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# Vertical distribution of *Calanus finmarchicus* and *C. helgolandicus* in relation to the development of the seasonal thermocline in the Celtic Sea

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## Abstract

The geographical distribution and annual mean abundance of *Calanus finmarchicus* (Gunnerus) and *C. helgolandicus* (Claus) in the northern North Atlantic Ocean were shown in relation to the seasonal and annual fluctuations of abundance of the species in the Celtic Sea from 1960 to 1981. These congeneric copepods, although showing allopatric distributions over most of their geographical range, have sympatric distributions in the Celtic Sea where they dominate the dry weight biomass of the plankton throughout the year. The two species respond differently to the development of the seasonal thermocline and halocline by taking up different vertical distributions in the water column. *C. finmarchicus* occurred in the colder, more saline water below the thermocline, while *C. helgolandicus* occurred in the warmer, less saline water above the thermocline. This behaviour is postulated as a mechanism by which these morphologically similar copepods more fully exploit the resources of their temporally and spatially heterogeneous environment and also minimise interspecific competition. The species have the same foraging techniques and are able to exploit the same size spectrum of particulates. The vertical depth strata in which the populations are found for most of the year in the Celtic Sea means that both species exploit the diatom bloom in early spring but, thereafter, *C. helgolandicus* grazes on the daily production of the autotrophs in the euphotic zone while *C. finmarchicus,* below the thermocline, has to rely for its food on sedimenting particulates (whole cells, detritus and faecal material). The isolating mechanisms whereby these two populations partition the habitat in the Celtic Sea are discussed.

## Introduction

*Calanus finmarchicus* and *C. helgolandicus* are two of the commonest species of copepod in the holoplankton of the northern North Atlantic Ocean (Edinburgh Oceanographic Laboratory, 1973). These congeneric species use the same foraging techniques and potentially share the same food. In areas where these morphologically similar species have sympatric distributions, such as the seasonally thermally stratified waters of most of the European continental shelf, how do they co-exist? What mechanisms, if any, can be observed in the copepods' behaviour which limit competitive interactions of the populations? Interspecific competition, habitat and niche selection are mechanisms which minimise competitive interactions and affect the structure of plankton communities. The results of previous observations made on the vertical distribution of these species in spring (Williams and Conway, 1980) from separate regions of the continental shelf around the British Isles (Celtic Sea and northern North Sea), suggest that when the species co-occur they are likely to demonstrate different behavioural strategies. These behavioural differences could expose them to different size ranges and quality of particulates if the populations take up different positions in the water column, thereby minimising interspecific competition for food and space. I have attempted to investigate these assumed behavioural traits from a site in the Celtic Sea where the species are known to have sympatric distributions. The objectives of this study are to demonstrate the partitioning of the habitat by these two species of *Calanus* and to suggest what characters are responsible for any differences observed in their behaviour.

## Materials and methods

The site chosen for the study in the Celtic Sea (CS2 – 53°30′N; 07°00′W; Fig. 1) was a region where the tidal stream amplitudes at spring tides were less than 0.5 m $s^{-1}$ (Sager and Sammler, 1968). The site has a depth of approximately 105 m and is strongly thermally stratified during the summer months. The position was occupied for 10 to 14 d periods in January, June/July, August and

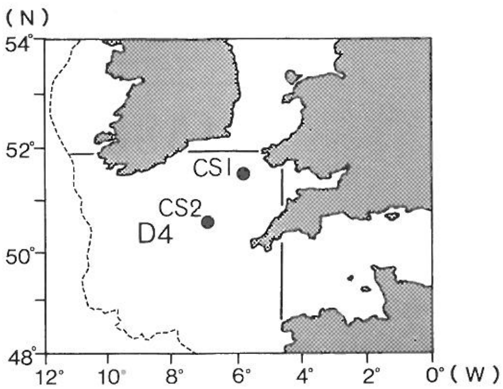


**Fig. 1.** Position of Celtic Sea sites (CS2 and CS1) and Standard Area D4 from the Continuous Plankton Recorder survey. Shelf edge (200 m contour) is indicated by dashed line

September/October 1982 and in April 1983 on board R.R.S. "Frederick Russell". Vertical profiles using standard hydrographic techniques were completed on each cruise to measure salinity, temperature, etc. Zooplankton samples were obtained with the IMER Double Longhurst-Hardy Plankton Recorder (DLHPR) (Williams *et al.*, 1983). The DLHPR was deployed to 5 m off 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 temperature, depth range and flow of water through each net (53 and 280 $\mu$m mesh) were recorded simultaneously with each plankton sample as the recorder was towed through the water column. The counts of the organisms per sample were converted to numbers $m^{-2}$ over the depth range sampled; usually 100 m to the surface. A night and day pair of DLHPR hauls, taken with the coarse mesh net system from each of the five cruise periods, were selected for use in this study.

Results from the Continuous Plankton Recorder (CPR) survey (Glover, 1967; Colebrook, 1982) were used to show the year to year and seasonal variability in numerical abundance at 10 m of *Calanus finmarchicus* (Gunnerus), *C. helgolandicus* (Claus) and phytoplankton in the Celtic Sea for a 22 yr period, 1960 to 1981. Surface temperature measurements for the Celtic Sea are based on data collated by my colleagues J. M. Colebrook and A. Taylor (IMER).

## Results

### Geographical distribution in the northern North Atlantic Ocean

Geographical distributions of plankton are primarily governed by latitudinal differences of temperature which affect successful breeding and survival of the species. Within the geographical boundaries of occurrence of these two species, the regions where they are numerically abundant (I assume) coincide with the optimum temperature for the species. The annual mean geographical distribution of *Calanus finmarchicus* in the northern North Atlantic Ocean is shown in Fig. 2. The 14 °C isotherm plotted represents its most northerly position in the summer (August: United States Naval Oceanographic Office, 1967); the water temperature to the north of this isotherm is less than 14 °C. This isotherm delineates the southern limit of the majority of the populations of *C. finmarchicus* in the North Atlantic Ocean, except on the shelf region to the south-west of the British Isles (Celtic Sea), the northern North Sea and the eastern seaboard of North America. The sea-surface temperature at the sampling site in the Celtic Sea in the summer months is ca. 18 °C.

*Calanus helgolandicus* is a southerly distributed species in the CPR survey. The geographical distribution and annual mean abundance of the species is shown in Fig. 3. The position of the 15.5 °C isotherm in August delineates the northern limit for the majority of the distribution of this species in the north-east Atlantic Ocean, though not for the northern North Sea. Sea-surface temperatures to the south of this isotherm range from 15.5° to ca. 27 °C within the survey area. *C. helgolandicus* is abundant in the Celtic Sea, especially in the latter half of the year (Colebrook, 1982; Williams and Conway, 1984).

In the open ocean the geographical distributions of these two species are essentially allopatric, but in the Celtic Sea they have overlapping (sympatric) distributions, as based on data of annual means from the CPR.

### Seasonal distribution in the Celtic Sea

One mechanism whereby competitive interactions between species may be minimised is the seasonal displacement of the breeding periods, and therefore of their numerical abundance. The mean monthly numerical abundance of

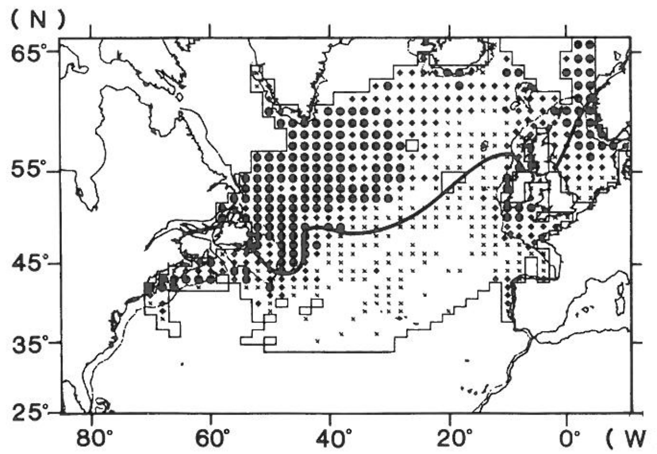


**Fig. 2.** *Calanus finmarchicus.* Annual mean distribution and abundance from sampling at 10 m depth by the Continuous Plankton Recorder (CPR). Data for all months sampled were combined to show the mean abundance from 1960 to 1981. Samples were assigned to rectangles 1° latitude by 2° longitude. Rectangle means are represented by three graded symbols. The absence of symbols (in the sampled area) indicates that the species were not found in Plankton Recorder samples. The boundary of the sampled area is shown by straight lines; position of the 14 °C isotherm in August is shown

*Calanus finmarchicus* and *C. helgolandicus* for Area D4 (i.e., Celtic Sea), based on sampling at 10 m with the CPR for a 22 yr period, is shown in Fig. 4. *C. finmarchicus* occurred more abundantly in the spring and winter and its distribution throughout the 22 yr period was sporadic compared with *C. helgolandicus,* which reached a seasonal maximum between April/May and October throughout the sampling period. There were large within-year and between-year differences in abundance of *C. helgolandicus,* although there was a general consistency in the timing of seasonal occurrence of the species at 10 m depth. In the majority of years, *C. helgolandicus* reached a maximum abundance in June, although occasionally it was abundant in late summer before presumably migrating away from the surface waters in October/November (Fig. 4 b).

If the seasonal succession and changes in numerical abundance of these two copepods observed at 10 m were reflected also in the populations at depth, then the species could be further partitioning the habitat and its resources. The appearance of *Calanus finmarchicus* at 10 m corresponded with the development of the phytoplankton bloom in spring (Fig. 5 a), to a greater extent than did the appearance of *C. helgolandicus.* The onset of the spring bloom of diatoms at 10 m, sampled by the CPR, occurred in early March and reached a peak in April in most years (Fig. 5 a) which was one to two months earlier than the peak of abundance of *C. helgolandicus,* the most abundant copepod herbivore species in the Celtic Sea. A large percentage (> 75%) of the autotrophic production in late spring and summer in the Celtic Sea is associated with phytoplankton < 5 $\mu$m (Joint and Pomroy, 1983; Joint and Williams, in press). *C. helgolandicus* may be utilising these small cells, especially the flagellates with flagella many times the body width, but this is not supported by published data on the feeding of herbivorous copepods (Marshall and Orr, 1956; Conover, 1978). The water temperature at the surface during the phytoplankton bloom was 10° to 12 °C, while in May to June it was 12° to 14 °C (Fig. 5 b) when the main peak of abundance of *C. helgolandicus* occurred. It is in May, June and July that the seasonal thermocline is established in the Celtic Sea and the deep chlorophyll maximum appears, after the spring phytoplankton bloom associated with the thermocline.

## Vertical distribution in the Celtic Sea

The vertical distribution and abundance of *Calanus finmarchicus* and *C. helgolandicus* (Copepodite Stages V and VI) in night and day hauls from the five cruise periods are shown in Fig. 6, together with salinity and temperature profiles. Total numbers in the profiles (nos. m$^{-2}$, over the depth range sampled) are shown for all hauls. It is apparent that the two species were present in roughly equal numbers at this site, throughout the year. This is contrary to the conclusion reached from the data given in Fig. 4, based on horizontal sampling at constant depth (10 m) with the CPR. *C. helgolandicus* is known to overwinter in the Celtic Sea, primari-

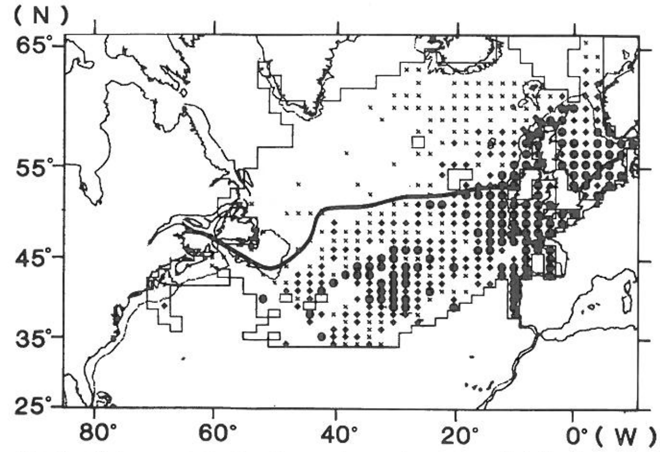


**Fig. 3.** *Calanus helgolandicus.* Annual mean distribution and abundance from sampling at 10 m depth with the CPR. The position of the 15.5 °C isotherm in August is shown. Further details as in legend to Fig. 2

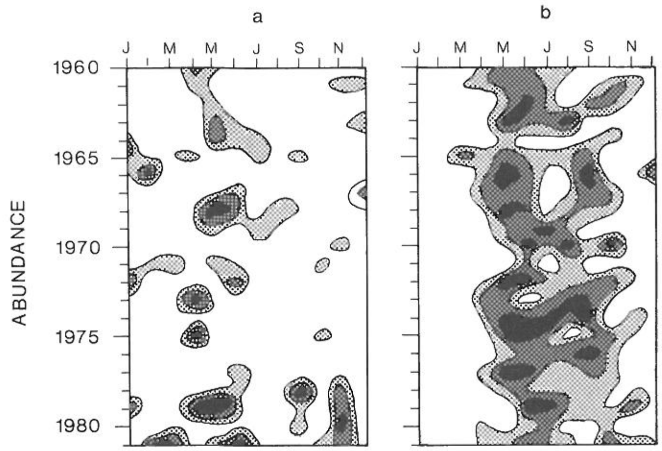


**Fig. 4.** *Calanus finmarchicus* (a) and *C. helgolandicus* (b). Seasonal abundance from 1960 to 1981 in the Celtic Sea at depth of 10 m in Standard Area D4 of the Continuous Plankton Recorder survey. Indices of abundance per sample were derived from averaging the means for each month in all rectangles (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 m$^3$

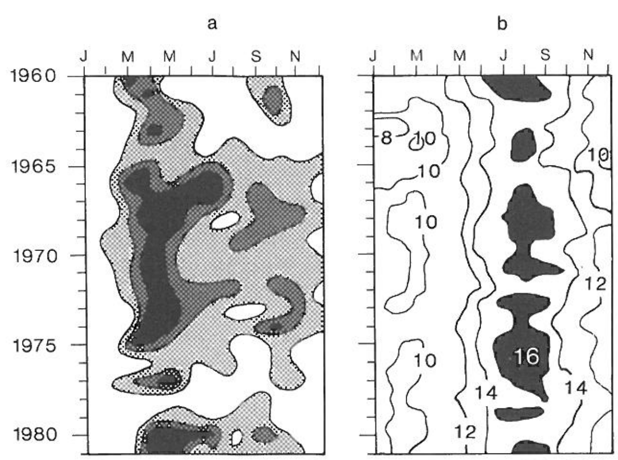


**Fig. 5.** Phytoplankton colour (a) and temperature, °C (b) in the Standard Area D4 of the Continuous Plankton Recorder survey. Phytoplankton colour is in arbitrary units of "greenness", the heaviest shading indicating the highest intensity

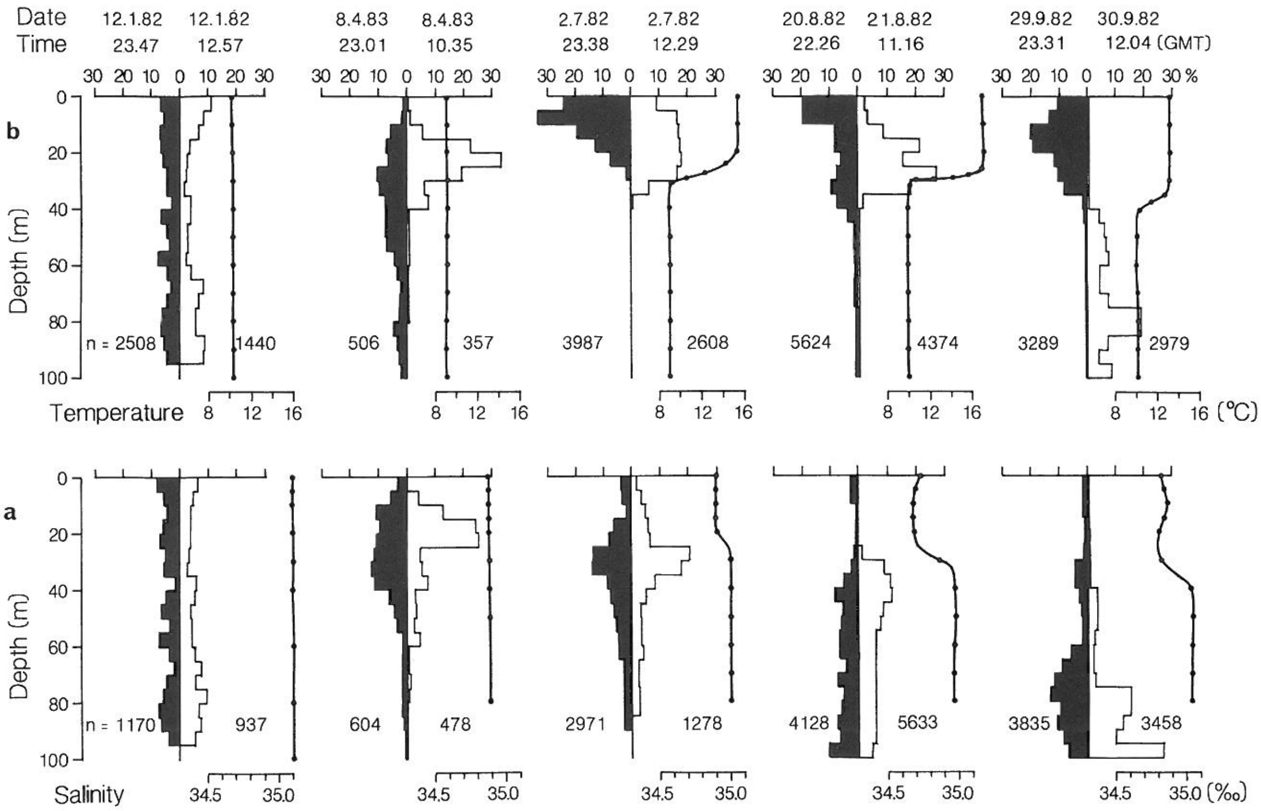


**Fig. 6.** *Calanus finmarchicus* (a) and *C. helgolandicus* (b). Vertical distribution of Copepodite Stages V and VI. Numbers in each night (black) and day (white) hauls are plotted in 5 m depth intervals as percentages of total numbers (*n*) present in the haul. Salinity and temperature profiles are shown for the day hauls. GMT: Greenwich Mean Time

ly as Stage V and adults (Williams and Conway, 1984), but it seems that *C. finmarchicus* also overwinters and reproduces in early spring. By the time the thermocline was well established in July, the populations of the two species had already vertically separated in the water column. The *C. finmarchicus* were associated with the colder (ca. 8.5 °C), more saline water below the thermocline, while the *C. helgolandicus* were distributed in the warmer, less saline water above the thermocline. At this sampling site, the water below 40 m hardly increased in temperature above the values measured in winter. Therefore, when the water column is thermally stratified, two separate water masses are formed; the upper wind-mixed and the lower tidally-mixed water. From July into autumn, *C. finmarchicus* remained below the thermocline in the colder water, presumably feeding on sedimented and tidally re-suspended particulates, whereas *C. helgolandicus* remained within the euphotic zone in close association with autotrophic phytoplankton.

## Discussion

The two congeneric copepods *Calanus finmarchicus* and *C. helgolandicus* are morphologically very similar and show little phenotypic divergence. As far as I am aware, no hybrids are produced between the species which demonstrates that their isolating mechanisms are fully evolved and the two species are distinct. They co-exist in the shallow waters of the Celtic Sea and, because they persist and reproduce in this locality, it is axiomatic that the species possess adaptations which enable the populations to exploit the habitat. The Celtic Sea is a temperate region and provides the environmental conditions required more by *C. helgolandicus* than by *C. finmarchicus*. The major portion of the oceanic population of the northern boreal species, *C. finmarchicus,* is found in waters with a summer temperature less than 14 °C (Fig. 2). The only reason that this northern species is able to persist in the Celtic Sea, which has a sea-surface temperature of ca. 18 °C, is because the sea becomes seasonally thermally stratified and a winter sea-temperature is retained below the thermocline.

At CS1 (Fig. 1), a sampling site to the north-east of CS2 close to the transitional water of the Irish Sea frontal boundary, only *Calanus helgolandicus* is found (Williams and Conway, 1984). The temperature of the bottom water at CS1 increases considerably over the winter sea-temperature, and sharp temperature discontinuities, similar to those seen at CS2, are not observed. The Stage V and VI copepodites of *C. helgolandicus* are found throughout the water column at CS1 during the summer months (Williams and Conway, 1984) and are not restricted to the mixed water above the thermocline.

The response by the two species to the increase in temperature and the development of the seasonal thermocline is shown when the populations separate above and below the thermocline. Although interspecific competition is minimised in the summer months, it must be present in the early spring and winter period when the water column is isothermal and the populations are mixed together. In April, the time of the onset of the spring diatom bloom in the Celtic Sea, the species have overlapping vertical distributions (Fig. 6). In feeding experiments, carried out on board ship with natural and cultured phytoplankton, it was observed that the two species were able to graze on the same size spectrum of particulates and therefore must, at times, be competing for the same food. Spring is a critical time for *Calanus finmarchicus* because it is the only period when the species reproduce in the Celtic Sea; although oocytes were seen in the oviducts of females from below the thermocline throughout the summer months. After the spring reproductive period, *C. finmarchicus* maintains itself below the thermocline as Stage V copepodites and adults. The presence of *C. finmarchicus* in the Celtic Sea cannot be explained in terms of an annual advective event of oceanic water, as suggested by Southward (1984) as a mechanism for controlling the change of abundance of the two congener species of *Sagitta* (*S. elegans* and *S. setosa*) off Plymouth. I consider that *C. finmarchicus* has penetrated and colonised the shelf sea from the main oceanic population rather than having co-evolved with *C. helgolandicus* in this region. The presence of *C. finmarchicus* together with *C. helgolandicus* throughout the winter months suggests that *C. finmarchicus* is a permanent resident of this region, the population perhaps being maintained by longer-term advection from the ocean. This process would maintain the gene flow from the oceanic population to the sub-population in the Celtic Sea and reinforce the very characters which separate these species.

The vertical distribution of the two species in the Celtic Sea is the result of the response by the individuals in the populations to the vertical temperature structure which is, itself, an expression of the physical processes acting within the ecosystem.

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