM (Hays *et al.*, 1994, 1995). Since normal DVM tends to increase in larger copepods, it might be expected that where larger species predominate, normal DVM should be more marked in the copepod community as a whole, and, similarly, where smaller species predominate, normal DVM should be less marked. Therefore, the spatial patterns of normal DVM and mean body size are compared. Second, as a step towards quantifying the biogeochemical impact of normal DVM over large spatial scales, the mean biomass of migrating copepods in different parts of the North Atlantic is estimated. Finally, seasonal changes in this migrating biomass are quantified and the relative contributions of different species are identified.

METHODS

Samples were collected by Continuous Plankton Recorders towed near the surface (mean recorded depth 6.5 m; Hays and Warner, 1993) from ships of opportunity and were analysed using standardised methods (see Warner and Hays, 1994). In the CPR survey, a number of numerically important copepod species such as *Calanus finmarchicus*, *C. helgolandicus*, *Euchaeta hebes*, *Euchaeta acuta* and *Undeuchaeta plumosa*, were identified to species level only in samples collected from 1958 onwards. Given this, the analysis of the CPR data was restricted to those samples collected between 1958 and 1992.

For each sample the local time that the sample was collected, the geographical location of that sample and the abundance of each of the 39 most common copepod taxa were recorded. These 39 taxa account for > 99.9% of all the copepod specimens in the CPR samples.

For some of the smaller copepod taxa, a proportion of the specimens that enter a CPR

will be lost through the 270 μm filtering mesh and thus their relative abundance may be underestimated if this loss is not accounted for. Using the relationship that has been established previously between the prosome width of copepods and their retention on the CPR mesh (Hays, 1994) and assuming the prosome widths given in Hays *et al.* (1994), corrections were made for this loss of small specimens through the CPR mesh and thus the abundance of the different taxa was calculated in that volume of water filtered to collect each sample. I estimated the wet weight of the different copepod taxa using the prosome width:wet weight relationship reported by Pearre (1980).

For each 2° latitude by 4° longitude area in the North Atlantic and adjacent seas, I then calculated the mean wet weight of copepods in those samples taken at midnight ± 3 h ("night" samples) and at midday ± 3 h ("day" samples). To calculate the mean proportion of the copepod biomass that migrated out of the near-surface layers between the night and the day ("Mean Community DVM"), I used the equation:

$$\text{Mean Community DVM} = \frac{\text{Mean night biomass} - \text{Mean day biomass}}{\text{Mean night biomass}} \quad (1)$$

I termed the mean size of all the copepods caught in different areas the "Mean Community Body Size". Thus the Mean Community Body Size was calculated as:

$$\text{Mean Community Body Size} = \frac{(N_1 \cdot W_1) + (N_2 \cdot W_2) + \dots + (N_{39} \cdot W_{39})}{N_1 + N_2 + \dots + N_{39}} \quad (2)$$

where N_1 – N_{39} were the total numbers of each of the 39 taxa in each area, and W_1 – W_{39} were the wet weights of each of these taxa.

RESULTS

Species occurrence in samples

A total of 129,269 CPR samples have been analysed from tows made between 1958 and 1992 in the North Atlantic bounded by 33–69°N and 76°W–13°E. The number of samples in which the different taxa (copepodite stages V–VI unless otherwise stated) were identified and the assumed prosome widths of the different groups are given in Table 1. For example, *Acartia* spp. were identified on 34,157 samples, *Anomalocera pattersoni* on 298 samples etc.

Diel differences in mean community body size

There was a major variation in the Mean Community Body Size in different areas. For example, if the analysis was restricted to those 2° by 4° areas within which ≥ 50 samples were collected during both the day and the night, the Mean Community Body Size varied between 0.17 and 2.44 mg wet weight (mean 0.77 mg) for night samples and between 0.12 and 1.14 mg wet weight (mean 0.44 mg) for day samples. The Mean Community Body Size for these night and day samples collected in the same areas were highly correlated: Mean Community Body Size for night samples = 2.08 (Mean Community Body Size for day samples) $- 0.14$ ($r^2 = 0.80$, $F_{1,122} = 493$, $P < 0.01$). While these night and day sizes were well correlated, the Mean Community Body Size was significantly higher at night (Paired *t*-test, $t_{123} = 8.9$, $P < 0.01$) (Fig. 1).

Table 1. The number of samples on which the different copepod taxa were identified and their assumed prosome width. Unless otherwise stated, copepodite stages are V and VI. The total number of analysed samples was 129,269

Species	Number of samples identified on	Prosome width (mm)
<i>Acartia</i> spp.	34,157	0.33
<i>Anomalocera pattersoni</i>	298	1.30
<i>Calanoides carinatus</i>	1101	0.75
<i>Calanus finmarchicus</i>	54,234	0.95
<i>C. glacialis</i>	999	1.00
<i>C. helgolandicus</i>	28,124	0.81
<i>C. hyperboreus</i>	949	2.70
<i>C. tenuicornis</i>	578	0.64
<i>Calanus</i> spp. I-IV	49,016	0.50
<i>Candacia armata</i>	3293	1.00
<i>Centropages bradyi</i>	454	1.00
<i>C. hamatus</i>	4394	0.52
<i>C. typicus</i>	18,461	0.63
<i>Clausocalanus</i> spp.	7382	0.47
<i>Corycaeus anglicus</i>	3445	0.43
<i>Eucalanus crassus</i>	538	0.95
<i>Euchaeta acuta</i>	1378	1.36
<i>E. hebes</i>	1640	1.04
<i>E. norvegica</i>	9476	2.68
<i>Euchirella rostrata</i>	1024	1.14
<i>Heterorhabdus norvegicus</i>	306	1.15
<i>Isias clavipes</i>	387	0.50
<i>Labidocera wollastoni</i>	675	1.00
<i>Metridia lucens</i>	20,862	1.05
<i>M. longa</i>	1663	1.60
<i>Metridia</i> spp. I-IV	1379	0.60
<i>Neocalanus gracilis</i>	1608	1.07
<i>Nannocalanus minor</i>	3220	0.74
<i>Oithona</i> spp.	33,973	0.27
<i>Pleuromamma abdominalis</i>	1949	1.28
<i>P. borealis</i>	3907	0.73
<i>P. gracilis</i>	2884	0.73
<i>P. piseki</i>	679	0.73
<i>P. robusta</i>	6028	1.46
<i>P. xiphias</i>	455	1.68
<i>Para-Pseudocalanus</i> spp. I-VI	50,162	0.44
<i>Rhincalanus nasutus</i>	851	1.14
<i>Temora longicornis</i>	17,868	0.62
<i>Undeuchaeta plumosa</i>	1638	1.33

Spatial patterns of DVM of body size

There was generally a strong positive relationship between the Mean Community Body Size of copepods in each 2° by 4° area and the Mean Community DVM. The unexplained variation in this relationship may have reflected inaccuracies in the estimates of either the Mean Community DVM or the Mean Community Body Size caused by low sampling intensities in certain areas. If this were the case, one would expect the correlation coefficient

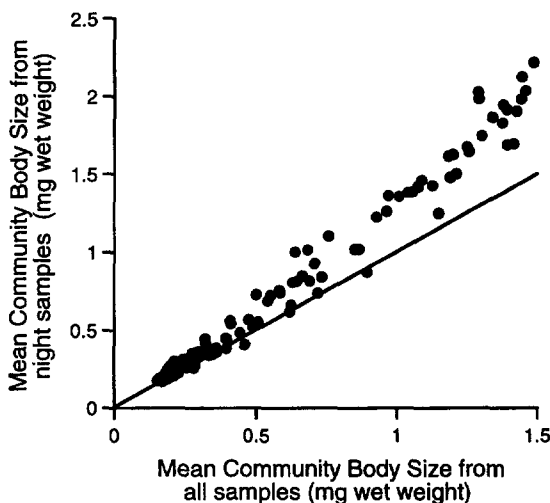


Fig. 1. Mean Community Body Size (equation (2)) calculated from samples collected at night versus the Mean Community Body Size calculated from all samples (i.e. those collected during both the day and the night) for those 2° by 4° areas within which ≥ 50 day and ≥ 50 night samples were analysed ($n =$ a total of 118 areas). The line of equivalence is shown. Most points lie above this line, indicating that the Mean Community Body Size was higher at night than during the day.

for this relationship to increase when only those areas that were well sampled were considered in the comparison, and this was, indeed, found to be the case (Fig. 2a). For example, when the comparison included all those areas within which ≥ 10 day and ≥ 10 night samples had been analysed, the correlation coefficient was only 0.32, but when this comparison was restricted to those areas in which ≥ 70 day and ≥ 70 night were analysed, the correlation coefficient was 0.70.

In plotting the spatial pattern of the Mean Community DVM, a compromise needed to be sought between (i) maximising the number of areas for which a value was plotted and (ii) minimising the inaccuracy in the estimated values. Given that the asymptote for the correlation coefficient of the relationship between the Mean Community Body Size and the Mean Community DVM in different areas was closely approached when there were ≥ 70 day and ≥ 70 night samples in each area, I used this as the minimum required sampling intensity when plotting the large-scale spatial patterns of these two parameters.

There was a total of 99 areas within which ≥ 70 day and ≥ 70 night samples were analysed. For these areas there was a clear spatial pattern in the Mean Community DVM (Fig. 3a). Mean Community DVM was highest in the oceanic area between Newfoundland and Iceland and lowest in the northeast Atlantic and in shallow coastal areas such as around U.K. and on the Grand Banks of Newfoundland.

The Mean Community Body Size showed a similar spatial pattern to that of Mean Community DVM (Fig. 3b), i.e. Mean Community Body Size was high between Newfoundland and Iceland and low in the northeast Atlantic and in shallow coastal areas.

Spatial patterns of migrating biomass

For CV–VI stages of members of the families Metridiidae, Calanidae, and Euchaetidae, I

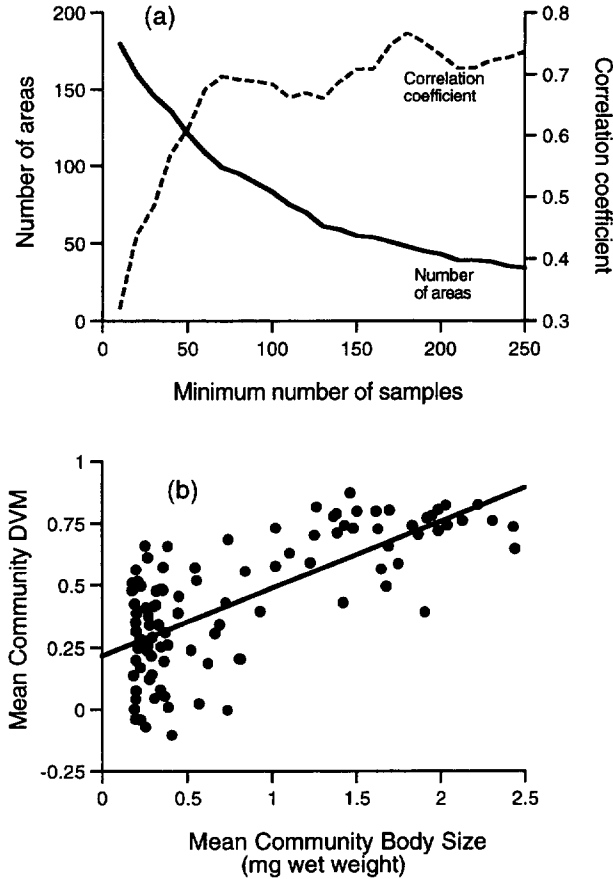


Fig. 2. (a) The variation in the correlation coefficient between the Mean Community DVM (equation (1)) and the Mean Community Body Size (equation (2)) (mg wet weight) for those 2° by 4° areas within which a certain minimum number of samples were analysed from both the day and the night. (b) For those 2° by 4° areas within which ≥ 70 day and ≥ 70 night samples were analysed, the relationship between the Mean Community Body Size (mg wet weight) for samples collected at night and the Mean Community DVM. Mean Community DVM = 0.27 (Mean Community Body Size) + 0.22 ($r^2 = 0.50$).

quantified the absolute biomass that migrated out of the near-surface layers between night and day. To do this, samples collected throughout the year were pooled and it was assumed that the filtration efficiency of the CPR was always 100% (i.e. the volume of water filtered equalled the inlet aperture multiplied by the length of tow) and thus that 3 m^3 was filtered in the collection of each sample. The mean absolute biomass that migrated followed the same pattern as that of the Mean Community DVM, with a generally high migrating biomass between Newfoundland and Iceland and a generally low migrating biomass in the northeast Atlantic and in coastal areas (Fig. 4a). On the basis of this map of the migrating biomass, I selected two areas within which to examine details of seasonal changes and also the relative contributions of different species. These two areas were the oceanic region between Newfoundland and Iceland (Area A) and the oceanic northeast Atlantic (Area B) (Fig. 4b).

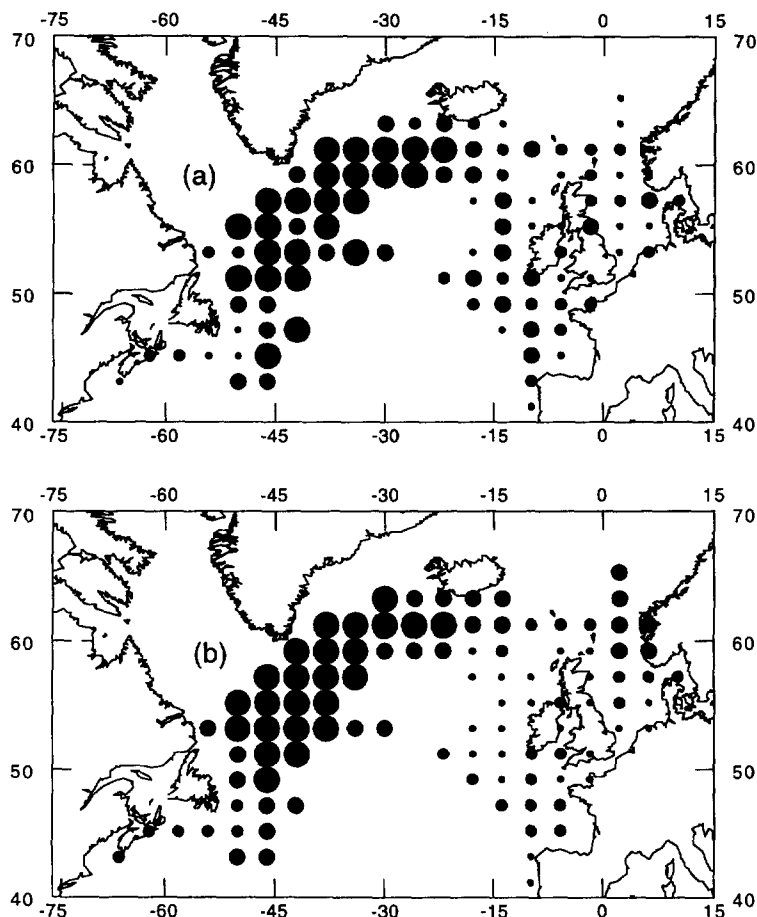


Fig. 3. (a) The Mean Community DVM (equation (1)) in the North Atlantic and adjacent seas. Symbol sizes: $\bullet = 0.09$ (range -0.10 – 0.24), $\bullet = 0.35$ (range 0.25 – 0.46), $\bullet = 0.57$ (range 0.47 – 0.70) and $\bullet = 0.77$ (range 0.71 – 0.87). Symbols are plotted for individual 2° by 4° areas within which there were ≥ 70 day and ≥ 70 night analysed samples. The range of values in the four plotted categories were selected so that there was a similar number of sample areas in each category. (b) The Mean Community Body Size (wet weight) of copepods collected at night. Symbol sizes: $\bullet = 0.21$ mg (range 0.17 – 0.27 mg), $\bullet = 0.34$ mg (range 0.27 – 0.45 mg), $\bullet = 0.94$ mg (range 0.52 – 1.43 mg), $\bullet = 1.88$ mg (range 1.46 – 2.44 mg).

Seasonal patterns of migrating biomass

In both Areas A and B there were marked seasonal changes in the mean copepod biomass that migrated out of the near-surface waters between the night and the day. In Area A, the mean biomass that migrated was lowest in winter (November, December, January and February) and increased progressively through March, April and May to reach a maximum in July and August, when an average of approximately 230 mg wet weight m^{-3} migrated daily (Fig. 5a). In Area B, the mean daily biomass that migrated was again lowest in winter but showed a bimodal seasonal pattern with maxima in April–May and in August–October, when approximately 18 mg wet weight m^{-3} migrated daily (Fig. 5b).

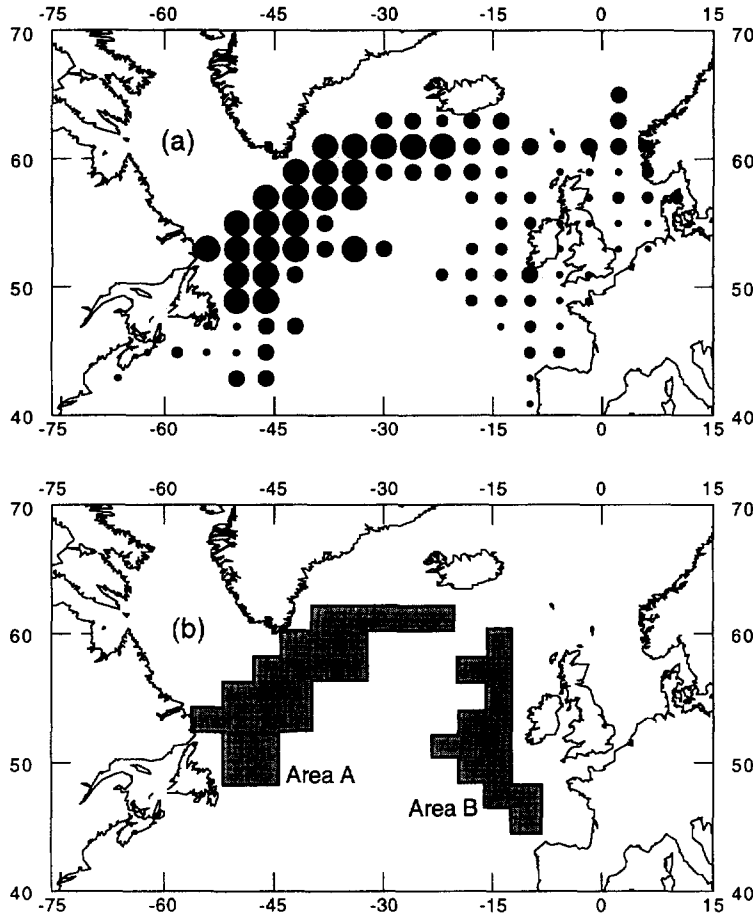


Fig. 4. (a) For copepodite stages CV–VI of members of the families Metridiidae, Calanidae, and Euchaetidae, the mean biomass (wet weight m^{-3}) that migrated out of the near-surface waters between night and day, calculated with the assumption that the volume of water filtered per sample was 3 m^3 . Symbol sizes: $\bullet = 1.9 \text{ mg m}^{-3}$ (SD = 5.1 mg m^{-3}), $\bullet = 11.0 \text{ mg m}^{-3}$ (SD = 2.3 mg m^{-3}), $\bullet = 36.4 \text{ mg m}^{-3}$ (SD = 13.4 mg m^{-3}), $\bullet = 91.3 \text{ mg m}^{-3}$ (SD = 32.0 mg m^{-3}). (b) The two areas selected for detailed examination of seasonal changes in the migrating biomass and also the relative contributions of different species.

These seasonal patterns in the mean biomass that migrated daily could reflect (i) seasonal changes in the near-surface abundance of copepods, or (ii) seasonal changes in the proportion of the community that migrated. To identify the relative importance of (i) and (ii), for each area the seasonal pattern in the mean migrating biomass was entered into a step-wise regression with the mean monthly night biomass and the mean proportion of the community that migrated in each month calculated as: $(\text{night biomass} - \text{daytime biomass}) / (\text{night biomass})$. In Area A the only factor that entered the resulting equation was the mean monthly night biomass, which explained $>99\%$ of the seasonal variation in the mean biomass that migrated daily (Fig. 5a). In Area B, the mean monthly night biomass explained 85.5% of the seasonal variation in the mean biomass that migrated daily, with a further

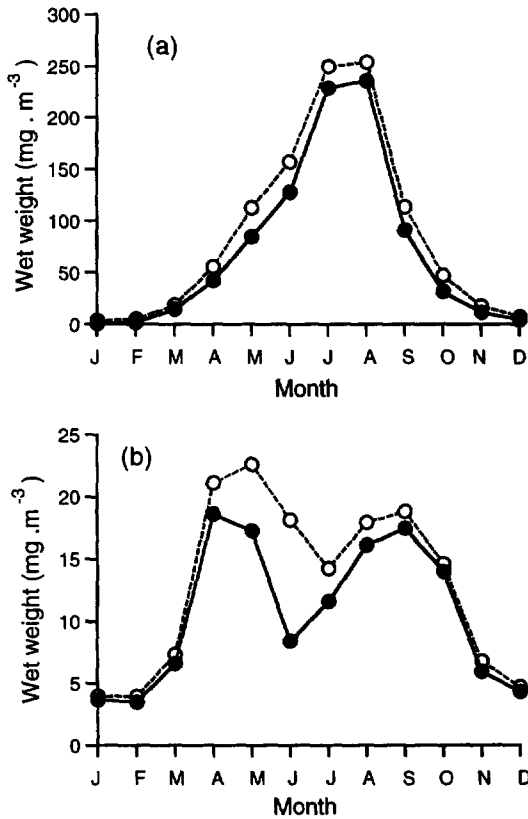


Fig. 5. For copepodite stages CV-VI of members of the families Metridiidae, Calanidae, and Euchaetidae, the seasonal variation in both the mean biomass (wet weight in mg m^{-3}) that migrated out of the near-surface waters between the night and the day (●-●) and the mean biomass at night (wet weight in mg m^{-3}) (○-○), for (a) Area A, and (b) Area B. The r^2 between these two measures was 99.4% in Area A and 85.5% in Area B.

14.3% being explained by seasonal changes in the proportion of the community that migrated (Fig. 5b).

Contribution of different taxa to the overall migrating biomass

For Areas A and B, I examined which species were most responsible for the differences in near-surface biomass between day and night samples. I restricted these analyses to the months April–October, i.e. to those months when the higher migrating biomasses were recorded (from Fig. 5). In Area A, in all of these months two species, *Calanus finmarchicus* and *Euchaeta norvegica*, accounted for > 85% of the total migrating biomass (Fig. 6a), with a smaller, but noticeable, contribution being made by *C. hyperboreus* in April and May. In Area B, *Metridia lucens* and *Euchaeta norvegica* were the most important contributors to the overall migrating biomass. *Pleuromamma robusta* was a third major contributor in August–October. *C. finmarchicus* and *C. helgolandicus* were noticeable contributors to the overall

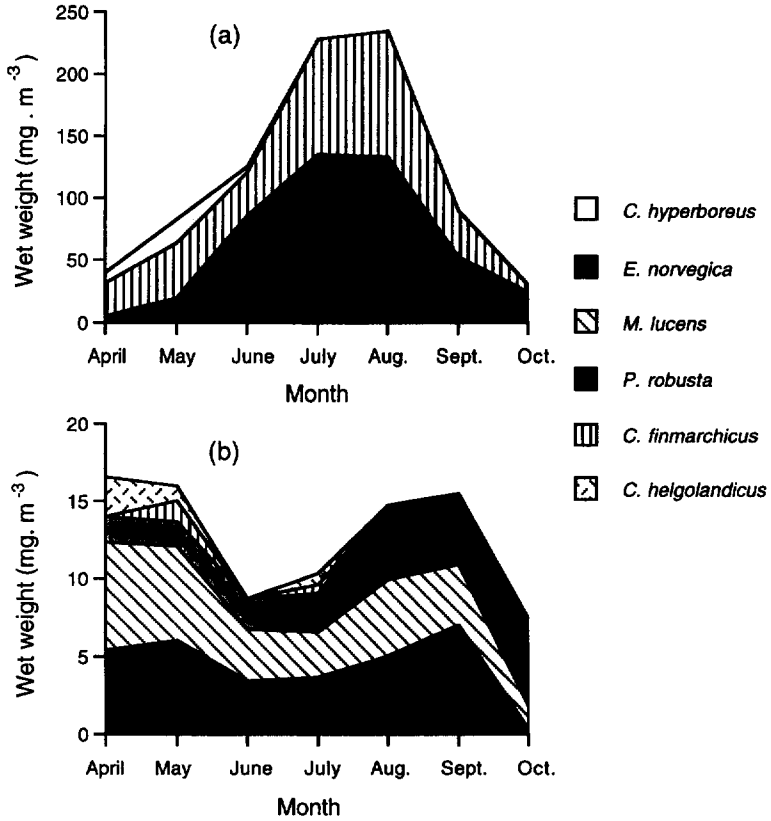


Fig. 6. (a) and (b). For CV–VI stages of members of the families Metridiidae, Calanidae, and Euchaetidae, the seasonal variation in the mean biomass (wet weight in $\text{mg} \cdot \text{m}^{-3}$) of different species that migrated out of the near-surface waters between the night and the day in Area A and Area B, respectively. The species plotted are those that contributed $\geq 5\%$ of the total migrating biomass in at least one of the months in that region. For example, in July in Area A, the migrating biomass of *Calanus finmarchicus* and *Euchaeta norvegica* was 92.6 and 135.5 $\text{mg} \cdot \text{m}^{-3}$, respectively, while in May in Area B, the migrating biomasses of *M. lucens* and *E. norvegica* were 6.9 and 5.4 $\text{mg} \cdot \text{m}^{-3}$, respectively.

migrating biomass only in April and May, although even in these months their contribution was relatively small (Fig. 6b).

DISCUSSION

While the geographical distributions of many species of zooplankton are well known (e.g. Oceanographic Laboratory, Edinburgh, 1973), these data have not been combined before to show the large-scale patterns in the mean size of species that occur in different areas. My calculations highlight first that the Mean Community Body Size shows a large spatial variation in the North Atlantic, with mean values within different 2° by 4° areas varying by over an order of magnitude. Second, there was a marked diel difference in the Mean Community Body Size, with the mean size of species near the surface being markedly higher

during the night (0.77 mg wet weight) compared to during the day (0.44 mg wet weight) (Fig. 1).

These calculations assume there are no body-size dependent diel differences in the avoidance of the CPR by different zooplankton taxa. For some plankton nets, however, it has been shown that net avoidance increases during the day compared to during the night, particularly for larger (and hence faster) species. Such differential day/night avoidance occurs, for example, because during the day an approaching net may be seen earlier, and hence avoidance behaviour initiated sooner, than during the night (McGurk, 1992). Differential day/night avoidance of the CPR has not been measured directly, and so the extent of this problem can only be inferred from studies made with other nets. McGurk (1992) was able to model the differential day/night avoidance of plankton samplers by herring larvae as a function of both the size of the larvae and the towing speed of the net. It was shown that at a towing speed of 2500 mm s^{-1} (the fastest speed examined), there was no differential day/night avoidance by larvae up to a size of approximately 10 mm. Since the CPR is typically towed at $> 6500 \text{ mm s}^{-1}$ (Hays and Warner, 1993) and copepods are likely to have a poorer avoidance ability than 10 mm herring larvae, by inference, the differential day/night avoidance of the CPR by copepods is likely to be negligible. Thus, this diel difference in the Mean Community Body Size is unlikely to be an artefact of size dependent differential day/night avoidance. Furthermore, this diel difference is readily explainable in terms of the known tendency for normal DVM to be more evident in larger copepods (Hays *et al.*, 1994). At night, both large and small species tend to be found near the surface, explaining why the Mean Community Body Size was relatively large, while during the day, the larger species tend to occur deeper (i.e. below the sampling depth of the CPR), explaining why the Mean Community Body Size was relatively small.

Mean Community Body Size and Mean Community DVM were found to co-vary in the North Atlantic (Fig. 2). This observation extends the previously reported relationship between the size of individual copepod species and their DVM behaviour to a community level, i.e. in areas where the copepod community consists of larger species, that community shows a stronger tendency to migrate than in areas where the community is composed of smaller species. However, even when poorly sampled areas were ignored, the Mean Community Body Size in different areas still explained only about 50% of the geographic variation in the Mean Community DVM (Fig. 2), suggesting that other factors, aside from body size, influence the tendency for species to migrate. This conclusion is consistent with results from a previous inter-specific comparison in a single area in which body size explained 47% of the variation in normal DVM, with much of the residual variation being explained by the pigmentation and morphology of the different taxa (Hays *et al.*, 1994). For example, small copepod species that show a strong tendency to migrate are typically heavily pigmented, while large species that do not migrate typically have a very elongate morphology (Hays *et al.*, 1994).

There were striking large-scale patterns for both the Mean Community Body Size and the Mean Community DVM (Fig. 3), with relatively large, strongly migrating copepods dominating in the oceanic region between Newfoundland and Iceland and relatively small, weakly migrating copepods dominating in the northeast Atlantic and in shallow coastal areas. One hypothesis to explain these patterns is that they are related to regional differences in sea surface temperature (SST). Ambient temperature is known to influence the size at maturity of many invertebrates, with individual species generally attaining a larger body size at colder temperatures (McLaren, 1963; Uye *et al.*, 1982). Furthermore, temperature has

also been suggested to determine the size of the species that predominate in any region (Sverdrup *et al.*, 1942). In accordance with this "Temperature Control Hypothesis", relatively larger species were observed to dominate in colder areas such as the northwest Atlantic, while relatively smaller species dominated in warmer areas such as the northeast Atlantic.

Alternatively, the observed patterns of Mean Community Body Size may be linked to geographic variations in the abundance of visual predators, which I term the "Predation Control Hypothesis". In freshwater environments considerable evidence has accumulated to suggest that the intensity of visual predation is the main ultimate factor determining the size spectrum of species within zooplankton communities. For example, in lakes where planktivorous fish are abundant, smaller zooplankton species predominate as a result of selective predation by fish on larger prey (Brooks and Dodson, 1965; Black and Hairston, 1988). However, this role of fish has received far less attention in marine environments. For commercially exploited planktivorous fish, such as Atlantic mackerel (*Scomber scombrus*) and Atlantic herring (*Clupea harengus*), reliable descriptions of their geographical range are known (Collette and Nauen, 1983; Whitehead, 1985; Whitehead *et al.*, 1988). Assessing the distributions of planktivorous fish species that are not commercially exploited is more problematic (Roger, 1994), but may be estimated in qualitative terms by the distribution of their predators such as small tunas. The Predation Control Hypothesis successfully accounts for the generally smaller body size of copepods that was observed in shallow coastal areas and in the oceanic northeast Atlantic, since these are areas where the abundance of either planktivorous fish or small tunas is high. For example, scombrids such as skipjack (*Scomber pelamis*), Atlantic bonito (*Sarda sarda*), albacore (*Thunnus alalunga*) and Atlantic mackerel (*Scomber scombrus*), as well as the planktivorous saury (*Scomberesox saurus*) are all generally abundant in the northeast Atlantic and around the U.K., but are not found in the northwest Atlantic (Wheeler, 1963; Collette and Nauen, 1983). Similarly, abundant planktivorous clupeoids such as herring (*Clupea harengus*), sprat (*Sprattus sprattus*), pilchard (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*), occur in shallow coastal areas around the U.K. but not in the oceanic area between Newfoundland and Iceland (Whitehead, 1985; Whitehead *et al.*, 1988).

The Predation Control Hypothesis may be readily extended to explain the observed spatial patterns of Mean Community DVM. In the northeast Atlantic and in shallow shelf seas, where the high intensity of visual predation causes small copepods to dominate, the Mean Community DVM may be low because the small size of these species alone minimises their risk of being perceived and hence consumed by visual predators. Conversely, between Newfoundland and Iceland where there is a lower intensity of visual predation and hence reduced selective predation on larger forms, larger forms may survive, but only by migrating vertically each day to minimise their risk of mortality.

Since SST and the inferred intensity of visual predation co-varied in the study region, it is not possible to readily distinguish which of these factors was the primary ultimate cause of the observed spatial patterns of Mean Community Body Size. Nevertheless, these results and interpretations do suggest that the well-established role of predation in determining the size structure of zooplankton communities in freshwater systems also needs to be critically assessed in marine environments.

While many smaller copepods, such as *Acartia* and *Pseudocalanus*, may exhibit normal DVM, their diel movements generally have a small amplitude (a few metres), and so these populations always tends to be relatively near (<50 m) the surface (Longhurst and

Williams, 1979; Frost and Bollens, 1992). In contrast, for members of the families Metridiidae and Euchaetidae, the amplitude of normal DVM may be several 100s of metres (Longhurst and Williams, 1979), while for members of the Calanidae the amplitude may be several 10s of metres (e.g. Frost, 1988). When examining seasonal variations in the migrating biomass and the relative contributions of different species, I therefore focused on the latter three families.

In both the northwest and northeast Atlantic there were marked seasonal cycles in the estimated biomass that migrated daily. In both regions, these seasonal changes were explained largely by the respective seasonal cycles in the total biomass of the epi-pelagic communities (Fig. 5). The implication, therefore, is that the observed seasonal changes in the migrating biomass occurred largely as a result of seasonal changes in the absolute abundance of epi-pelagic zooplankton, which, in turn, are known to be caused both by reproduction in spring and summer and also by seasonal vertical migrations involving the overwintering of populations at great depths (> 1000 m; Longhurst and Williams, 1992).

In the northwest Atlantic, two species, *Calanus finmarchicus* and *Euchaeta norvegica*, accounted for the majority of the migrating biomass. These two species are well known to be abundant in the northwest Atlantic (Oceanographic Laboratory, Edinburgh, 1973). *E. norvegica* is a large carnivorous species that typically exhibits very strong normal DVM (Longhurst and Williams, 1979). Normal DVM is generally weaker in *C. finmarchicus* (Hays, 1995), but due to its high absolute abundance this species makes a strong contribution to the overall migrating biomass.

In the northeast Atlantic, the normal DVM behaviour of many zooplankton species has been documented for one month of the year by Longhurst and Williams (1979). They used a Longhurst–Hardy Plankton Recorder to quantify day/night differences in the vertical distribution of zooplankton in August and found that the copepods that contributed most to the total migrating biomass were *E. norvegica*, *M. lucens* and *P. robusta*, with a much smaller contribution from *C. finmarchicus*. These results are in close agreement with those I obtained using the CPR data from the northeast Atlantic in August (Fig. 6). In addition, the CPR data shows that these three species are important contributors to the overall migrating biomass throughout April–October, although the relative importance of *P. robusta* is less during the spring and early summer. Thus, in contrast to the northwest Atlantic, in the northeast Atlantic the contribution of *C. finmarchicus* to the overall migrating biomass is very small.

The results from the present study strongly suggest that the CPR data set provides the potential for mapping, over large spatial scales, the vertical elemental fluxes caused by normal DVM. For example, species such as *M. lucens* and *P. robusta*, which show a marked diel variation in abundance in the CPR samples, typically migrate several hundreds of metres to reach the surface at night and so, for example, in the northeast Atlantic in summer, where the surface mixed layer extends only to about 50 m (Longhurst and Williams, 1979; Taylor *et al.*, 1993), these species will cross the thermocline daily and so may contribute to the net removal of nitrogen from the surface mixed layer. To proceed further with this use of CPR data to assess the removal of nitrogen from the surface mixed layer by vertical migrants will require a number of refinements to the use of this data set. First, it is not sufficient to assume that the filtration efficiency of the CPR is 100%, since it is well known that the filtration efficiency of net systems may vary markedly, e.g. due to material clogging the meshes (McQueen and Yan, 1993). Therefore, the flow rate through the CPR will need to be quantified on operational tows, as this will allow the absolute abundance of

zooplankton (and hence also the absolute migrating biomass) to be accurately determined. Second, the relationship between the abundance of zooplankton at the mean sampling depth of the CPR (6.5 m) and the overall mean abundance of zooplankton in the surface mixed layer will need to be estimated. This will allow the migrating biomass determined from the CPR samples to be extrapolated to the total biomass migrating in and out of the surface mixed layer. Third, in addition to copepods, the interpretation of the CPR data will need to include an assessment of the importance of other zooplankton groups. For example, Longhurst and Williams (1979) have shown that in the northeast Atlantic, euphausiids may be important contributors to the total migrating biomass.

In summary, the results from the CPR survey show that the extent of normal DVM within copepod communities is spatially variable in the North Atlantic. Mean Community DVM is most marked in the northwest Atlantic and less marked in shallow coastal areas and in the northeast Atlantic. These patterns co-vary with variations in the Mean Community Body Size, with larger species predominating where Mean Community DVM is strongest.

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