Marine Biology 79, 63–73 (1984)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Vertical distribution, and seasonal and diurnal migration of *Calanus helgolandicus* in the Celtic Sea

R. Williams and D. V. P. Conway

Natural Environment Research Council, Institute for Marine Environmental Research; Prospect Place, The Hoe, Plymouth PL1 3DH, Devon, England

Abstract

The vertical distribution and migration (seasonal, diel and ontogenetic) of *Calanus helgolandicus* are described from the shallow (100 m) shelf-seas to the south-west of the British Isles. In 1978 and 1979, the overwintering population of *C. helgolandicus* consisted primarily of Stage V copepodites and adults. By late winter/early spring the copepodites had moulted to adult females (> 90%), which matured and bred the first cohorts of the year, prior to onset of the spring phytoplankton bloom in April/May. *C. helgolandicus* reached a peak of numerical abundance in August of 20×10^3 copepodites m^{-2} (over the depth range sampled – 0 to 70 m), which was 200 times the population in winter. The seasonal peak of abundance occurred 4 mo after the peak of the bloom of phytoplankton in spring. The yearly development of the copepod was not always out of phase with the diatom bloom, as seen when the data from 1978 was placed in the context of a longer time-series collected at 10 m over 22 yr (1960–1981, inclusive). Large vertical migrations were observed in the younger copepodites (CI and II) in May from below to above the thermocline. In the remainder of the year, the CI and CII stages behaved differently and were located above the thermocline within the euphotic zone. The largest vertical displacements of biomass were seen in the summer months due to the migrations of the CV stages and adults, which had developed from the spring cohorts. It was contended that the seasonal and vertical migrations of *C. helgolandicus* are part of a more complex pattern of inherent behavior than has been reported previously and that, however difficult this is to discern in the natural populations, it always expresses itself.

Introduction

This paper is an interpretation of the migratory behaviour (seasonal, diel, and ontogenetic) of *Calanus helgolandicus* as it develops throughout the year, established from data collected in the shallow seas to the south-west of the British Isles. It is assumed that the vertical migrations by the copepod are fully realised in deep ocean waters but, to some extent, this behaviour must be modified and constrained by the shallow waters (100 to 200 m) of the Celtic Sea. Briefly, what is known and generally accepted about *C. helgolandicus* is as follows: the younger the copepodite stage the shallower its distribution; the younger copepodite stages show little evidence of vertical migration; the older stages migrate diurnally and feed in the euphotic zone at night; adult males occur deeper than females; and in northern latitudes the populations overwinter mainly as Copepodite V and adult stages. Rarely have these observations been placed in the context of a detailed seasonal study. Usually, isolated observations have been made, or sampling has been carried out over a limited period, which has given rise to many seemingly contradictory conclusions being derived for the behaviour of this copepod.

Calanus helgolandicus is an important component of the biomass of the plankton in the shelf-seas to the south-west of the British Isles. As a grazing omnivore it occupies the trophic level between the autotrophs/microheterotrophs and the large fish populations of sprat [*Sprattus sprattus* (L.)], pilchard [*Sardina pilchardus* (Walbaum)], scad [*Trachurus trachurus* (L.)] and mackerel (*Scomber scombrus*, L.) which occur in this region. A proper understanding of its migratory patterns is therefore necessary for a wider understanding of trophic relationships in the ocean.

Materials and methods

Zooplankton samples were obtained by oblique hauls with the Longhurst Hardy Plankton Recorder (LHPR) (Longhurst and Williams, 1976; Williams *et al.*, 1983). The LHPR was deployed as near as possible to the sea bed using an IOS (Institute of Oceanographic Sciences) acoustic telemetry system, and samples were collected at approximately 5 m depth intervals to the surface. The mesh of the

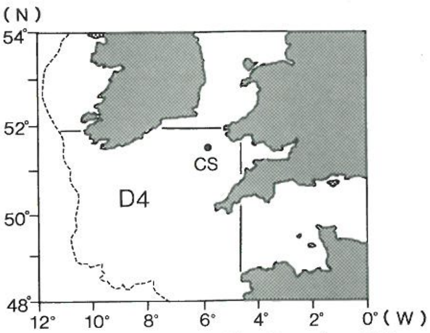

Fig. 1. Position of Celtic Sea site (CS) and Area D4 from the Continuous Plankton Recorder Survey. Shelf edge (200 m contour) is indicated by dotted line

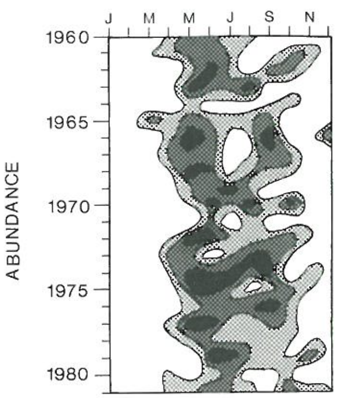

Fig. 2. *Calanus helgolandicus.* Seasonal abundance from 1960 to 1981 in Celtic Sea at depth of 10 m in "standard area" D4 of the Continuous Plankton Recorder Survey. Indices of abundance per sample were derived by averaging the means for each month in all rectangles (1° × 2°) in the standard area. Contour levels of lightest to heaviest shading are < 4, 4 to 8, 8 to 16 and > 16 copepods per sample of 3.0 m³

plankton net and filtering gauze used in the cod-end was 280 μm. The temperature, depth range and flow of water through the mouth of the net were recorded simultaneously with each plankton sample. The counts of organisms were corrected to numbers m^{-2} over the depth range sampled. The plankton samples were collected from the R.R.S. "John Murray" and R.R.S. "Challenger" during 8 cruises in 1978 and 1979 at or around the centre (51°30′N, 05°52′W) of an 8 × 10 nautical mile site (51°26′N, 06°00′W; 51°26′N, 05°44′W to 51°34′N, 05°44′W; 51°34′N, 06°00′W) in the Celtic Sea (Fig. 1). The 19 LHPR hauls used to illustrate the changes in abundance and vertical distribution of *Calanus helgolandicus* were selected from a larger series of hauls taken during these cruises.

Results from the Continuous Plankton Recorder (CPR) survey (Glover, 1967; Colebrook, 1982) were used to show the year-to-year and seasonal variability in abundance of *Calanus helgolandicus* in the Celtic Sea from 1960 to 1981 (Fig. 2).

Continuous measurements on pumped sea-water from 3 m were taken of temperature and salinity with a Plessey thermosalinograph (6600T), and levels of chlorophyll *a* were recorded with a Turner Mark III fluorometer with a flow-through cell attached. These instruments were calibrated frequently by collecting water samples for subsequent measurement of salinity using an Autolab inductively coupled salinometer (Model 601 Mark III), and for chlorophyll *a* spectrophotometric determinations (Strickland and Parsons, 1972) after filtration onto glass-fibre (GFC) papers. Measurements were also taken of particle size distribution and concentration with a TA II multi-channel Coulter counter with a population accessory; water samples were preserved in Lugol's iodine for identification of phytoplankton species. Vertical profiles were taken for all the variables determined horizontally.

Results

Seasonal development of the population

The mean seasonal variability in abundance and geographical distribution of *Calanus helgolandicus* in the northern North Atlantic Ocean from sampling with the CPR at 10 m are given by Colebrook (1982). The species was most abundant in the Celtic Sea and reached a seasonal maximum between May and October (Fig. 2). A more detailed analysis of the results from the CPR survey for the Celtic Sea from 1960 to 1981 revealed large differences in the abundance between years and also large within-year variability in abundance of this copepod (Fig. 2). Although there was considerable variability in the numerical abundance of *C. helgolandicus,* there was generally a consistent picture in the timing of the seasonal development of the population. The copepod first appeared in the samples at 10 m in April and became abundant in May/June and/or in late summer before disappearing from the surface waters in October. The numerical abundance of *C. helgolandicus* averaged over the whole of the Celtic Sea in 1978 was low compared with previous years.

The maximum numbers of *Calanus helgolandicus* sampled by the LHPR occurred in the summer months; the numerical peak was in August and the peak of dry weight (mg m^{-2}) in early October (Fig. 3) (Williams and Conway, 1982). The seasonal numerical peak of *C. helgolandicus* occurred 3 mo after the May spring bloom of diatoms.

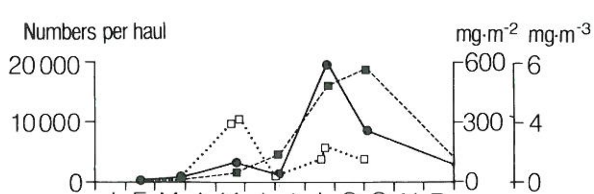

Fig. 3. Seasonal variability of numerical abundance (numbers per haul; ●) and dry weight biomass (mg m^{-2}; ■) of *Calanus helgolandicus* and chlorophyll *a* (mg m^{-3}; □) from the Celtic Sea site during 1978

Winter conditions

A LHPR haul taken during the night (early morning) of 15 February, 1978 (Fig. 4) showed that Stage V (CV) copepodites and adults were distributed throughout the water column. There were greater numbers below 40 m and the numerical peak occurred between 60 and 65 m; a few Stage IV copepodites were present in the haul. The sea-surface temperature was 7.7 °C and the water column was isothermal. A day and a night haul taken on 20/21 January, 1979 (see Fig. 3 of Williams and Conway, 1982) showed similar distributions of Stage V and VI copepodites as the previous haul. The sea-surface temperature was 9.4 °C and the water column isothermal. The temperature of the sea had still to decrease to its winter minimum, which occurred in the Celtic Sea in February.

Analysis of the guts of CV and adult stages from the January hauls indicated that the copepod had been feeding. The contents of the guts of a number of specimens from these hauls were black. Analysis of this gut-material showed that the copepod had been feeding on detritus which had presumably been resuspended from the sea-bed by the mixing processes in winter. The chlorophyll values measured from the shelf in winter ranged from 0.3 to 0.6 mg m^{-3} throughout the water column.

In contrast, off the shelf, in the deep oceanic waters the overwintering population of *Calanus helgolandicus* occurred below 400 m. In a LHPR haul taken at mid-day on 14 January, 1982 (48°16′N; 10°24′W) the *C. helgolandicus* population consisted of 7% CIV, 92% CV and 1% adults. The CV copepodites were distributed from 400 m to the maximum depth of the haul at 870 m and were abundant from 520 to 850 m. The temperature was 12 °C from the surface to 150 m and decreased from 11 °C at 450 m to 9.6 °C at 870 m. The maximum numbers of *C. helgolandicus* occurred in water with a temperature of 10 °C ± 0.2 C°. Chlorophyll values measured were 0.2 to 0.3 mg m^{-3} between the surface and 100 m.

Spring conditions

By early spring in the Celtic Sea the CV copepodites had moulted and matured into adults. A good example of this maturation of the overwintering population is seen in a pair of oblique hauls taken on 23/24 March, 1979, when all but a few specimens were adult females (Fig. 5). A vertical migration was observed at night, when a large proportion of the female population migrated from below 60 m to the upper 25 m of the water column (Williams and Conway, 1982). We consider this to be a breeding migration when eggs were liberated in the surface waters. Although eggs have been observed in females collected throughout winter, it is only in March that eggs and nauplii were found in the water column. The water temperature was 8.3 °C and the water column was isothermal from the surface to 100 m.

Young copepodites (CI–IV) were observed earlier in the Celtic Sea in 1978 than 1979. An oblique haul taken on 27 March sampled all stages of copepodites throughout the whole sampling depth (0 to 80 m) and showed CI to III to be most abundant between the surface and 5 m, CIV and V between 15 and 20 m and adults between 20 and 25 m (Fig. 6). The numbers of *Calanus helgolandicus* sampled in this haul were approximately tenfold higher than the values in winter. The appearance of young copepodites in late March implied that egg liberation and successful development had taken place at least 2 to 3 wk previously. Therefore, the onset of breeding and development of the *C. helgolandicus* population preceded the spring phytoplankton bloom. The levels of chlorophyll in late March, associated with particulate matter equal to or greater than 1 μm, was 0.26 ± 0.08 mg m^{-3}; this value can be considered to be equivalent to the winter baseline values for the shelf-sea. Although breeding and development of the copepod commenced in winter (i.e., early March) it was not until late spring/early summer that numbers increased appreciably.

The sea-surface temperature by the latter half of May was 12.3 °C and a thermocline was well established between 15 and 20 m. Total numbers of *Calanus helgolandicus* had risen fourfold over the numbers present in March due to the numbers of Copepodites CI, CII, and CIII (Fig. 7). *C. helgolandicus* from 5 hauls taken between

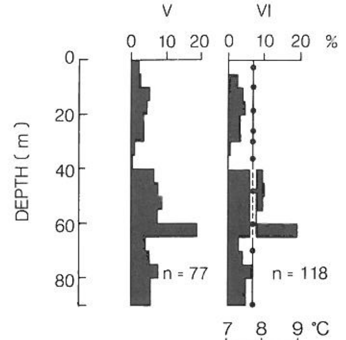

Fig. 4. *Calanus helgolandicus.* Vertical distribution (as % of total numbers) of Copepodite Stages V and VI from a night LHPR oblique haul at 06.32 hrs Greenwich Mean Time (GMT) on 15 February 1978 from the Celtic Sea site. Temperature profile (circles) is also shown

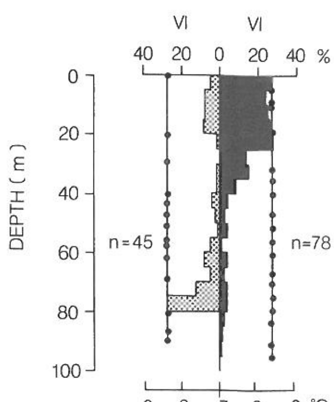

Fig. 5. *Calanus helgolandicus.* Vertical distribution of adults from a day (11.53 hrs GMT on 24 March, 1979; stippled) and a night (23.31 hrs GMT on 23 March, 1979; black shading) LHPR oblique haul from the Celtic Sea site. Associated temperature profiles (circles) are also shown

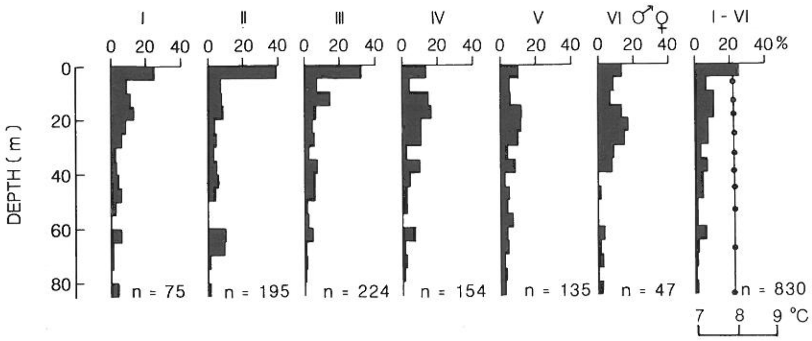

Fig. 6. *Calanus helgolandicus.* Vertical distribution of Copepodite Stages I–VI from a night LHPR oblique haul at 22.30 hrs GMT on 27 March, 1978 from the Celtic Sea site. Temperature profile (circles) is also shown

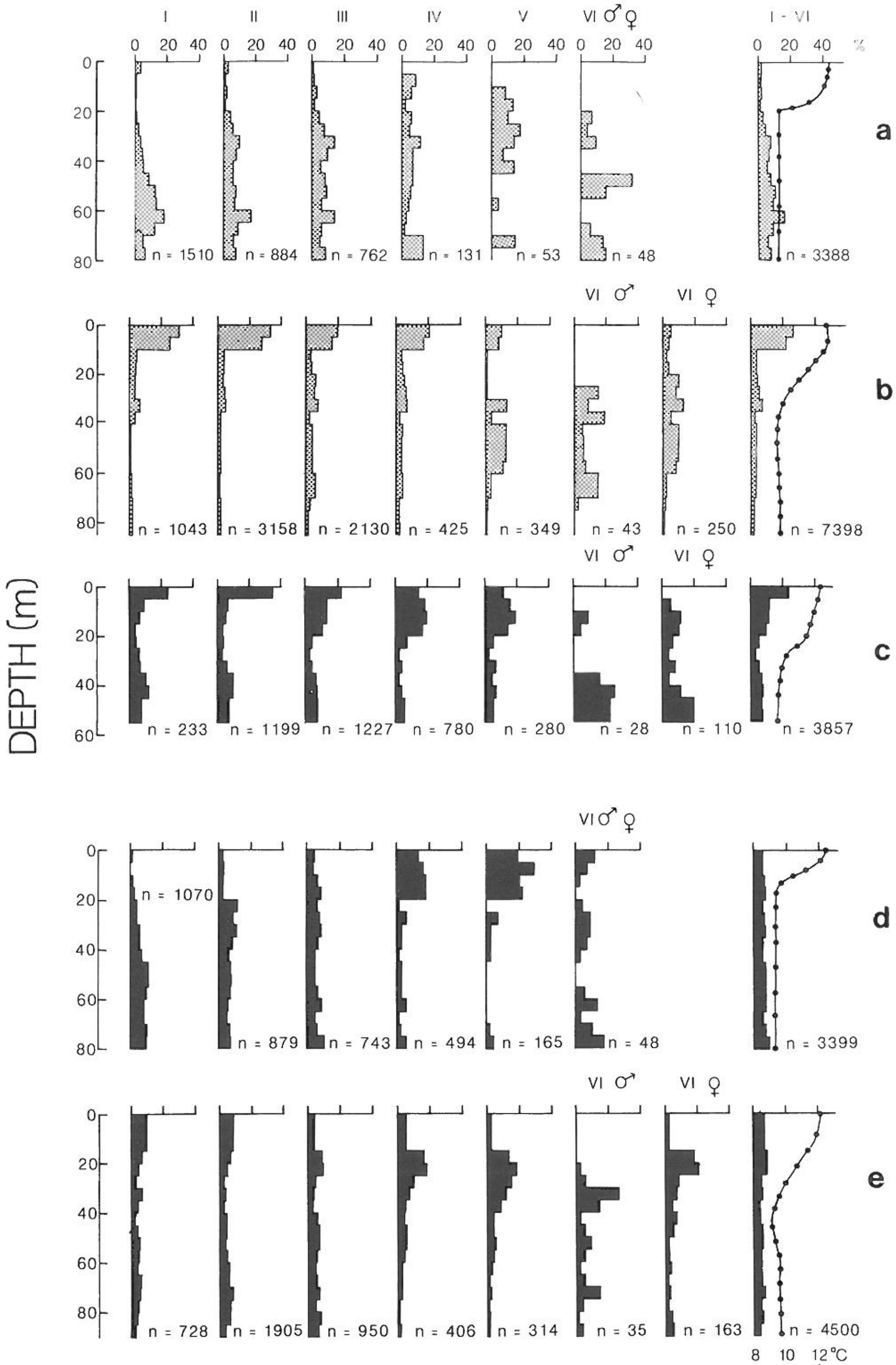

Fig. 7. *Calanus helgolandicus.* Vertical distribution of Copepodite Stages I–VI from LHPR oblique hauls taken at (a) 10.03 hrs GMT on 21 May, (b) 17.04 hrs GMT on 17 May, (c) 21.47 hrs GMT on 17 May, (d) 22.15 hrs GMT on 21 May, and (e) 03.41 hrs GMT on 18 May, 1978. Numbers in each day (stippled) and night (black shading) hauls are plotted in 5 m depth intervals, as percentages of total numbers (*n*) present. Temperature profiles (circles) are also shown. Approximate times for sunrise and sunset over period 17 to 21 May, 1978 were 20.00 hrs and 04.30 hrs local time, respectively

17.04 hrs (17 May) and 22.15 hrs (21 May), show complex changes in vertical distribution and evidence of migration throughout a 24 h period (Fig. 7). If the vertical structure of *C. helgolandicus* had been described from one or even two of these hauls, then an incomplete picture and understanding of the population would have been obtained. The vertical distributions of the young copepodites (CI–III) and the majority of the older stages in the early day haul (Fig. 7 a) were below the thermocline and euphotic zone, where the temperature of the water was still at a winter level. Similar vertical distributions of the younger copepodites underlying the older copepodites were observed during May in the Celtic Sea in 1977 (Williams and Conway, 1980) and in subsequent years. By late afternoon the majority of the copepodites (CI and II) had completed large vertical migrations from below the thermocline to the upper 5 m of the water column (Fig. 7 a, b); they remained shallow until twilight (Fig. 7 c), before sinking away from the near-surface waters at night (Fig. 7 d). The younger the copepodite stage the deeper the mean of its vertical distribution. Just before dawn (Fig. 7 e), the copepodite stages (CI–III) were more evenly distributed throughout the water column. We suggest that there were two migrations by the younger stages (CI and II) into the upper waters during a 24 h period. One migration was in late afternoon and the other at dawn, each for a period of approximately 6 h duration. We conclude from these hauls that the copepodite stages (CI and II) were deepest at midday and midnight. Copepodites Stages IV and V made pronounced vertical diurnal migrations from deeper water to or above the thermocline (Fig. 7). By nightfall (Fig. 7 d), 90% of the population resided above 20 m and by dawn (Fig. 7 e) the majority of CIV and V were below 15 m and sinking away from the surface waters. The Copepodite Stages IV and V spent approximately 9 out of 24 h within the euphotic zone. Low numbers of adults were found in these hauls (48 to 293 m^{-2}), but migration of part of the adult female population from below to above the thermocline was observed during the night hours; the majority of the population remained below the thermocline. Adult males were distributed deeper than the females and did not migrate above the thermocline; the ratio of males:females was 1:5.

The spring bloom of phytoplankton, estimated as chlorophyll *a*, at 3 m occurred during the latter half of May (Fig. 3). Surveys on 16 and 23 May gave values of chlorophyll *a* of 4.02 ± 2.1 mg m^{-3} ($n=30$) and 4.28 ± 2.16 mg m^{-3} ($n=30$). Samples taken from water bottles deployed at 9 depths showed maximum particulate concentration at the surface (1 m) on 16 May and at 5 m on 22 May, 1978 (Fig. 8). The increase in particle volume observed in the latter profile was due to an increase of diatoms in the samples taken from 1 to 15 m. The species identified were *Thalassiosira* spp., *Rhizosolenia delicatula* and *Nitzschia closterium.* Diatoms made up 70% of the particles at 1 m and 50% between 5 and 20 m. Large amounts of detritus were present throughout the water column, representing 20% of all particulate material between 1 and 20 m and 40% below 20 m; the remaining particulates consisted of naked dinoflagellates and flagellates. The high particulate volumes observed in the deepest samples of the profile ($6.01\ \mu m^3 \times 10^6\ ml^{-1}$) below 80 m on 22 May (Fig. 8) are typical of profiles taken in this area, and at certain times of the year can be higher than the volumes observed in the near-surface samples.

Summer conditions

By early July the sea-surface temperature had risen to 14.4 °C and a 3 C° thermocline existed between 25 and 35 m (Fig. 9). The temperature below the thermocline had risen to 11°–11.4 °C from a minimum in winter of less than 8 °C, suggesting mixing of this sub-thermocline water. Copepodites (CI to IV) from a day (11.13 hrs) and a night (23.08 hrs) haul were found above the thermocline (Fig. 9). The portion of CV and adults which were distributed below the thermocline during the day migrated above it at night. Total numbers of *Calanus helgolandicus* in the July hauls were lower than in the May hauls, but the numbers of adults had increased (Figs. 7, 9). The mean dry weights of CV and the adults were heavier [the heaviest recorded for the year (Bottrell and Robins, 1984) and the dry weight biomass of the population (mg m^{-2}) was approximately three times heavier than in May (Figs. 3, 13).

Early in July the phytoplankton, as measured by chlorophyll *a*, reached a summer minimum at 3 m of 0.44 ± 0.43 mg m^{-3} ($n=30$). These low values were also measured throughout the water column. Vertical profiles (0 to 70 m) taken on 1 July had an integrated value of 14.2 mg chlorophyll *a* m^{-2} (range 3.9 to 30.5 mg m^{-2}). The primary production associated with this standing crop was low. The result of a ^{14}C incubation experiment on 2 July gave a value of 19.45 mg C m^{-2} h^{-1} (0 to 18 m), with a production peak at 5 m; approximately 20% of the production was related to particulate material $< 8\ \mu m$ (I. Joint, personal communication).

By late August the sea-surface temperature was 17.0 °C and *Calanus helgolandicus* reached its seasonal peak of numerical abundance in 1978 (Fig. 3). The distribution of the developmental stages of *C. helgolandicus* in August is shown in four oblique hauls taken between 23.58 hrs on 22 August and 05.49 hrs, 24 August (Fig. 10). The distributions of CI to IV showed no evidence of large diel migrations and remained above the thermocline, while CV copepodites were observed throughout the water column by day and night. Most of the adults were distributed below the thermocline, with a high density of females (> 200 m^{-3}) between 65 and 70 m in the noon haul (Fig. 10 a). At night and early morning the females were evenly distributed from the thermocline depth to 70 m, the maximum depth of sampling (Fig. 10 c, d). Adult males were identified from the morning and evening hauls and were present in a ratio of 1:7 with the females. The males were only found below the thermocline.

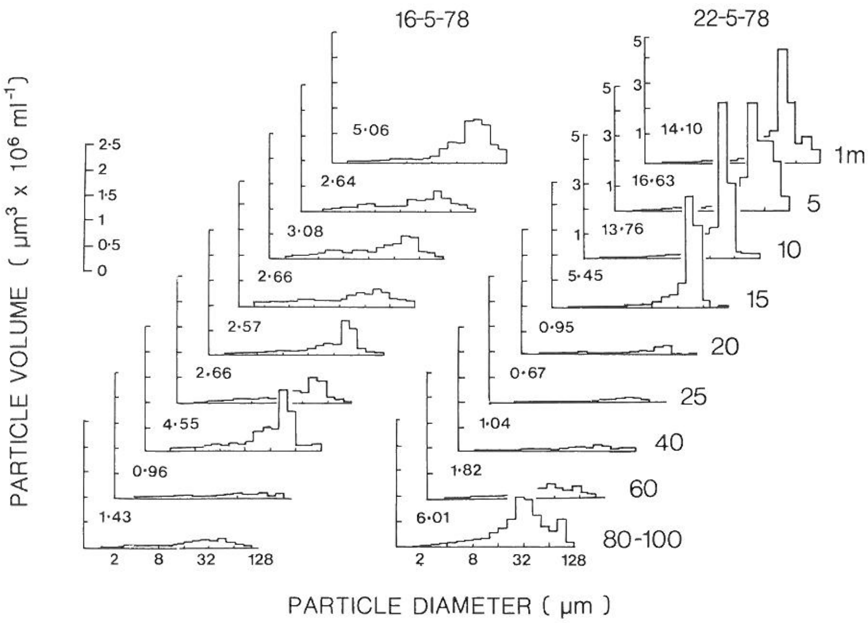

Fig. 8. Particle volumes (parts per million) and particle diameters (18 size classes from 1.59 to 128.0 μm equivalent spherical diameters) of particulates from two water-bottle profiles (9 depths from 1 to 80–100 m) taken on 16 May and 22 May, 1978 at the Celtic Sea site. Total particulate volumes at each depth are given

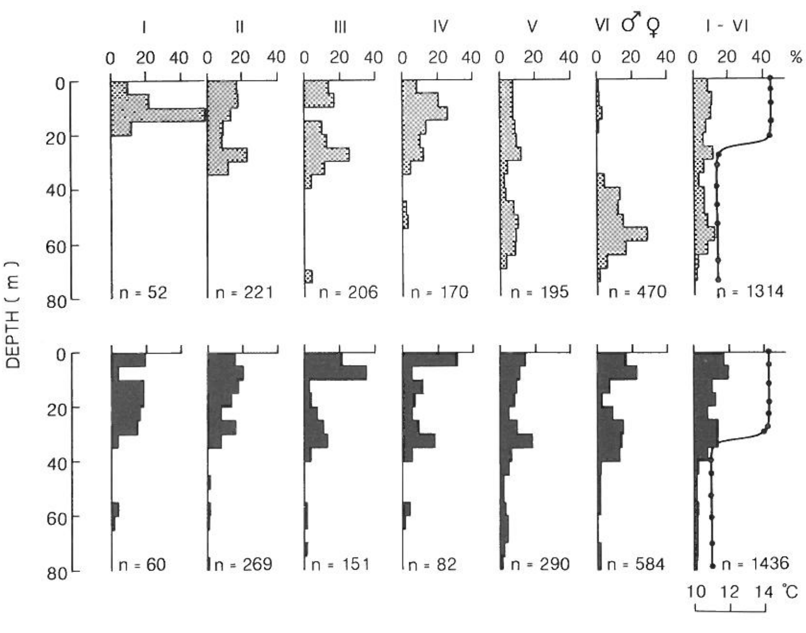

Fig. 9. *Calanus helgolandicus.* Vertical distribution of Copepodite Stages I–VI from a day (11.13 hrs GMT; stippled) and a night (23.08 hrs GMT; black shading) LHPR oblique haul from the Celtic Sea site on 3 July 1978. Temperature profiles (circles) are also shown

Chlorophyll *a* at 3 m measured during two horizontal surveys on 18 and 20 August (1.48±0.84 and 2.29±2.03 mg m^{-3}, respectively, $n=60$) had increased five times over the July value and the mean integrated value from five vertical profiles taken on 21/22 August was 50.8 mg m^{-2} (range 41.4 to 118.4 mg m^{-2}). This higher standing crop showed corresponding higher values of production of 51.8 and 203.7 mg C m^{-2} h^{-1} measured from two ^{14}C incubation experiments on 22 and 23 August; 23.3 and 10.0%, respectively of the production was associated with cells < 8 μm. An indication of the particulate material available as food for *Calanus helgolandicus* during this month can be assessed from a "typical" profile taken on 21 August 1978 (1 to 70 m) (Fig. 11). Dinoflagellates and naked flagellates contributed 60% of the identified particulates in the shallower waters of the profile (1 to 20 m) and decreased in abundance with depth. The unarmoured dinoflagellate *Gyrodinium aureolum,* with a diameter of 20 to 40 μm, was one of the most abundant species in the summer bloom. Diatoms made a contribution of 18% at 30 m, reducing to 11.5% at 70 m – which was the depth at which *C. helgolandicus* adults were concentrated (Fig. 10). The effects of these larger-sized diatoms can be seen in the particle size distributions from 30 to 70 m (Fig. 11). The remaining particulate material was unidentified detritus and contributed up to 30% of all particulates from 1 to 10 m and was present at > 50% in the remaining water column.

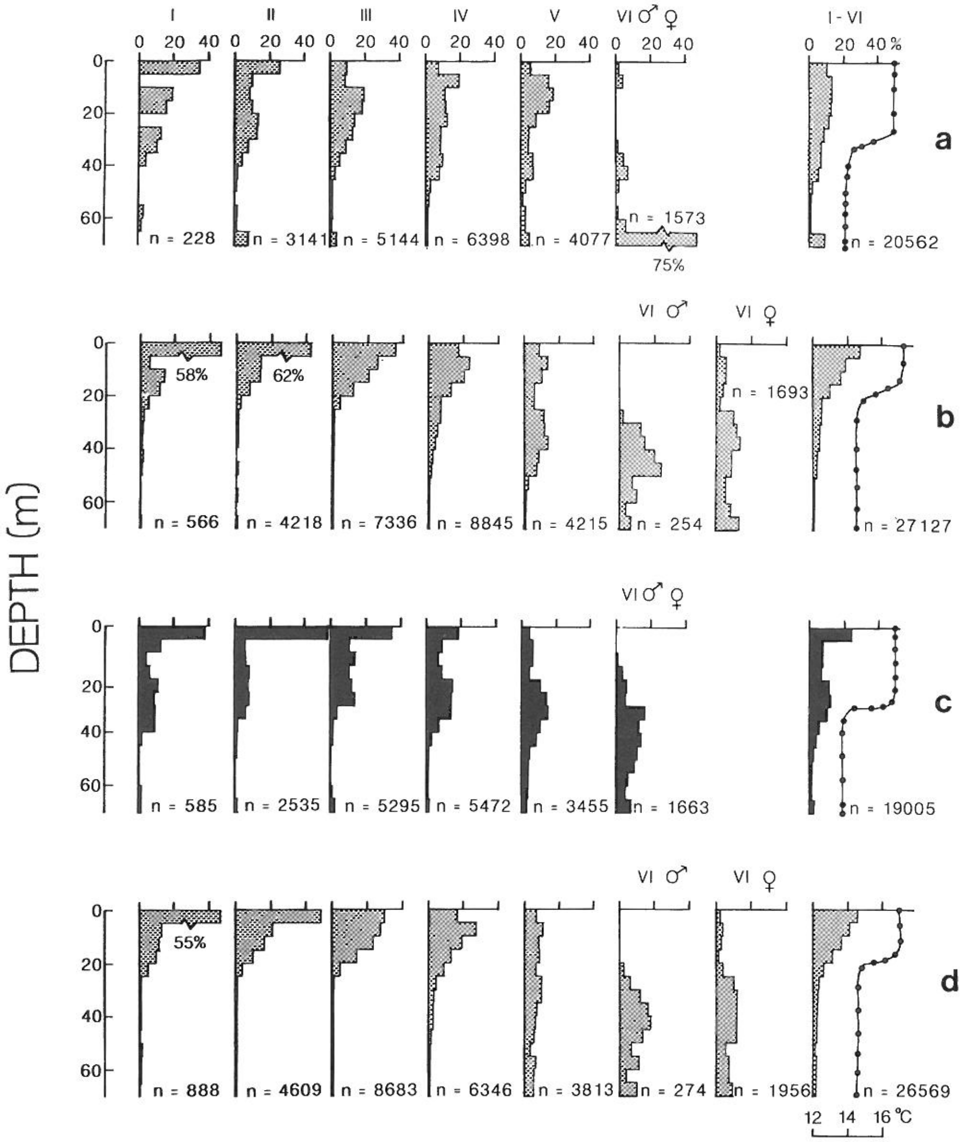

Fig. 10. *Calanus helgolandicus.* Vertical distributions of Copepodite Stages I–VI from LHPR oblique hauls taken on (a) 12.05 hrs GMT on 23 August, (b) 17.50 hrs GMT on 23 August, (c) 23.58 hrs GMT on 22 August, and (d) 05.49 hrs GMT on 24 August, 1978 from the Celtic Sea site. Temperature profiles (circles) are also shown

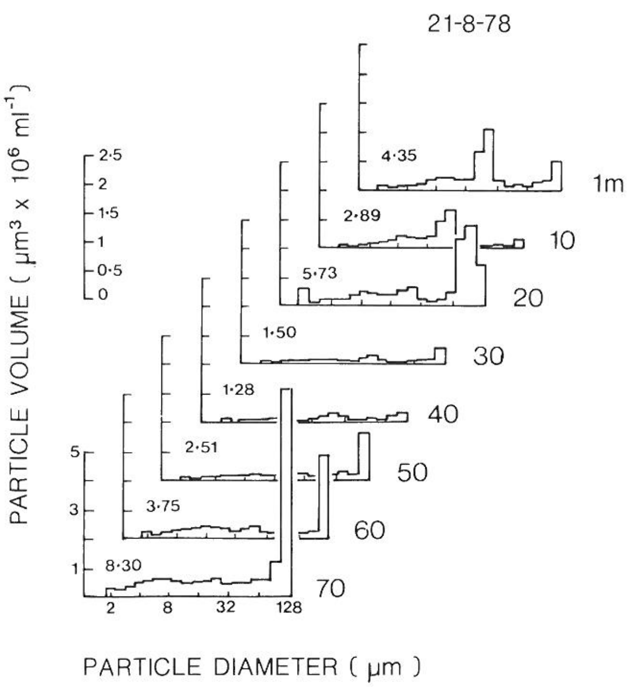

Fig. 11. Particle volumes (parts per million) and particle diameters of particulates from a water-bottle profile (8 depths between 1 and 70 m) taken on 21 August, 1978 at the Celtic Sea site. Total particulate volumes at each depth are given

Autumn conditions

The vertical distribution of *Calanus helgolandicus* in autumn is shown from four hauls taken at 6 h intervals from 23.33 hrs on 1 October to 17.01 hrs on 2 October 1978 (Fig. 12). The majority of the copepodite stages were found above the thermocline, although CV and CVI females tended to aggregate at the thermocline in the early evening. The thermocline was at a depth of 40 to 45 m by day and 35 to 45 m by night: a 12 h series of vertical profiles demonstrated the influence of the tidal cycle on the depth of the thermocline. The sea-surface temperature on 2 October was 13.8 °C, which was 3.2 C° less than the summer temperature; it was also less than the temperature below the thermocline in August. CIV and CV were the

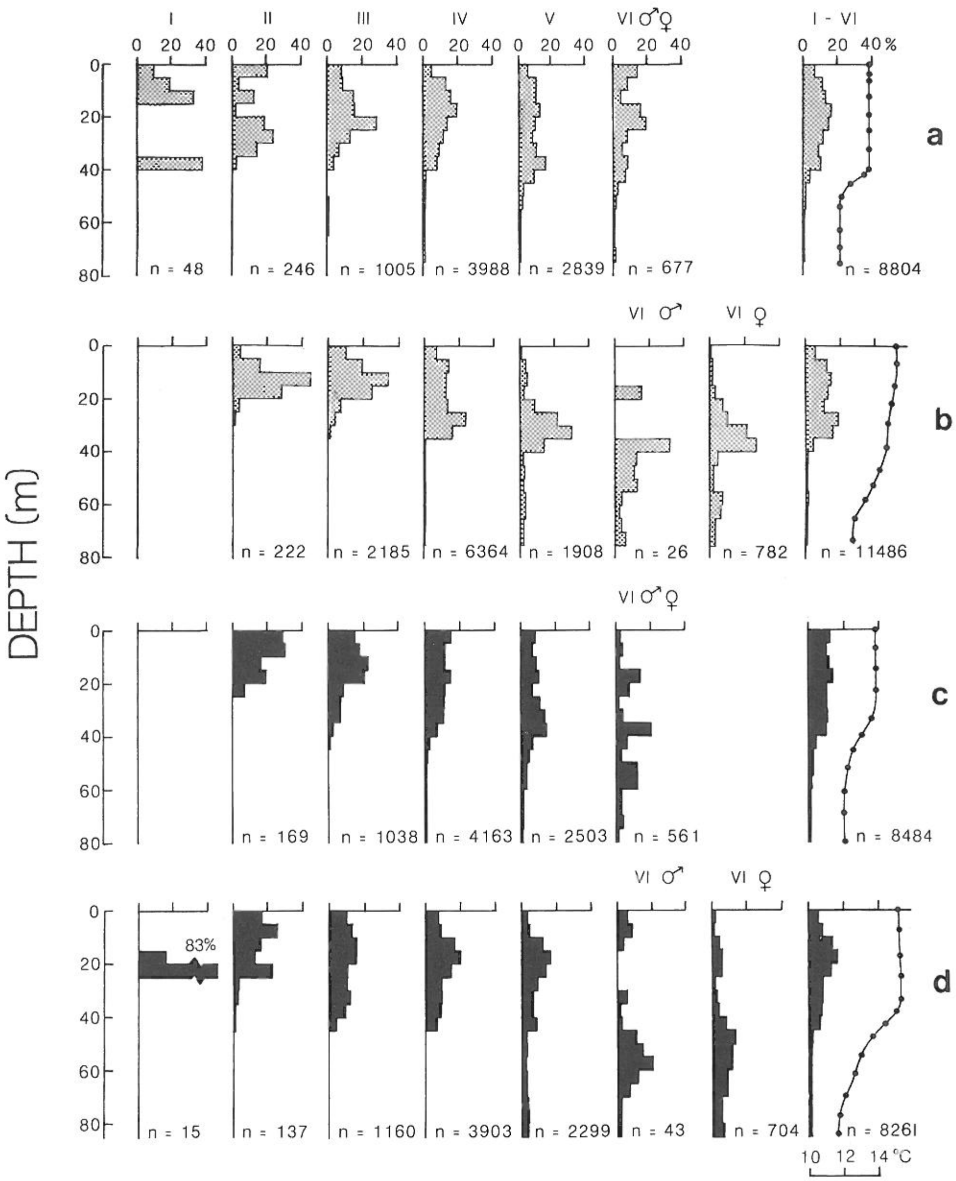

Fig. 12. *Calanus helgolandicus.* Vertical distributions of Copepodite Stages I–VI from LHPR oblique hauls taken on (a) 11.09 hrs GMT on 2 October, (b) 17.01 hrs GMT on 2 October, (c) 23.33 hrs on 1 October, and (d) 05.42 hrs GMT on 2 October, 1978 from the Celtic Sea site. Temperature profiles (circles) are also shown

numerically dominant stages in these four hauls, and while the total number of all stages was half the August value, the mean individual weight of the older stages and adults was more than double for the same total length (Bottrell and Robins, 1984). The peak of biomass for the population in 1978 therefore occurred in October, when these older copepodites were laying down energy reserves for winter. There is net heat loss from the sea through autumn and, with the winter gales, the temperature structure of the water breaks down, becoming isothermal.

Length/dry weight relationships were determined for the copepodite stages of *Calanus helgolandicus* from all the series of LHPR hauls. The weights were used to obtain profiles of dry weight biomass (Williams and Conway, 1982). Day and night LHPR hauls taken in spring, summer and autumn were selected (Fig. 13) to demonstrate the vertical migration of *C. helgolandicus* and the subsequent changes in vertical distribution of the biomass. The temperature, chlorophyll *a* and particulate volume profiles associated with the LHPR hauls are also shown. Over the winter and early spring period the population of *C. helgolandicus* consisted predominantly of CV and CVI; therefore, vertical profiles of biomass mirror numerical profiles during these periods (Fig. 13) more than at other times of the year (Fig. 3). In spring and early summer a large proportion of the older copepodites made extensive diurnal vertical migrations, which were reflected in the changes of the day and night profiles of dry weight biomass (Fig. 13). By late summer and autumn the vertical distributions of the older copepodite stages changed little over 24 h and the numerical and biomass profiles were similar.

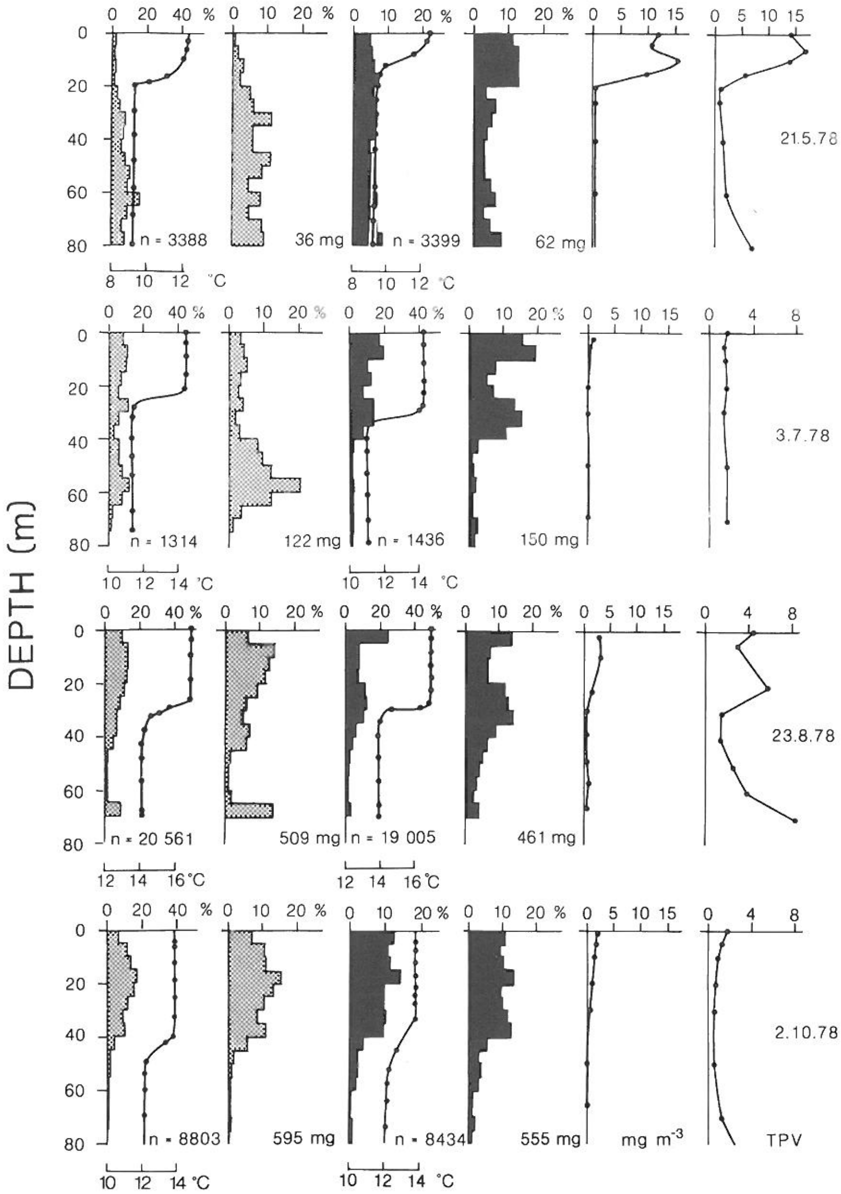

Fig. 13. *Calanus helgolandicus.* Vertical distributions of numbers and dry weight biomass of four day and night pairs of LHPR oblique hauls from the Celtic Sea. Numbers of each day (stippled) and each night (black shading) hauls are plotted in 5 m depth intervals as percentages of total numbers (n) and total biomass (mg) present. Temperature profiles are also shown, together with chlorophyll a profiles (mg m^{-3}) and total particulate volume (TPV, μm$^3 \times 10^6$ ml^{-1})

Discussion

The Celtic Sea sampling site has a water depth of approximately 100 m and becomes seasonally thermally stratified from late spring until autumn. The tidal stream amplitudes are not large, ranging from 0.38 to 0.75 m s^{-1} at spring tides (Sager and Sammler, 1968). Nevertheless, the hydrographic and biological data collected in spring and summer were sometimes very variable. One of the factors contributing towards this variability was the influence on the sampling site of the Celtic Sea front (Pingree *et al.*, 1976; Simpson, 1976; Pingree and Griffiths, 1978; Simpson *et al.*, 1978). Movements of large-scale features associated with the frontal region have been observed from satellite infrared imagery (Simpson *et al.*, 1978) and, on occasions, these features were transported into the sampled area.

The *Calanus helgolandicus* sampled in the Celtic Sea during 1978 developed from a small population (100 individuals m^{-2}, 0 to 90 m) in winter to a numerical peak of abundance in August (20 000 individuals m^{-2}, 0 to 70 m). This sequence of development was also observed in the longer time-series of data collected at 10 m with the CPR. In this 22-yr series of data, *C. helgolandicus* most frequently reached a seasonal numerical peak in late spring/early summer, with the occasional peak occurring in late summer, as we recorded in 1978. From the LHPR hauls we illustrate what we believe to be a "typical" pattern of seasonal development, vertical distribution and migration of this copepod in the shallow Celtic Sea. These characteristics are expressed by the population irrespective of whether there is an early or late seasonal numerical peak of abundance.

It has been assumed until now that the younger copepodite stages are limited to vertical migrations of small amplitude within the euphotic zone and for all intents and purposes are non-migrating. The series of hauls taken in May clearly show large vertical migrations, in relation to the depth of the water column, for all stages and considerable translocations of biomass into the euphotic zone at night. In fact, the largest amplitudes were shown by CI and CII copepodites. Similar migrations were not seen in the younger copepodites in other seasons of the year. It was in spring that the younger copepodites of *Calanus helgolandicus* were found in the colder deeper water, distributed below the older stages (Williams and Conway, 1980). The migration of the younger stages into the warmer waters of the upper 15 m of the water column we assume to be a feeding migration enabling the copepodites to graze on the algal bloom. In the remainder of the year, when there is low standing crop the majority of the younger copepodites behave differently and are located above the thermocline within the euphotic zone. The temperature profiles in the hauls in May show something of the variability of the physical regime which can be observed in this region. In early to mid-summer, the most abundant copepodite stage was adult (male and female). In consequence, these profiles show the largest displacement of biomass observed at night through the migration of the CV and CVI stages, which have developed from the spring cohorts.

In 1978 the population reached a numerical peak in August, when the copepodites were present in the 0 to 5 m depth range at a density > 1 000 individuals m^{-3}. The modes of the vertical distributions of the CI to CIV stages changed over 24 h, but remained within the euphotic zone. The biomass peak of the population occurred in the autumn hauls, taken in October, even though there were half the number of copepodites present compared with August. The mean dry weights of the CV and CVI stages in August were the lowest measured through the year; the mean weights of the older copepodites in October were more than twice the August values for the same overall length (Bottrell and Robins, 1984). It is obvious that errors can arise in calculating biomass and zooplankton production if single mean weights are applied to population data determined for a seasonal cycle, or even if weights are taken from the literature and are not applicable to the area of study. Similarly, this degree of variability must be taken into account when weight-specific growth rates of length classes are determined from dry weights derived from length/weight relationships.

From these hauls it can be seen that the seasonal and vertical migrations of *Calanus helgolandicus* are part of a more complex pattern of behaviour than has been suggested in the earlier literature i.e., simplistic nocturnal migrations of older copepodite stages. The copepod responds to its changing environment by exhibiting different patterns of behaviour i.e., feeding migrations, egg-laying migrations, migrations which presumably give a net gain in energy, and non-migrating patterns which potentially conserve energy. It can be observed from our results that large sections of the population are not migrating on a daily basis and that even the simple diel vertical migration is far from being the normal practice. Food availability and temperature are considered to be the most important variables governing the successful development of copepods (Vidal, 1980 a, b) but more precisely it is the effects of these two variables in combination which are critical for development and growth. It is the response of the population to the changes of these variables which governs the success of the species each year.

Our observations of year-to-year fluctuations in abundance of *Calanus helgolandicus* in the Celtic Sea show that the average abundance and timing of the seasonal maxima of the standing stock can be extremely variable. The sea-surface temperature on the other hand does not show the same degree of variability and it is highly unlikely that temperature would correlate with any measured parameters of the copepod population. What should be realised is that many of the laboratory experiments and field studies conducted with *C. helgolandicus* have related growth of the copepod to single temperature values or a narrow range of temperature. The effects on growth, development and general physiology of *C. helgolandicus* of varying the temperature regime over 6 h or shorter/longer periods have not been investigated. The copepodite stages, when they migrate in the stratified waters, are exposed to wide ranges of temperature over short time-periods. The main development of *C. helgolandicus* in the shelf-seas around the British Isles takes place in water with large vertical temperature gradients; up to 8 C°. There are other regions where *C. helgolandicus* occurs, such as the Black Sea, where the temperature gradients are even larger. The behaviour shown by *C. helgolandicus* in our series of LHPR hauls provides one of the possible reasons why this copepod does not exhibit isochronal development.

As well as the complexity of the effects of the temperature regime, there are the problems of deciding what is food for *Calanus helgolandicus*. Food can be measured as mean phytoplankton population density, chlorophyll *a* or particulate organic carbon. There are difficulties in relating copepod growth to mean densities of phytoplankton obtained over many metres (Klein Breteler *et al.*, 1982). Our own results show that *C. helgolandicus* can occur in high numbers in narrow depth zones. There is also the quality of the food itself to take into consideration. It is the vertical and horizontal variability in these physical and biological components of the marine system which create the heterogeneity in abundance of *C. helgolandicus* and other species of zooplankton. Within this complex distribution of *C. helgolandicus* there is an inherent behavioural pattern which always expresses itself, dependent on the maturity of the copepod.

Acknowledgements. We wish to acknowledge the help given to us by our colleagues at IMER who participated in the Celtic Sea programme. We would also like to thank the masters and crews of the NERC research vessels. This work forms part of the Production Processes Programme of the Institute for Marine Environmental Research, a component body of the Natural Environment Research Council.

Literature cited

Bottrell, H. H. and D. B. Robins: Seasonal variations in length, dry weight, carbon and nitrogen of *Calanus helgolandicus* from the Celtic Sea. Mar. Ecol. Prog. Ser. *14,* 259–268 (1984)

Colebrook, J. M.: Continuous plankton records: seasonal variations in the distribution and abundance of plankton in the North Atlantic Ocean and the North Sea. J. Plankton Res. *4,* 435–462 (1982)

Glover, R. S.: The continuous plankton recorder survey of the North Atlantic. Symp. zool. Soc. Lond. *19,* 189–210 (1967)

Klein Breteler, W. C. M., H. G. Fransz and S. R. Gonzalez: Growth and development of four calanoid copepod species under experimental and natural conditions. Neth. J. Sea Res. *16,* 195–207 (1982)

Longhurst, A. R. and R. Williams: Improved filtration systems for multiple-serial plankton samplers and their deployment. Deep-Sea Res. *23,* 1067–1073 (1976)

Pingree, R. D. and D. K. Griffiths: Tidal fronts on the shelf seas around the British Isles. J. geophys. Res. *83,* 4615–4622 (1978)

Pingree, R. D., P. M. Holligan, G. T. Mardell and R. N. Head: The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic Sea. J. mar. biol. Ass. U.K. *56,* 845–873 (1976)

Sager, G. und R. Sammler: Atlas der Gezeitenströme für die Nordsee und den Kanal und die Irische See, 58 pp. Rostock: Seehydrographischer Dienst der DDR 1968

Simpson, J. H.: A boundary front in the summer regime of the Celtic Sea. Estuar. cstl mar. Sci. *4,* 71–81 (1976)

Simpson, J. H., C. M. Allen and N. C. G. Morris: Fronts on the Continental Shelf. J. geophys. Res. *83,* 4607–4614 (1978)

Strickland, J. D. H. and T. R. Parsons: A practical handbook of seawater analysis., 2nd ed. Bull. Fish. Res. Bd Can. *167,* 1–310 (1972)

Vidal, J.: Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. Mar. Biol. *56,* 111–134 (1980 a)

Vidal, J.: Physioecology of zooplankton. II. Effects of phytoplankton concentration, temperature, and body size on the development and molting rates of *Calanus pacificus* and *Pseudocalanus* sp. Mar. Biol. *56,* 135–146 (1980 b)

Williams, R., N. R. Collins and D. V. P. Conway: The double LHPR system, a high speed micro- and macroplankton sampler. Deep-Sea Res. *30,* 331–342 (1983)

Williams, R. and D. V. P. Conway: Vertical distributions of *Calanus finmarchicus* and *C. helgolandicus* (Crustacea: Copepoda). Mar. Biol. *60,* 57–61 (1980)

Williams, R. and D. V. P. Conway: Population growth and vertical distribution of *Calanus helgolandicus* in the Celtic Sea. Neth. J. Sea. Res. *16,* 185–194 (1982)

Date of final manuscript acceptance: January 19, 1984.
Communicated by J. Mauchline, Oban