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Distribution patterns of mesozooplankton biomass in the North Sea

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ABSTRACT: During spring 1986 and winter 1987, zooplankton samples were collected over the entire North Sea by means of a multi-closing net-system. Before taxonomic treatment, wet weight estimates and carbon content conversions were carried out. From this data set, 4 962 522 tons zooplankton biomass (dry weight) were estimated for the whole North Sea during the spring survey. High biomasses (more than 100 mg C/m^3) were located in areas between the Orkneys and the Shetlands, off the mouth of the Firth of Forth, the Channel and the river Rhine. Considerable zooplankton biomass was also found parallel to the Danish west coast. Furthermore, a narrow tongue of high biomass (partly greater than 200 mg C/m^3) intruded from the north, between 1 °E and 4 °E, into the northern North Sea, turning to the east at 56 °N, and continuing into deeper water layers to form a left turning "helix" of high biomass in the central part of the North Sea. During the winter survey the carbon content of the zooplankton stock was a factor 10 lower than in summer. Altogether, 519 340 tons of zooplankton biomass (dry weight) were estimated in winter. Centres of relatively high biomass were located off the mouth of the rivers Rhine, Weser and Elbe and off the British east coast moving in a cyclic way across the Dogger Bank into the central North Sea. A further maximum of zooplankton abundance was found in the Skagerrak region. However, an intrusion of zooplankton from the shelf edge into the North Sea was not observed in winter. A qualitative analysis of species composition showed that small copepods dominated the zooplankton in the southern and eastern North Sea. The "eddy" of high biomass in the northern North Sea observed in spring, however, was mostly shaped by the large copepod *Calanus finmarchicus* (70–90 %). The distribution of zooplankton biomass in the North Sea is discussed in relation to the hydrographic conditions and to the biology of the dominant species.

INTRODUCTION

Within the framework of the interdisciplinary ZISCH-Project (Circulation and Pollutant Transfer in the North Sea), various parameters were measured over the entire North Sea during two extremes of seasonal activity (spring/winter).

The mesozooplankton is one of the very important compartments of the ecosystem in the North Sea. It drives the whole system of carbon-transport through the food-web by grazing on the phytoplankton (Steele, 1974). Moreover, vertical diurnal migration of the mesozooplankton in combination with metabolic processes strongly influences the distribution of organic matter. Hence, knowledge of both horizontal and vertical zooplankton distribution is necessary.

Taxonomic analysis of nearly 1000 net-samples from both surveys is quite time consuming. Therefore, a preliminary evaluation of wet weight estimates was carried out, the results of which are presented here together with qualitative statements about species composition.

MATERIAL AND METHODS

Sampling method

The zooplankton samples were generally collected with the "Meßhai" (HYDROBIOS), a multi-closing net-system that allows a subdivision of the water column into five steps by means of oblique hauls. Temperature, salinity and depth were recorded simultaneously by sensors installed in the gear.

During bad weather conditions, an alternative multi-closing-net was used to perform vertical hauls from on board the drifting vessel. In shallow coastal areas, as well as over the Dogger Bank, the simple WP-2-Net was used. All nets had mesh sizes of 200 μm.

During May/June 1986, samples were collected at 127 stations (Fig. 1). Two stations were cancelled because of bad weather. At 73 stations the water column was sampled with the "Meßhai". The filtration of approximately 3700 m^3 water resulted in 315 samples from different depth ranges. At 28 stations the vertical multi-closing-net was used, while at 26 very shallow stations samples were taken with the WP-2-Net.

During January–March 1987 (Fig. 5), eight stations were cancelled because of bad weather conditions. At 120 stations the "Meßhai" was used. 9150 m^3 water were filtered at these stations, yielding 418 samples from different depth ranges. Sampling by means of the WP-2-Net took place at 19 stations in the case of bad weather or shallow depths.

Qualitative statements on species composition

Immediately after collection, the living plankton material was inspected under the microscope on board the research vessel. For each sample the most important zooplankton species (or groups) were ranked according to their relative contribution to the total zooplankton stock in the sample, symbolized in the figures by solid circles of six different sizes.

Wet weight estimates

The wet weights of the samples were determined on land with a micro-balance (PAG OERLIKON AG, Zürich) using the preserved material.

The samples were washed on a piece of gauze. The water was carefully sucked off so that the organisms remained undamaged for subsequent taxonomic determination. Large medusae which now and then occurred in the samples were removed, since their high water content would falsify the results of the wet weight estimates. The results of the measurements were related to the flow meter data of the "Meßhai", giving wet-weight per m^3. Finally, this data material was converted to carbon content by means of a conversion factor given by Cushing et al. (1958).

RESULTS

Biomass distribution patterns

The distribution of the carbon content of the zooplankton samples from the spring cruise is shown in Figures 2–4 for three depth ranges (0–20 m, 20–60 m, 60–150 m). The distribution patterns are outlined as iso-lines.

In the 0–20 m layer, high biomasses of more than 100 mg C/m^3 were located in the areas between the Orkneys and Shetlands, off the mouths of the Firth of Forth, the Channel and the river Rhine. Additionally, in the eastern North Sea proceeding from the river mouths of Weser and Elbe, along the Danish west coast considerable zooplankton-concentrations were found. A narrow tongue of high biomass (partly higher than 200 mg C/m^3) was recorded between 1 °E and 4 °E. It enters the North Sea from the north and turns to the east at 56 °N. Finally, it seems to join the high biomasses of the Skagerrak region. In deeper layers (Figs 3, 4), this "eddy" of high biomass seems to continue, so that a large "funnel" – or rather a left turning "helix" of high biomass coming from the north and gradually shifting into deeper layers is perceptible in the northern and central North Sea during spring. Altogether, during the spring survey in the North Sea a zooplankton biomass of 4 962 522 tons dry weight was estimated.

During the winter survey, a zooplankton biomass of 519 340 tons dry weight was found in the North Sea. Thus, as a rule, the carbon content of the zooplankton stock at that time was lower by a factor of about 10 compared to the spring. Nevertheless, centres of high biomass were also observed in winter (Figs 6–8), located off the mouths of the rivers Rhine, Weser and Elbe and in the Skagerrak region. Further, an area of high biomass was observed from the British east coast over the Dogger Bank into the central North Sea. In deeper layers, this area of high biomass continued and turned further north into the open North Sea. The tongue of high zooplankton biomass observed in spring coming from the shelf edge could not be detected in winter.

Qualitative statements about species composition

Figures 9–27 give an impression of the dominance of some important species and zooplankton groups during both cruises. From this, we gather that *Calanus finmarchicus* s. l. (Figs 9, 10) formed large stocks only in the northern North Sea, i.e. in water bodies of Atlantic origin. Also in winter this copepod was predominantly found in the northern North Sea. However, considerable stocks occurred only in the Norwegian Trench at that time. The small copepod *Temora longicornis* (Figs 11, 12), on the other hand, dominated in the southern part of the North Sea both in spring and in winter, i.e. in the pure North Sea water. Likewise, the small copepod *Acartia* spp. (Figs 13, 14) constituted an important part of the zooplankton stock during both seasons in the southern and south-eastern North Sea. An exception was the area north of Scotland, where *Acartia* spp. also occurred in large numbers. The *Pseudocalanus* group (Figs 15, 16), consisting of the small copepods *Pseudocalanus elongatus* and *Paracalanus parvus*, dominated primarily in the southern and eastern North Sea and, like *Acartia* spp., also in the Orkney-Shetland-Region. Nevertheless, during winter these copepods seem to be dominant everywhere in the North Sea. Euphausiacea and *Oikopleura* spp. (Figs 17–20) accounted for a certain

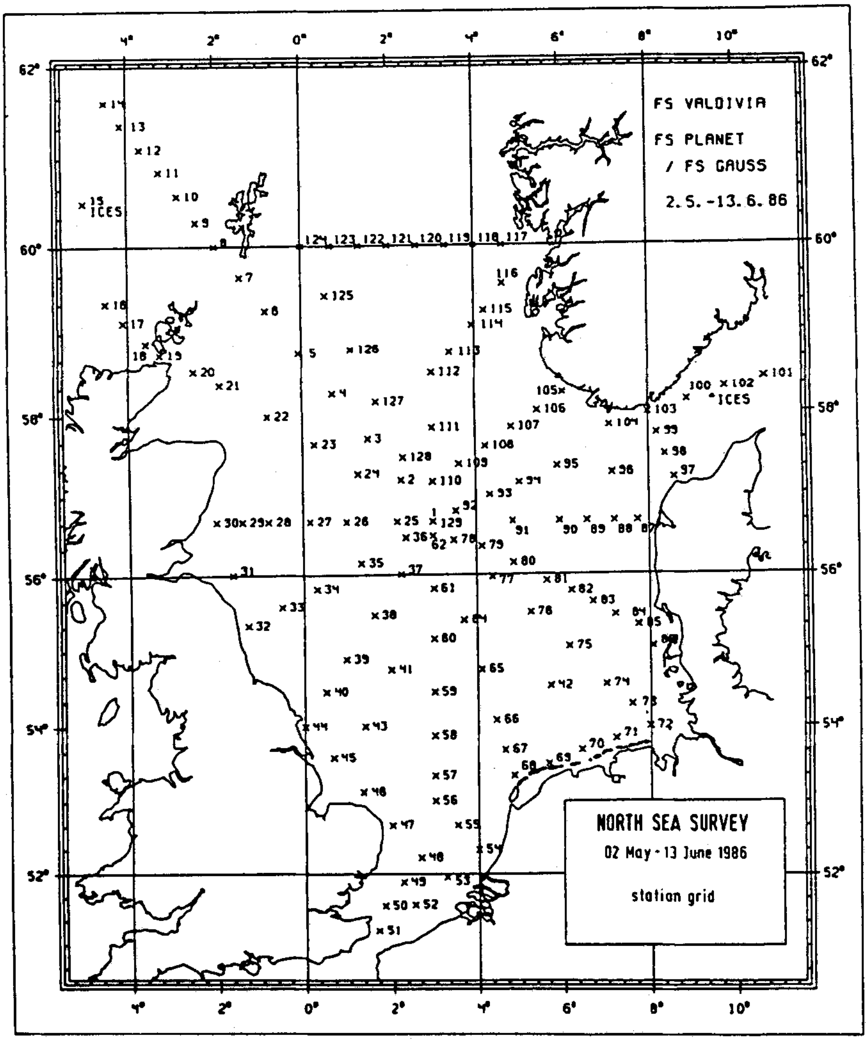

Fig. 1. Station-grid during the spring cruise 1986

proportion of the zooplankton stock in the northern North Sea and in the Skagerrak region during both cruises. The tiny carnivorous cyclopoid copepod *Oithona* spp. (Figs 21, 22) seems to be an inhabitant of the central and northern North Sea, where it represents an important part of the zooplankton stock. This was especially evident during the winter cruise. Actually, in winter, carnivorous groups like Amphipoda, Chaetognatha, *Aglantha* and *Pleurobrachia* (Figs 23–26) were conspicuous in the zooplankton material. During that season also, eggs and larvae of fishes prevailed in the samples in the southern North Sea (Fig. 27).

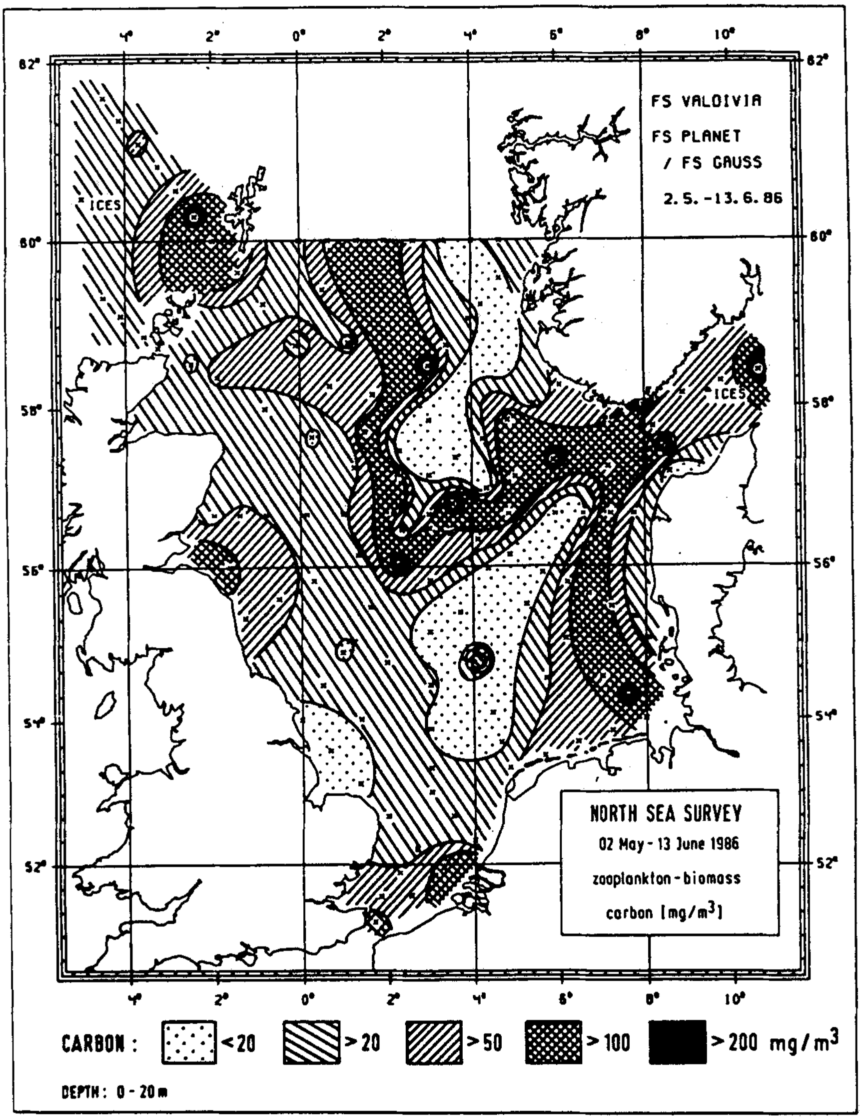

Fig. 2. Distribution patterns of zooplankton biomass (mg C/m^3) in the 0–20 m layer of the North Sea during the spring cruise 1986

DISCUSSION

A qualitative inspection of the zooplankton material resulted in characteristic horizontal distribution patterns of species and groups. From this we can conclude that *Calanus finmarchicus* and some species of the Euphausiacea as well as *Oikopleura* sp. characterize the zooplankton stock of the northern North Sea. On the other hand, small

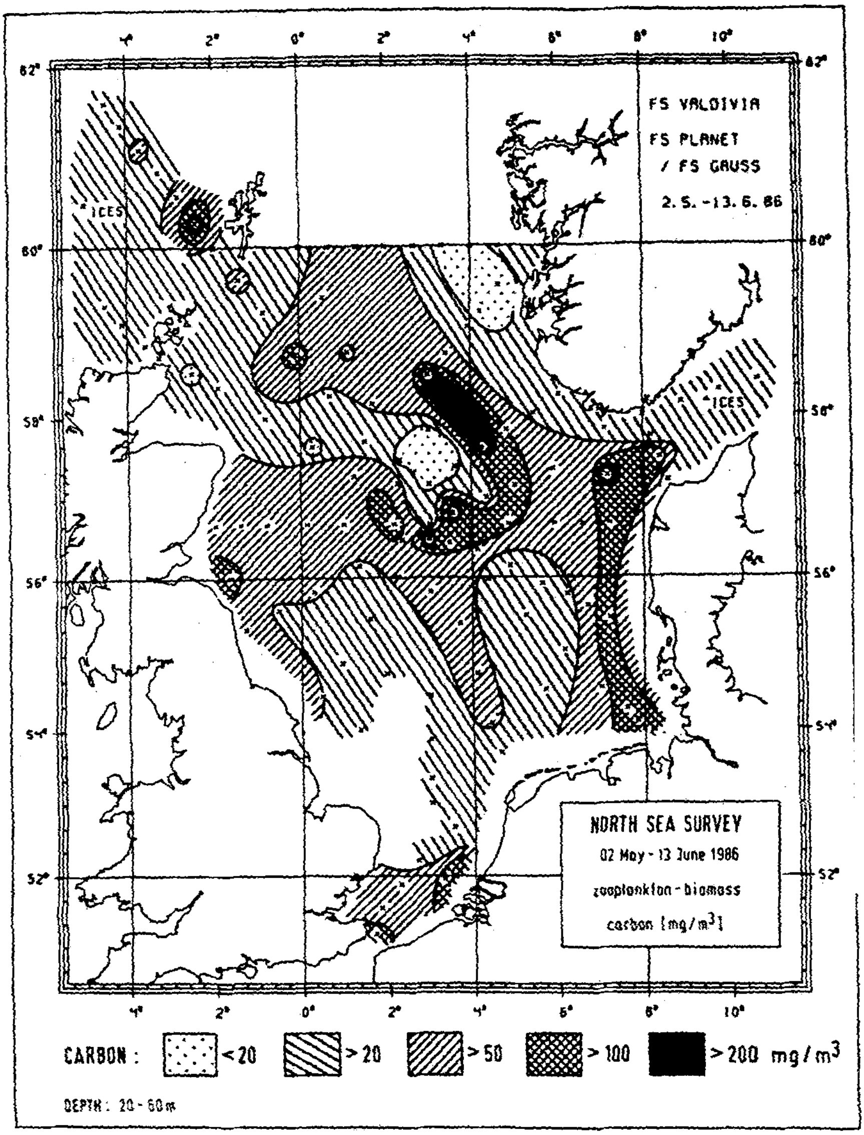

Fig. 3. Distribution patterns of zooplankton biomass (mg C/m^3) in the 20–60 m layer of the North Sea during the spring cruise 1986

calanoid copepods like *Temora longicornis*, *Acartia* spp. and the *Pseudocalanus* group were typical inhabitants of the southern and eastern North Sea. This fact, however, does not mean that these small species always formed the centres of high biomass found in the southern North Sea. It should be mentioned that especially in winter large organisms in low individual numbers, like Hyperiids or *Aglantha*, were sometimes able to dominate the zooplankton biomass.

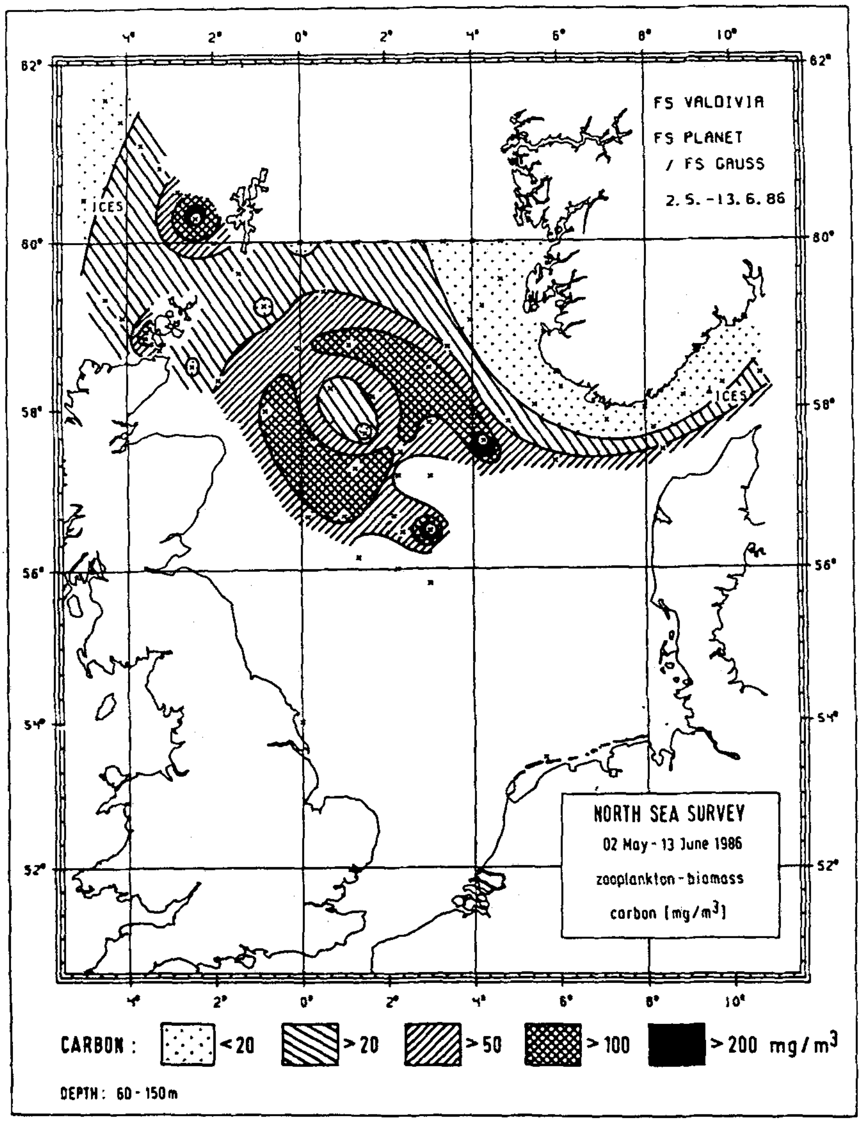

Fig. 4. Distribution patterns of zooplankton biomass (mg C/m^3) in the 60–150 m layer of the North Sea during the spring cruise 1986

From Rees (1949) and Matthews (1969) it is known that *Calanus finmarchicus* is an inhabitant of the northern North Sea at least during summer. Glover (1957) observed an intrusion of this copepod from the north with the Atlantic water between the Shetlands and the Norwegian Trench. It is also well known, for example from publications of Kraefft (1910), Rae & Fraser (1941), Rae & Rees (1947), Colebrook et al. (1961) and others, that small copepods do have large stocks in the southern and eastern areas of the North Sea.

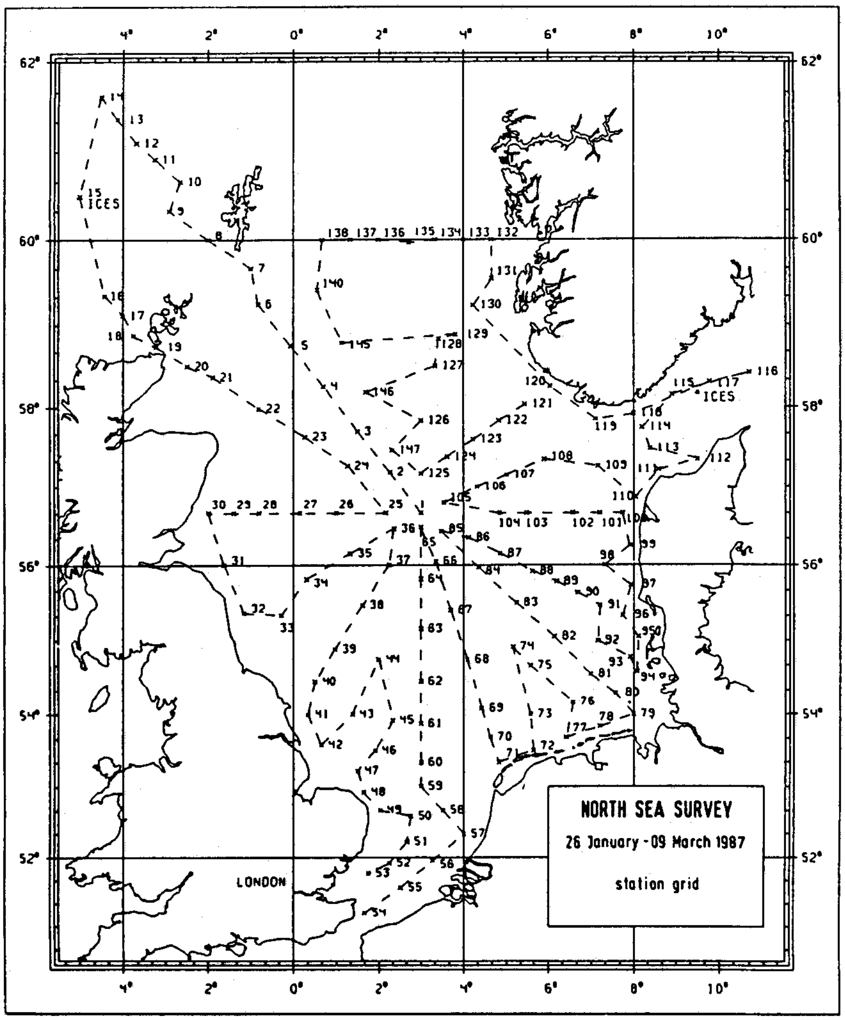

Fig. 5. Station-grid during the winter cruise 1987

Rae & Fraser (1941) reported that in the southern North Sea the *Pseudocalanus* group forms by far the largest part of the copepod stock. In the Hoofden, they found the winter months to be even more productive than summertime. Particularly in January, large concentrations were recorded along the Dutch coast. Thus, they assume propagating periods of these copepods during autumn and winter. In several publications, *Pseudocalanus* spp. is described as a detritus feeder, which fits it for surviving in winter. *Acartia* spp. was found by Rae & Fraser (1941) more commonly in the southern areas than in the central North Sea. According to them, the numerical difference between winter- and summer-populations is not marked very strongly, so they suggest reproduction periods all the year round. *Acartia* spp. is known as a herbivorous copepod that is able to

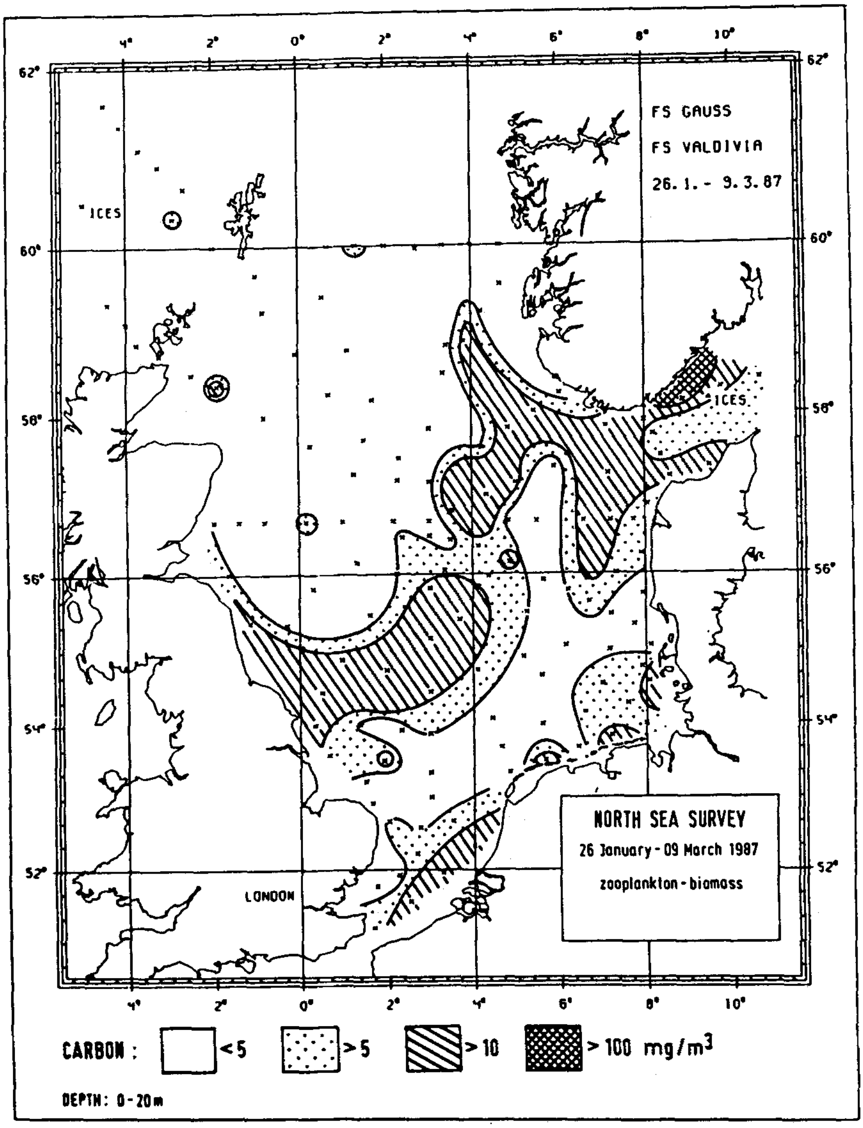

Fig. 6. Distribution patterns of zooplankton biomass (mg C/m^3) in the 0–20 m layer of the North Sea during the winter cruise 1987

survive as a mixed food consumer during unfavourable seasons. According to Timm (1896), *Temora longicornis* is to be found near Helgoland all the year round with maxima from November until April. Likewise, Rae & Fraser (1941) emphasize that during winter *T. longicornis* is well represented in Dutch coastal waters.

The tiny carnivorous cyclopoid copepod *Oithona* spp. seems to be an inhabitant of the central North Sea. It was noticed particularly in the samples from the winter cruise.

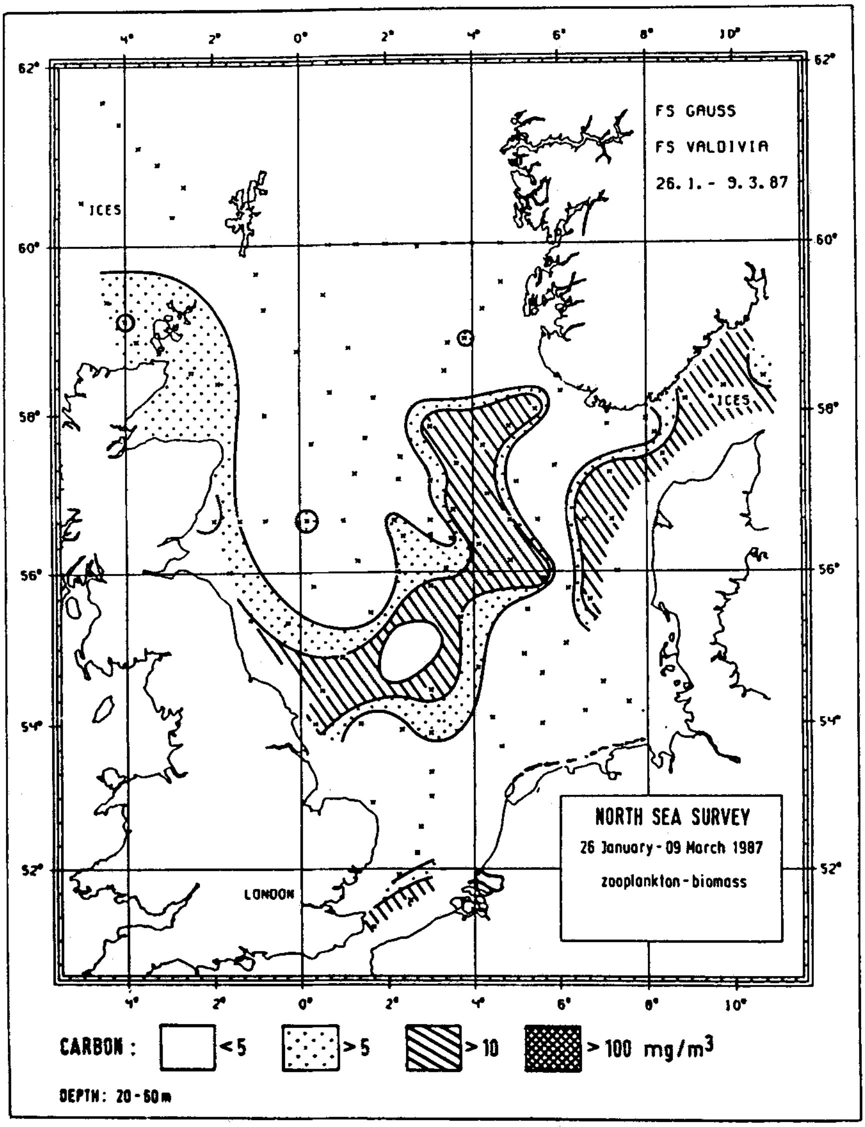

Fig. 7. Distribution patterns of zooplankton biomass (mg C/m^3) in the 20–60 m layer of the North Sea during the winter cruise 1987

Actually, at that time carnivorous groups like Chaetognatha, Amphipoda, *Aglantha* and *Pleurobrachia*, were conspicuous in the zooplankton material. Thus, we may state that detritus feeders (like *Pseudocalanus*) and carnivorous species dominated the zooplankton in the North Sea during winter.

A quantitative taxonomic analysis of the gained zooplankton samples is in progress but could not be finished up to this day. Therefore, at first, a statement of zooplankton

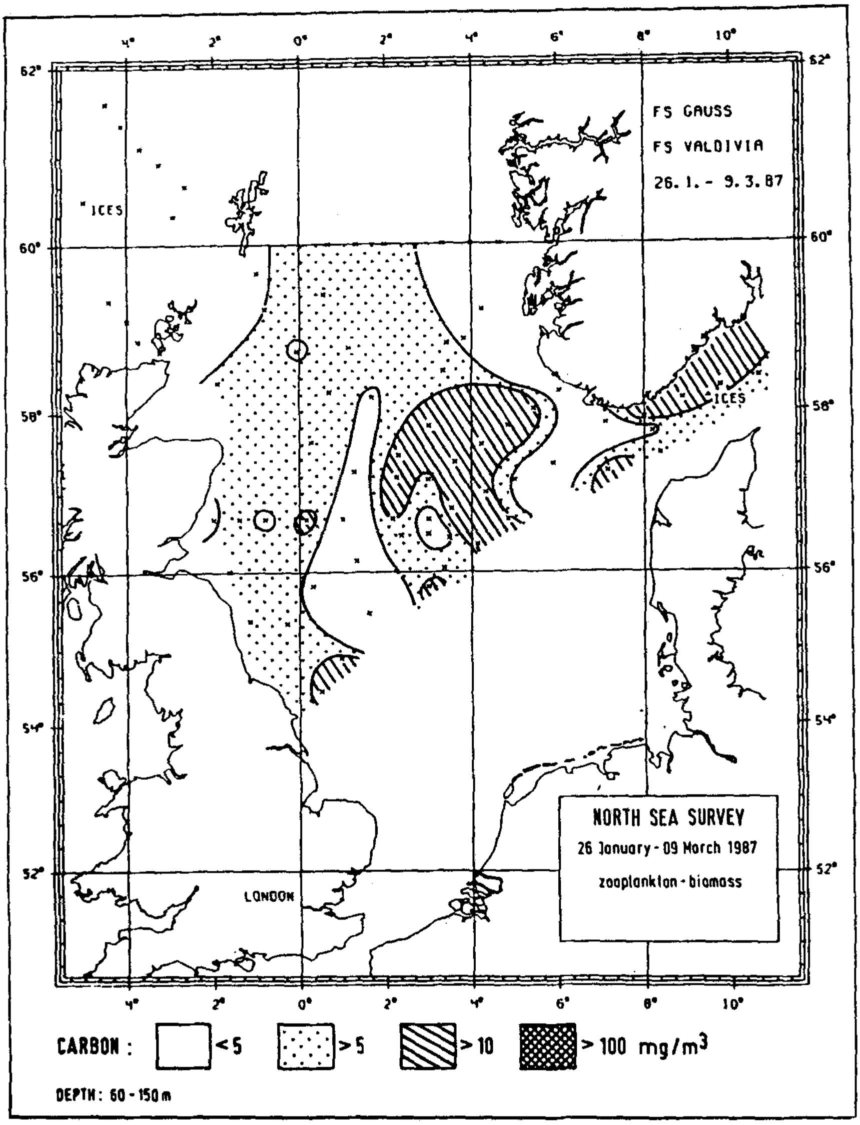

Fig. 8. Distribution patterns of zooplankton biomass (mg C/m^3) in the 60–150 m layer of the North Sea during the winter cruise 1987

distribution in the entire North Sea should be made by wet weight estimates. It should be mentioned that there are drawbacks, if wet weight is estimated on preserved zooplankton material, for after fixation a reduction of biomass is usually observed. Several authors (e.g. Omori, 1970, 1978; Morris, 1972; Durbin & Durbin, 1978) report that the leaching of organic contents (lipids and proteins) from zooplankton preserved in formaldehyde-seawater solution differs depending upon species and their chemical composition. Fur-

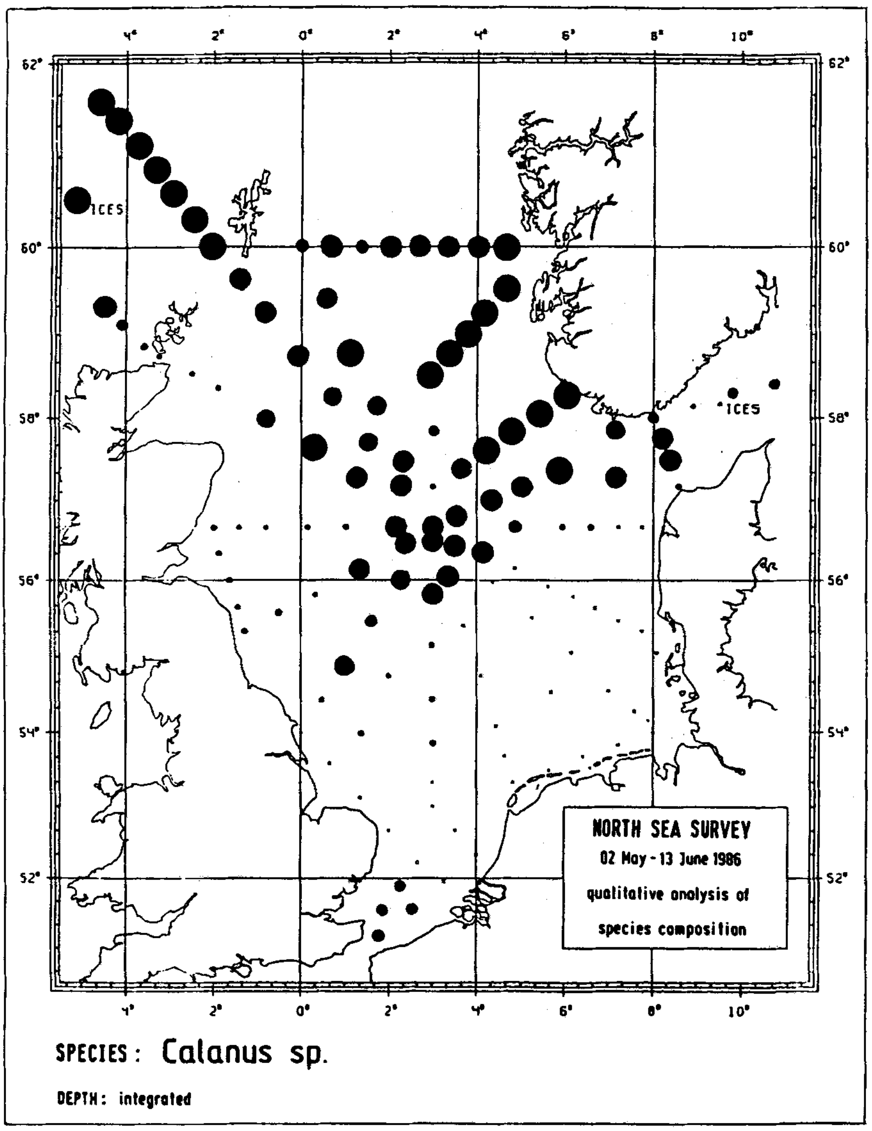

Fig. 9. Relative dominance of *Calanus finmarchicus* in the zooplankton stock during the spring cruise symbolized by the sizes of solid circles

thermore, seasons, temperature, geographical distribution and diets may have an influence (e.g. Omori, 1969; Ikeda, 1974; Beers, 1976).

Daro & van Gijsegem (pers. comm.) undertook dry weight estimates with *Temora longicornis* and *Centropages hamatus* using freshly captured animals as well as preserved material. On an average, they recorded a reduction of dry weight of 43 % after fixation. Landry (1978) found a loss of 37 % after prolonged preservation of *Acartia clausi*.

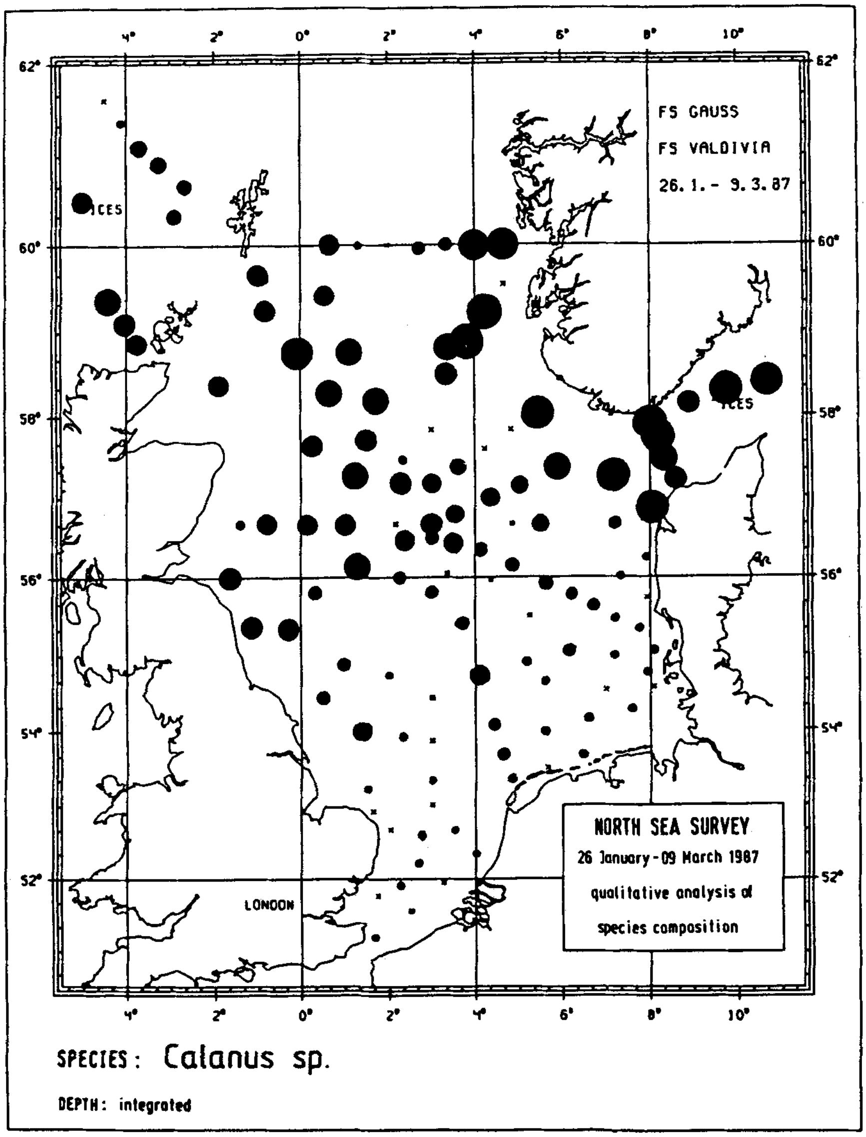

Fig. 10. Relative dominance of *Calanus finmarchicus* in the zooplankton stock during the winter cruise symbolized by the sizes of solid circles

Durbin & Durbin (1978) determined a decrease of only 21 % in the same species. Even the choice of the buffer solution, which usually is added to the formaldehyde, seems to influence the dry-weight. Omori (1978) reports that the loss of organic content is much greater in borax-buffered zooplankton material than in samples treated with hexamethylenetetramine-buffered formaldehyde solution. Hopkins (1968) found out that satiated

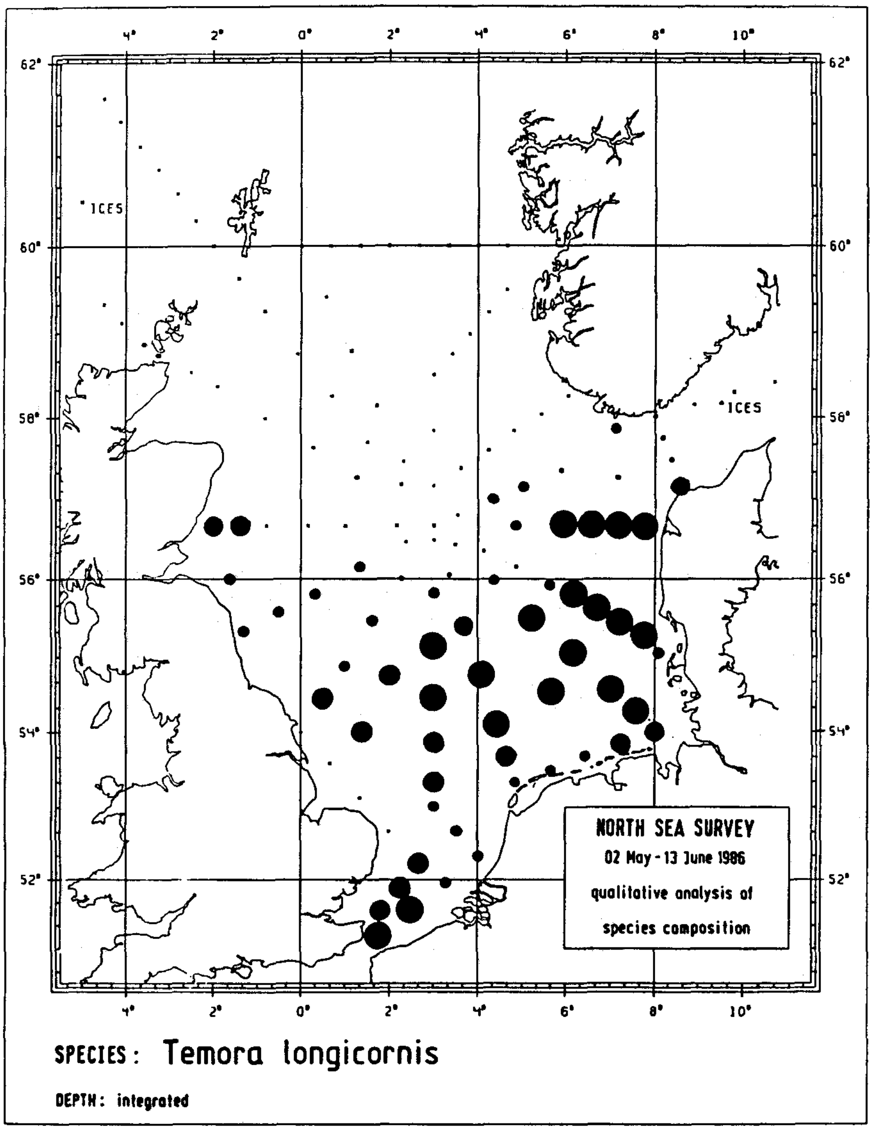

Fig. 11. Relative dominance of *Temora longicornis* in the zooplankton stock during the spring cruise symbolized by the sizes of solid circles

hexamethylenetetramine in formaldehyde solution effects an increase in dry-weight of 10–25 % in many zooplankton-groups, e.g. Copepoda, Euphausiacea and Chaetognatha.

Thus, we can assume that part of the reduction of weight caused by the formaldehyde-fixation will have been compensated by the influence of hexamethylenetetramine. Since our zooplankton samples were preserved with a 4 % solution of formal-

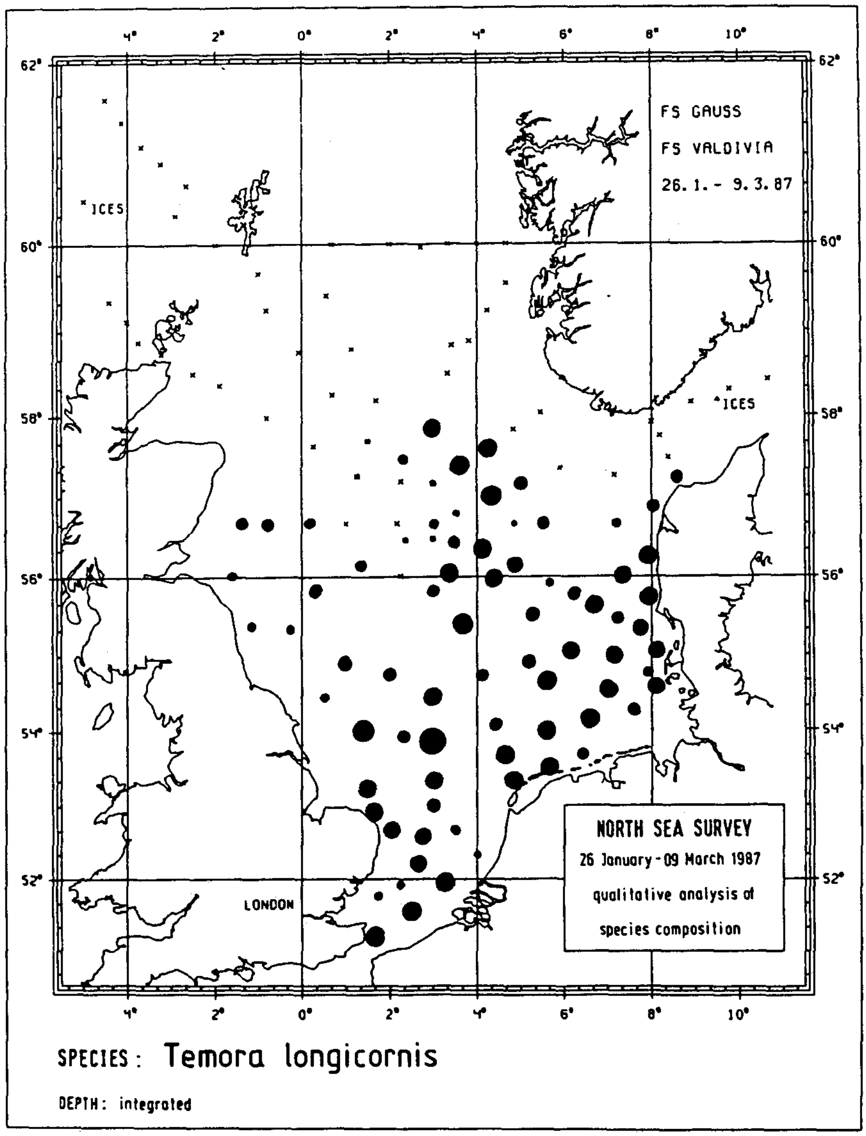

Fig. 12. Relative dominance of *Temora longicornis* in the zooplankton stock during the winter cruise symbolized by the sizes of solid circles

dehyde in sea water buffered with satiated hexamethylenetetramine, we can hope that there were no considerable weight losses after fixation.

Summing up, it seems that no precise knowledge is available on the effects of formaldehyde-fixation on weight estimates. Probably a multitude of factors is responsible for the considerable variability of the results. After having investigated this problem in

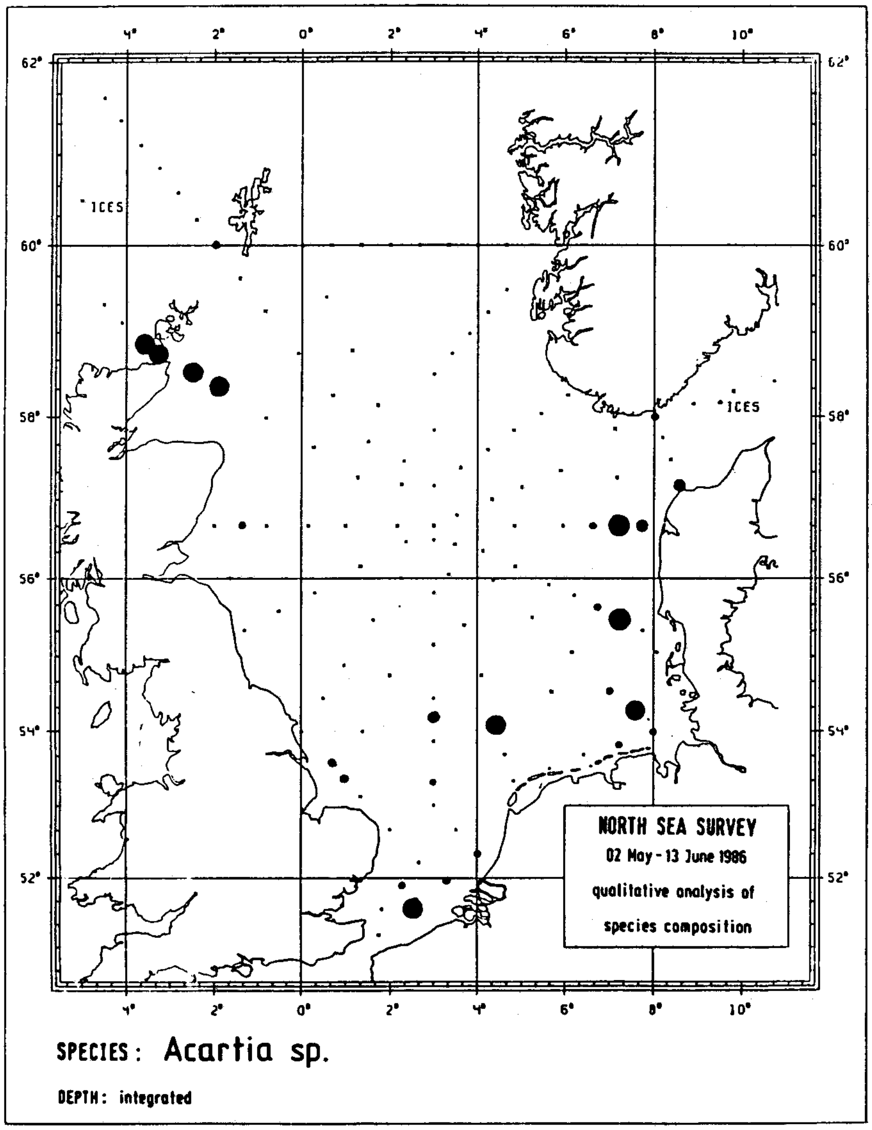

Fig. 13. Relative dominance of *Acartia* sp. in the zooplankton stock during the spring cruise symbolized by the sizes of solid circles

detail, Sonnenberger (1982) concluded that further extensive experiments are necessary in order to judge definitively whether a correction of weight estimates gained from preserved material is possible by means of suitable conversion factors.

With the above mentioned insufficiencies in mind, we have used our wet weight estimates for a first presentation of a quasi synoptical distribution of zooplankton biomass in the North Sea, both in the horizontal and the vertical, respectively.

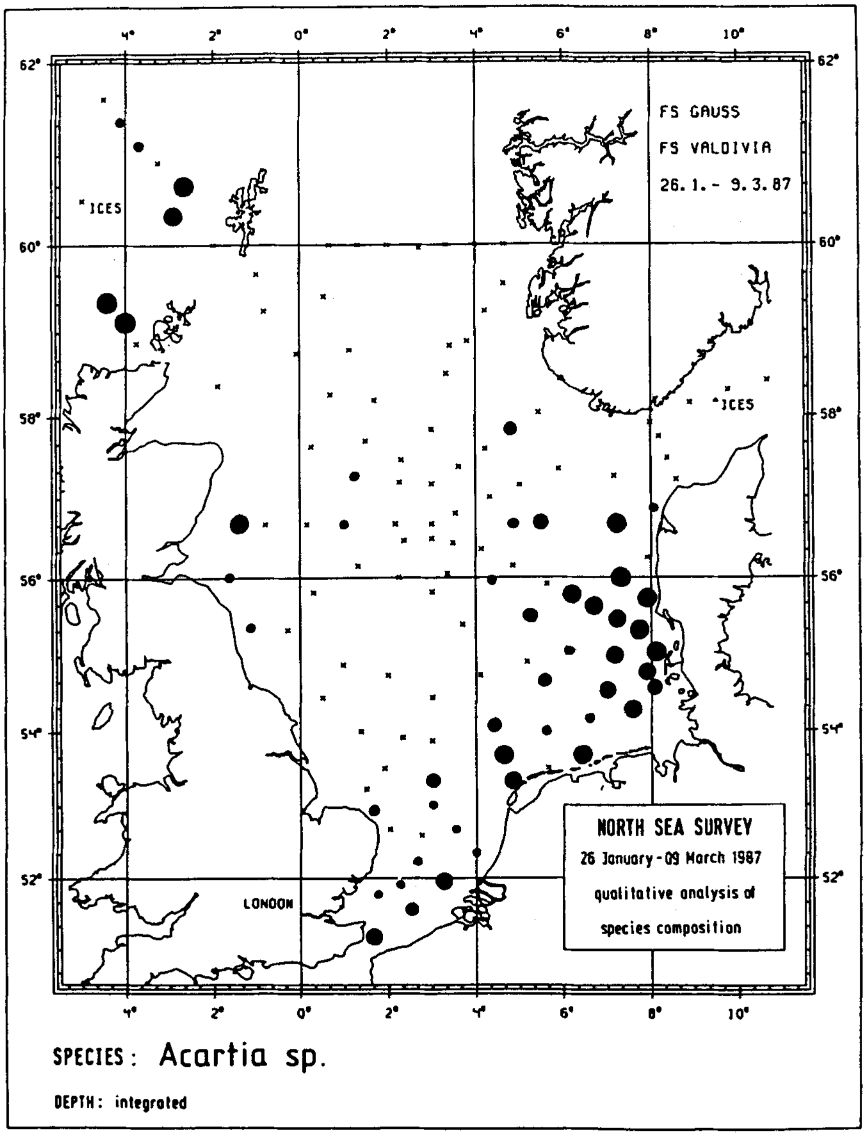

Fig. 14. Relative dominance of *Acartia* sp. in the zooplankton stock during the winter cruise symbolized by the sizes of solid circles

In the central North Sea, the distribution patterns of zooplankton-biomass during both surveys (spring/winter) resulted in cyclical courses. They are likely caused by the topography and the prevailing current system of the North Sea, which normally takes an anti-clockwise course. As described already by Böhnecke (1922), the water masses entering the North Sea from the North split up into several branches: the eastern mass turns towards the Skagerrak region at 57 °N, whereas the western branch flows farther

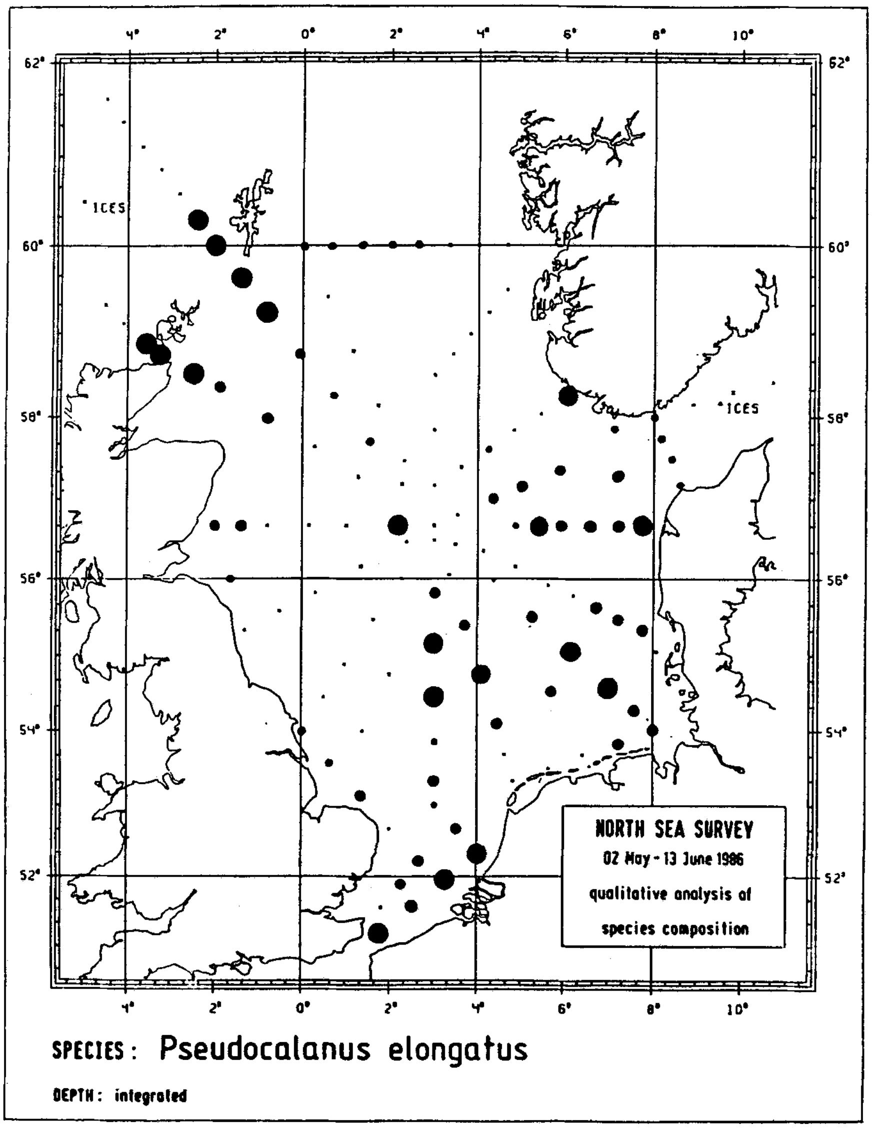

Fig. 15. Relative dominance of the *Pseudocalanus* group in the zooplankton stock during the spring cruise symbolized by the sizes of solid circles

south along the British east-coast and does not turn to an north-easterly course until reaching the Dogger-Bank region (Fig. 28). Subsequent writers like Backhaus (1984) stated several modifications of this current system mainly caused by distinct wind conditions. Nevertheless, the basic patterns of the currents in the North Sea can be considered as described by Böhnecke (1922).

According to this, it seems that during the spring condition the pure Atlantic water

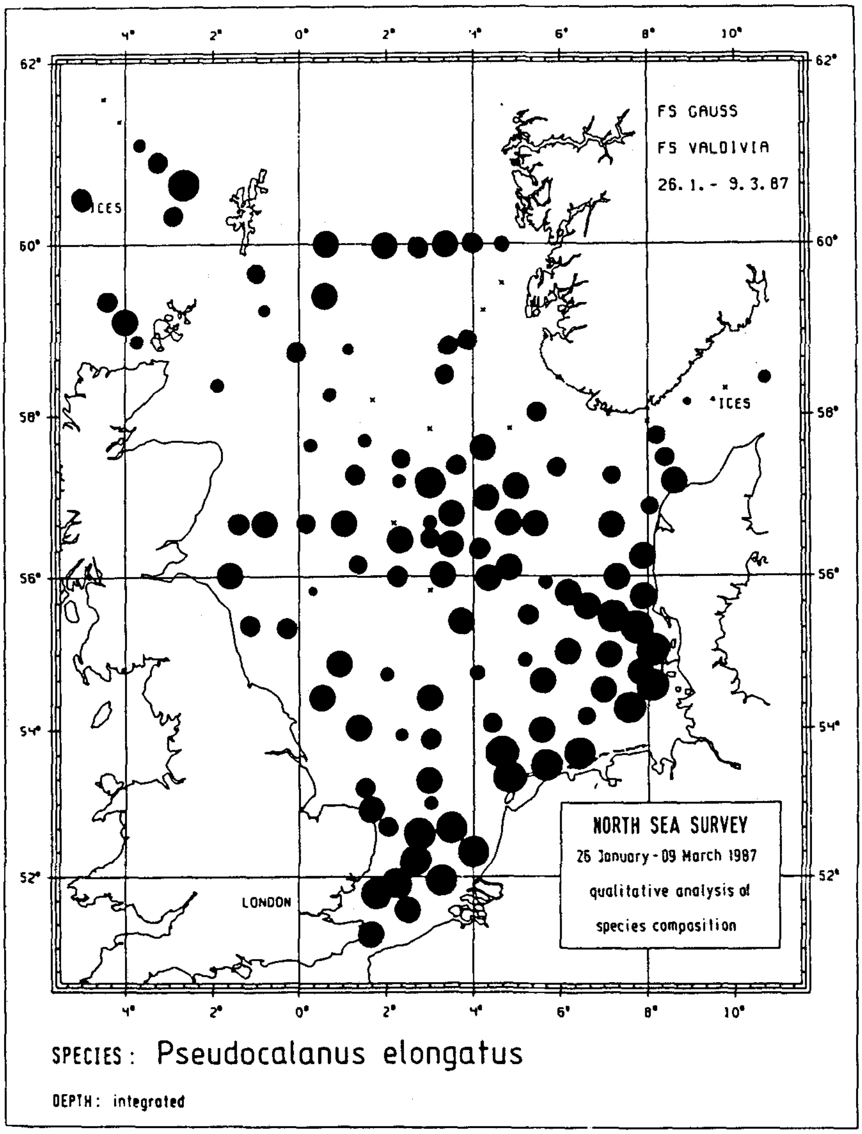

Fig. 16. Relative dominance of the *Pseudocalanus* group in the zooplankton stock during the winter cruise symbolized by the sizes of solid circles

flowing into the North Sea between the Shetlands and the Norwegian Trench determined the zooplankton patterns in the northern and central North Sea. These water masses contain nutrients in abundance (e.g. Radach et al., 1990) and they turn to the north-east at 57 °N. On the other hand, the mixed waters of coastal and Atlantic origin flowing in between the Orkneys and the Shetlands and subsequently proceeding along the British east-coast up to the Dogger Bank characterized the distribution patterns of

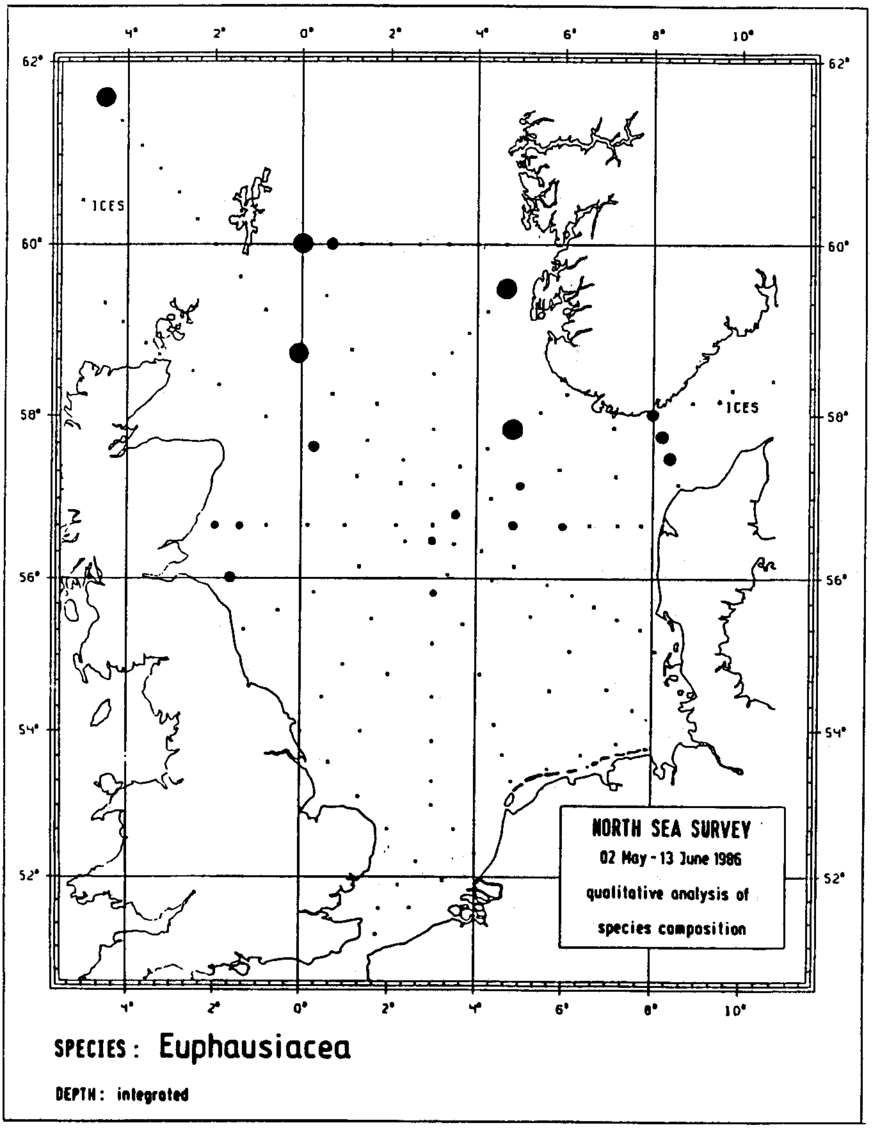

Fig. 17. Relative dominance of the Euphausiacea in the zooplankton stock during the spring cruise symbolized by the sizes of solid circles

zooplankton in winter. Thus, we can assume in principle that the Atlantic inflow from the north plays an important role in the zooplankton productivity in extensive areas of the northern and central North Sea.

The large "eddy" of high zooplankton biomass found in the northern and central North Sea during spring consisted predominantly of *Calanus finmarchicus* (70–90 %), which hibernates in large numbers at the shelf edge of the Norwegian Sea at depths

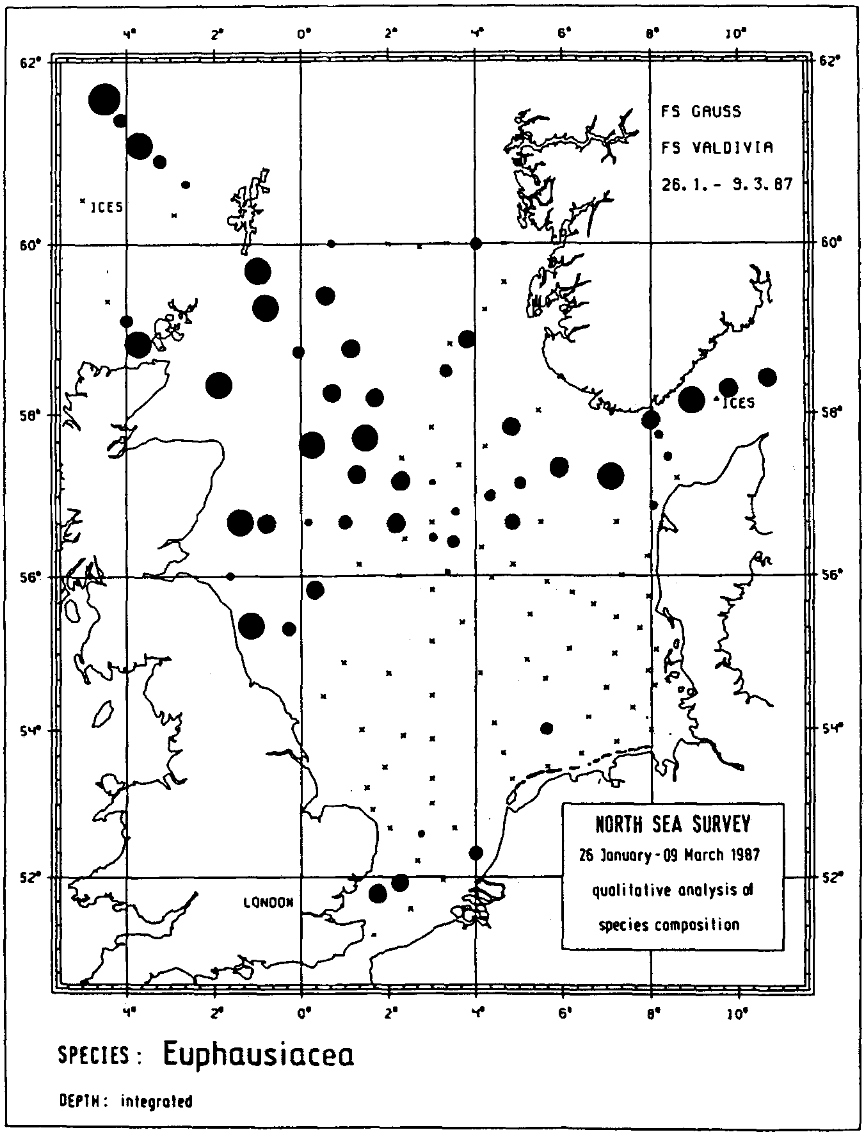

Fig. 18. Relative dominance of the Euphausiacea in the zooplankton stock during the winter cruise symbolized by the sizes of solid circles

between 400 and 700 m, i.e. in the transitional zone between Atlantic water and Arctic bottom water (Östvedt, 1955; Krause, 1978). In February/March, the hibernating organisms move into the surface layer for propagation (Sömme, 1934; Marshall & Orr, 1955), where they might be seized by the surface currents. In this way, these stocks and their subsequent summer-generations may be transported by the oceanic current (Dooley, 1974) into the North Sea. Svansson (1980) located this inflow between 2 °E and 3 °E.

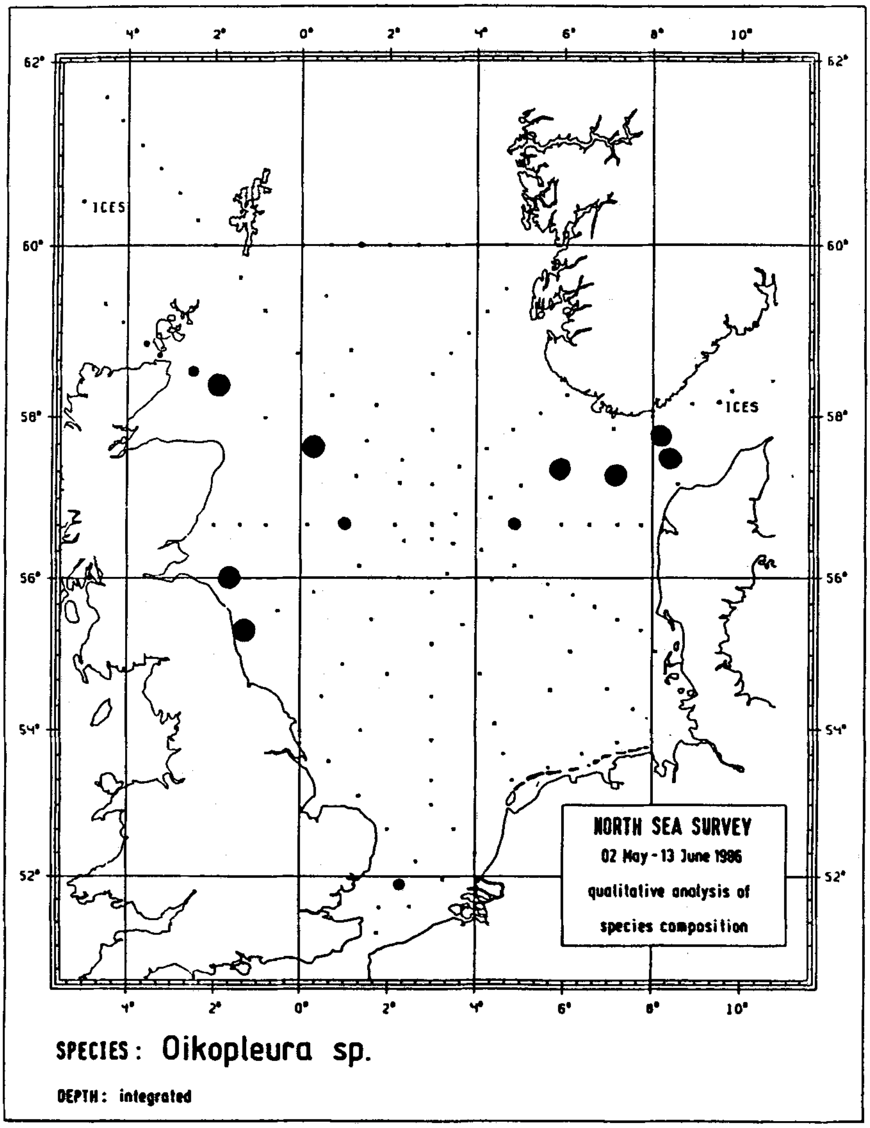

Fig. 19. Relative dominance of *Oikopleura* sp. in the zooplankton stock during the spring cruise symbolized by the sizes of solid circles

In the Skagerrak region, these stocks seem to join a further *Calanus*-population which probably hibernated in deep water layers of the Norwegian Trench. Possibly, however, their resting stages have been swept by deep counter currents of the Norwegian Trench from the shelf edge to the Skagerrak region during winter (e.g. Hirche, 1984). Nevertheless, during the winter survey (February 1987) this large copepod obviously had already completed its ascent to the surface layer. Sufficient nourishment is

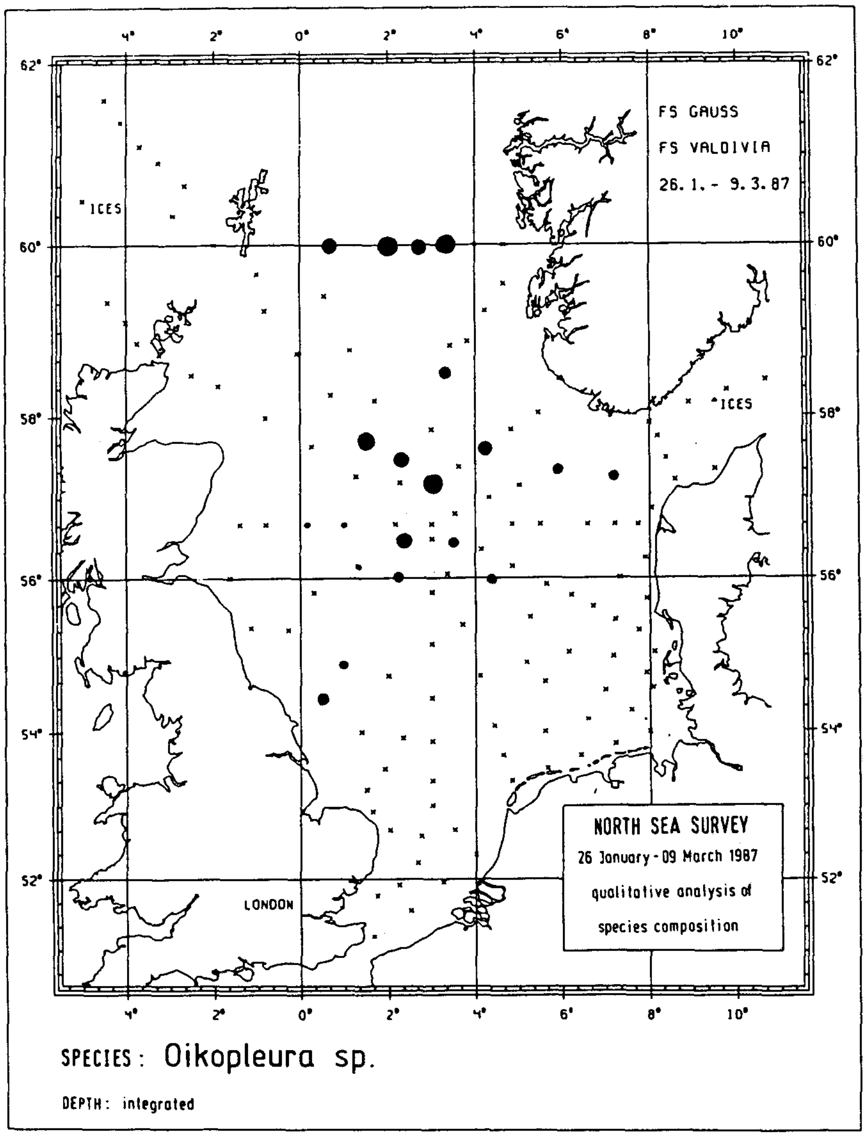

Fig. 20. Relative dominance of *Oikopleura* sp. in the zooplankton stock during the winter cruise symbolized by the sizes of solid circles

already available in this region in February because of an early diatom bloom based on special hydrographic conditions (e.g. Kattner et al., 1983). Thus, at that time, high concentrations of zooplankton biomass (> 10 to > 100 mg C/m^3) could already be detected in the Skagerrak region.

The biomass produced in the Skagerrak seems to spread not only northwards with the Norwegian Coastal Current but also to the south into the shallow North Sea (Figs

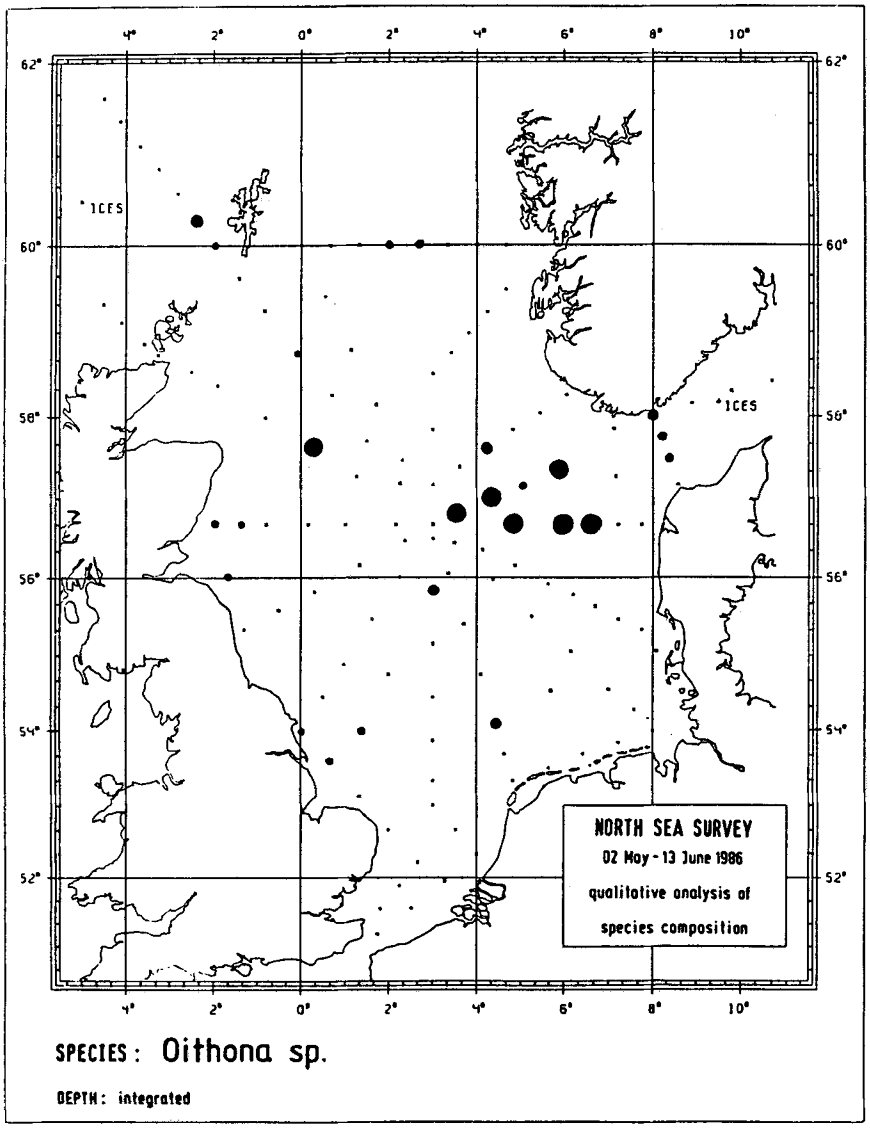

Fig. 21. Relative dominance of *Oithona* sp. in the zooplankton stock during the spring cruise symbolized by the sizes of solid circles

6–8). Especially in the deeper layer (20–60 m), an enlarged tongue of high biomass is visible along the Danish coast. This becomes understandable regarding the publication of Aure & Saetre (1981), who described the blocking effects of water masses in the Skagerrak when westerly winds prevail. Only when winds blow from the east does a considerable outflow of Skagerrak water set in. These blocking effects possibly may cause a reverse current into the shallow North Sea.

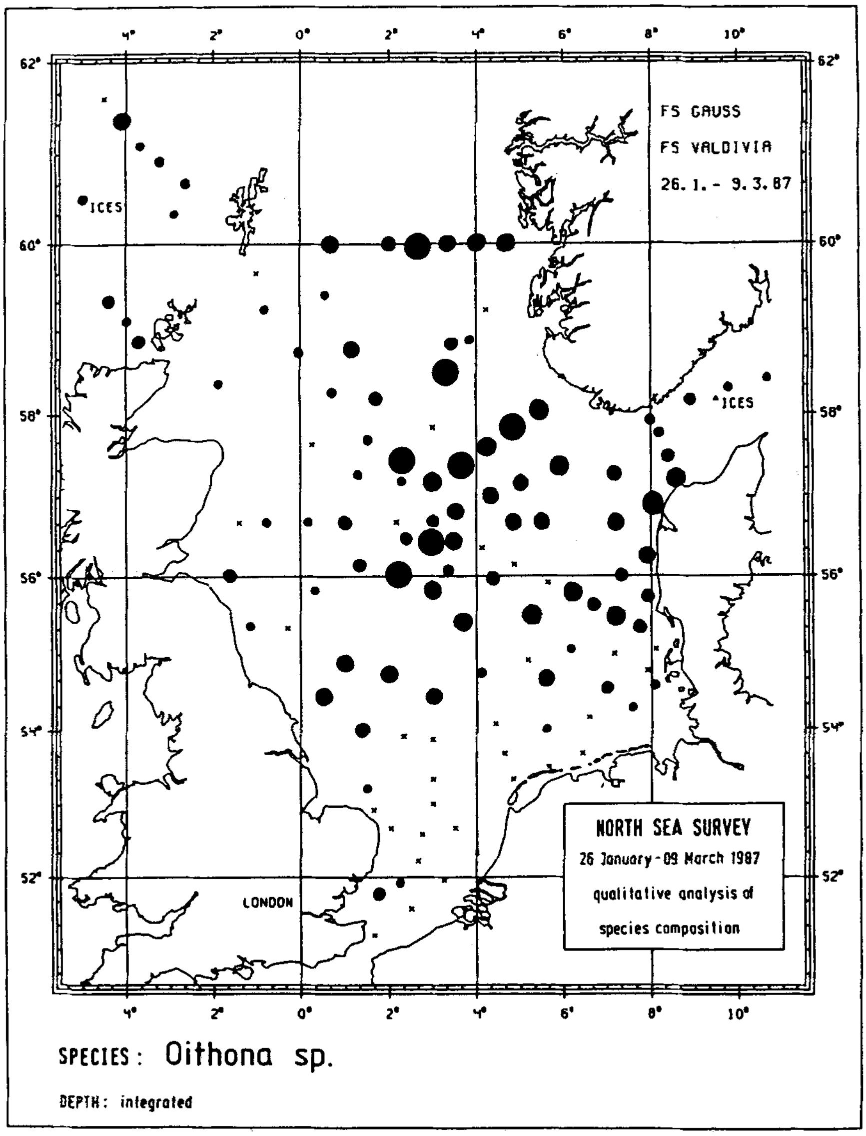

Fig. 22. Relative dominance of *Oithona* sp. in the zooplankton stock during the winter cruise symbolized by the sizes of solid circles

An inflow of high zooplankton biomass from the shelf edge into the shallow North Sea was not observed during the winter cruise. However, a left turning centre of biomass, starting from the British east coast and spreading over the Dogger Bank and farther north into the central North Sea, was visible (Figs 6, 7). Further centres of relatively high biomass were recorded in the Southern Bight (mouths of the Channel and the river Rhine) and in the German Bight (mouths of the rivers Weser and the Elbe).

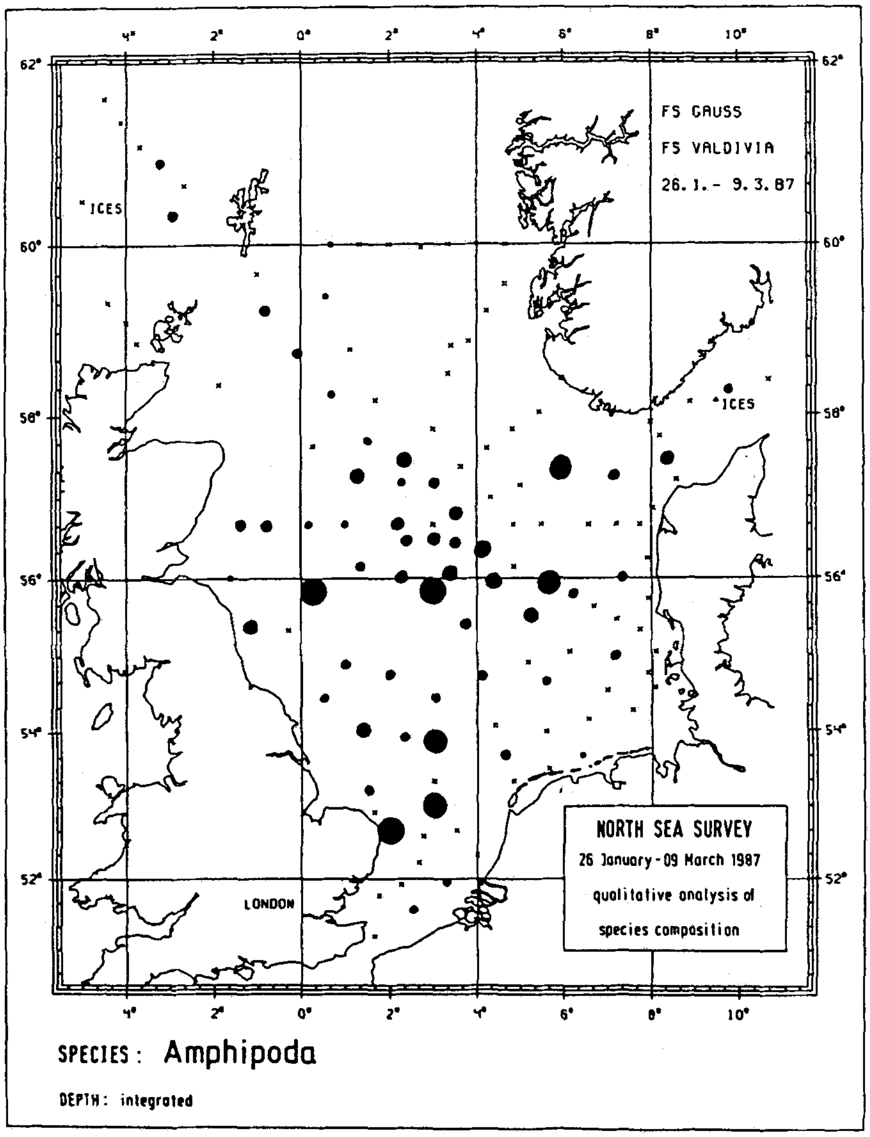

Fig. 23. Relative dominance of Amphipoda (Hyperiids) in the zooplankton stock during the winter cruise symbolized by the sizes of solid circles

The cyclic distribution patterns of high zooplankton biomass observed during the spring and winter cruises gradually shifted to deeper water layers, forming a large left turning helix in the central and northern North Sea. This particularly became visible through the spring survey (Figs 2–4); but also in winter, the deepest layer (60–150 m) shows relatively high biomass in extensive areas of the northern North Sea (Fig. 8). Thus, we could imagine that in this region large amounts of organic particles particularly

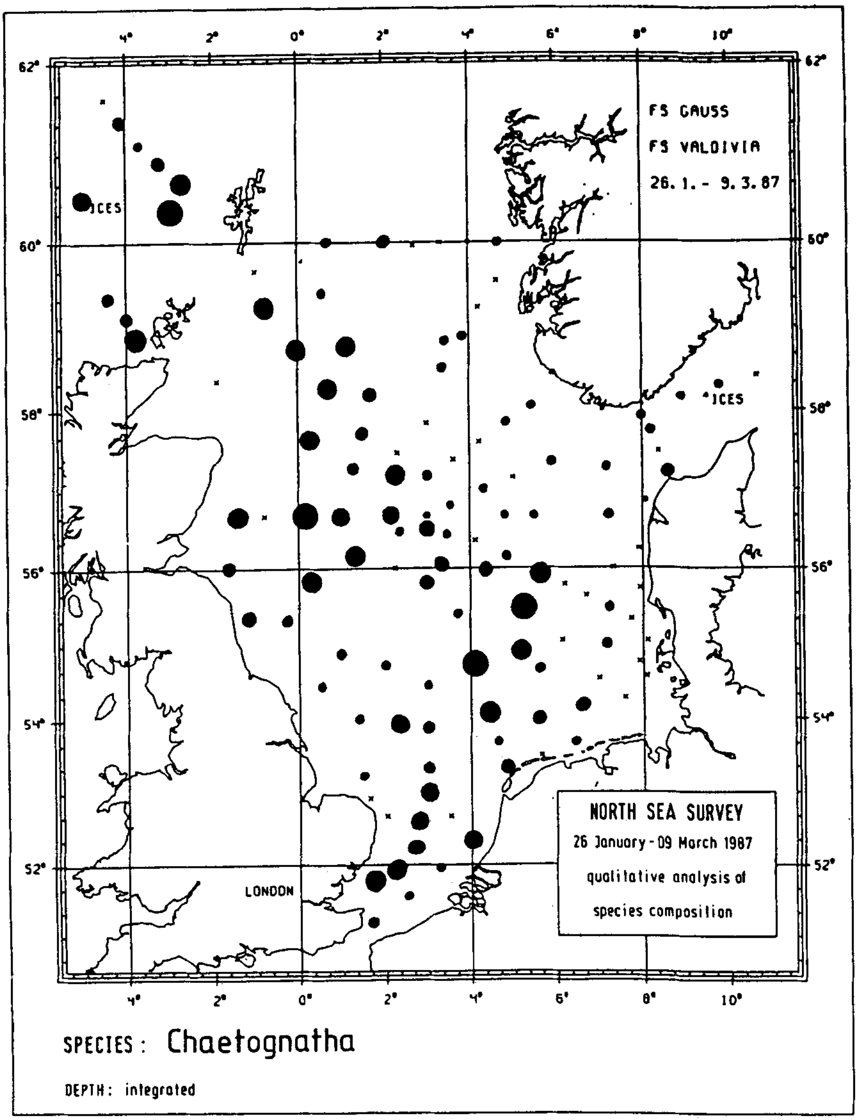

Fig. 24. Relative dominance of Chaetognatha (*Sagitta* sp.) in the zooplankton stock during the winter cruise symbolized by the sizes of solid circles

produced in the inflowing current system will be gradually transported to deeper regions and to the bottom.

The downward flux of the organic material may be advanced by the Baltic Water, which in summer spreads far to the west as far as the Greenwich Meridian and thus overlays the Atlantic waters. During winter, however, the Baltic water draws back to the Norwegian coast (Dietrich, 1950), Accordingly, during spring the centre of high biomass

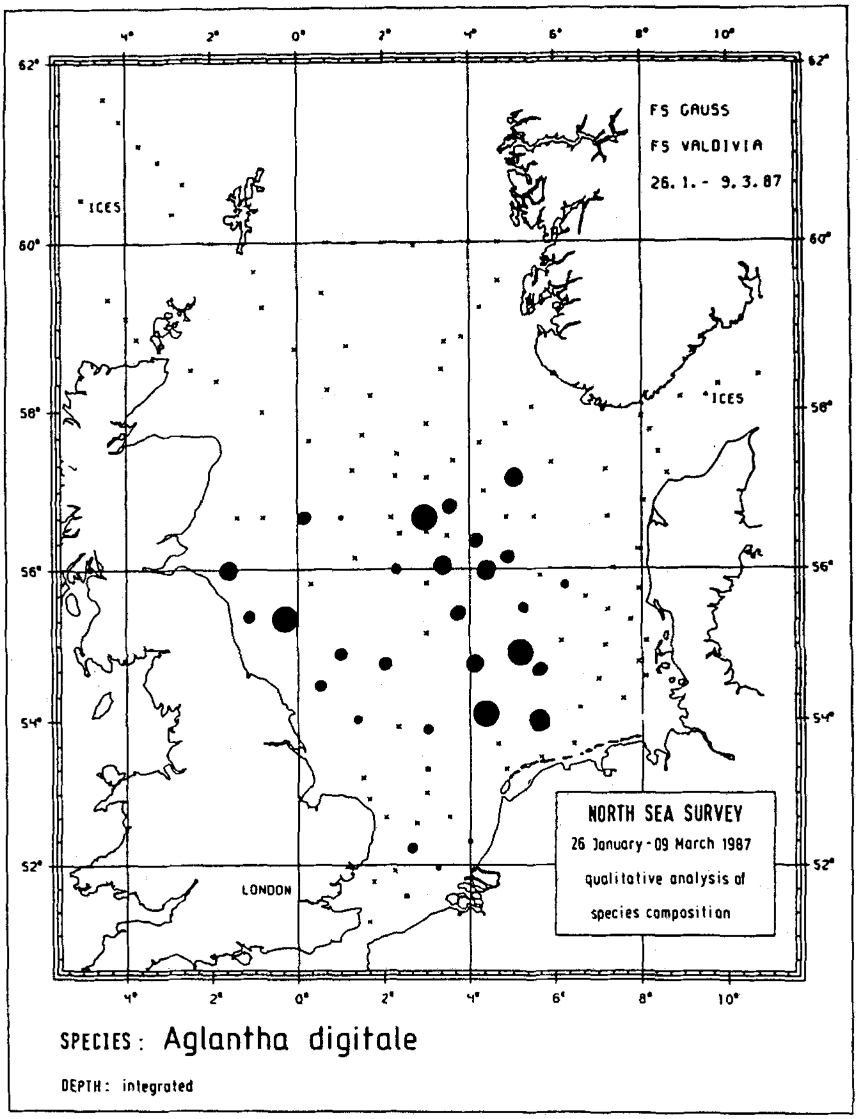

Fig. 25. Relative dominance of *Aglantha digitale* in the zooplankton stock during the winter cruise symbolized by the sizes of solid circles

in the deepest layer (60–150 m) was displaced about 80 sea miles further to the west than observed in the winter survey.

Even the behaviour of *Calanus finmarchicus* itself, which is the most important copepod of the northern North Sea, may be a promotion for the downward flux of organic material. Based on own investigations (Krause, 1978; Krause & Radach, 1989), we know that *C. finmarchicus* – after having grazed off the diatom spring bloom – starts to

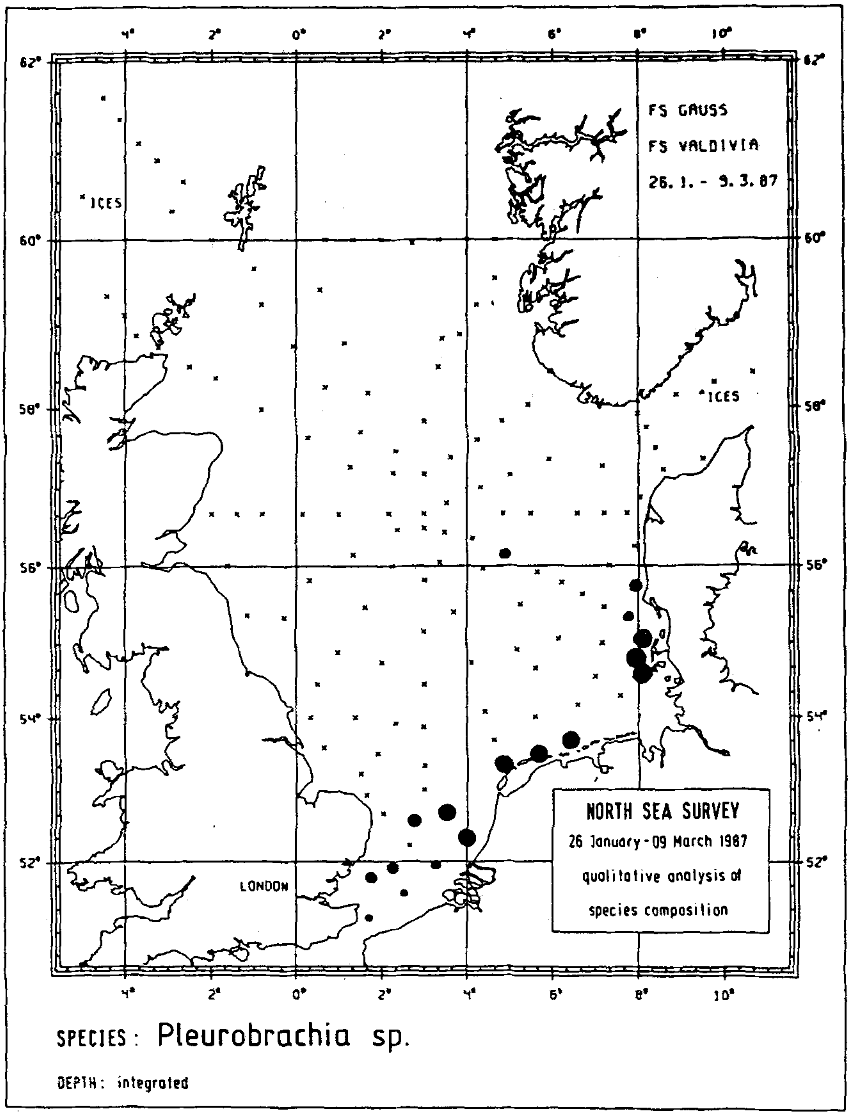

Fig. 26. Relative dominance of *Pleurobrachia* sp. in the zooplankton stock during the winter cruise symbolized by the sizes of solid circles

emigrate from the surface to deeper layers as early as June/July. From this, it becomes clear that large stocks of this copepod accumulating in the cyclic current system of the northern North Sea gradually reach the sea floor (available for the predatory bottom organisms?).

In this respect, reference must be made to the fact that in large areas of the northern and central North Sea considerable amounts of pollutants like heavy metals have been

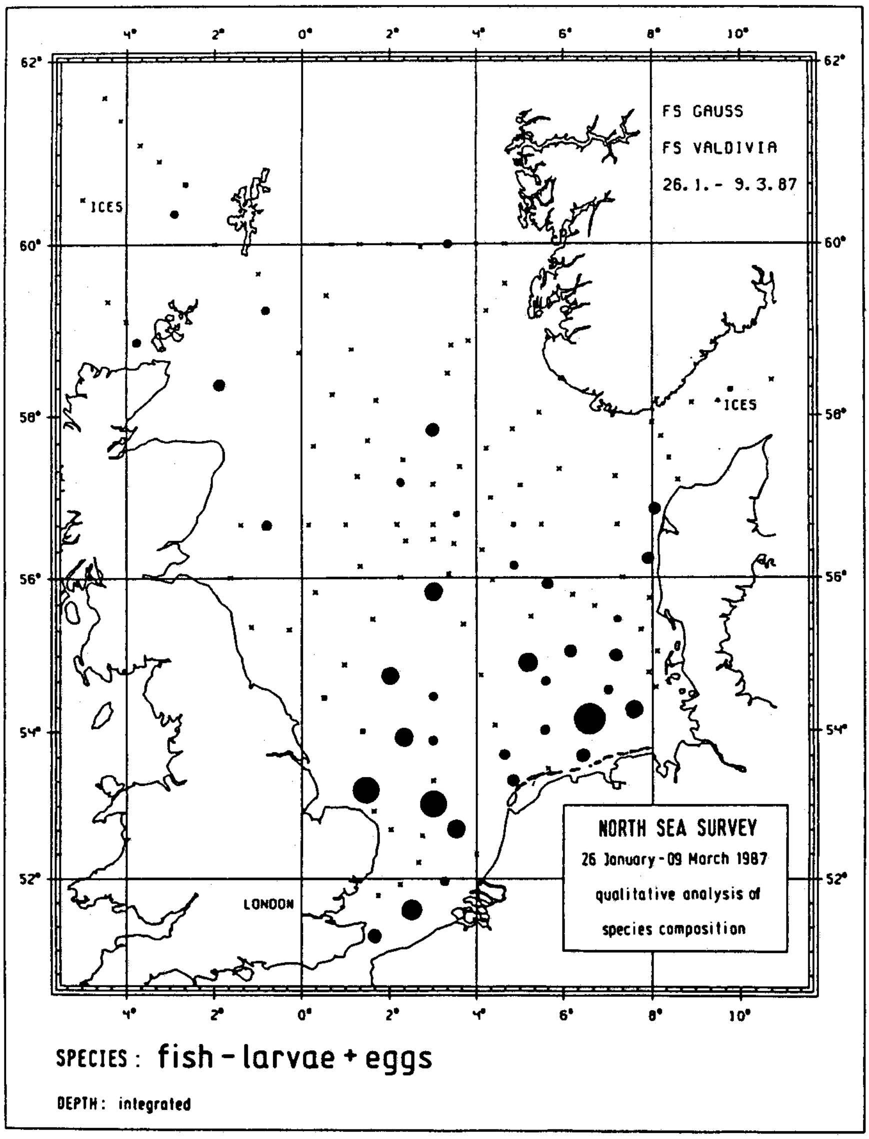

Fig. 27. Relative dominance of fish larvae and eggs in the zooplankton stock during the winter cruise symbolized by the sizes of solid circles

found in benthic organisms (Karbe et al., 1988) and in the sediment (Kersten & Klatt, 1988). There might be a connection between the intensified vertical flux of organic material and the contaminated sea floor in this region. The patterns of high zooplankton biomass implicate a high productivity of phyto- and zooplankton in the nutrient-rich current system of the northern and central North Sea. Hereby, the organisms might accumulate considerable amounts of several pollutants from the surrounding water,

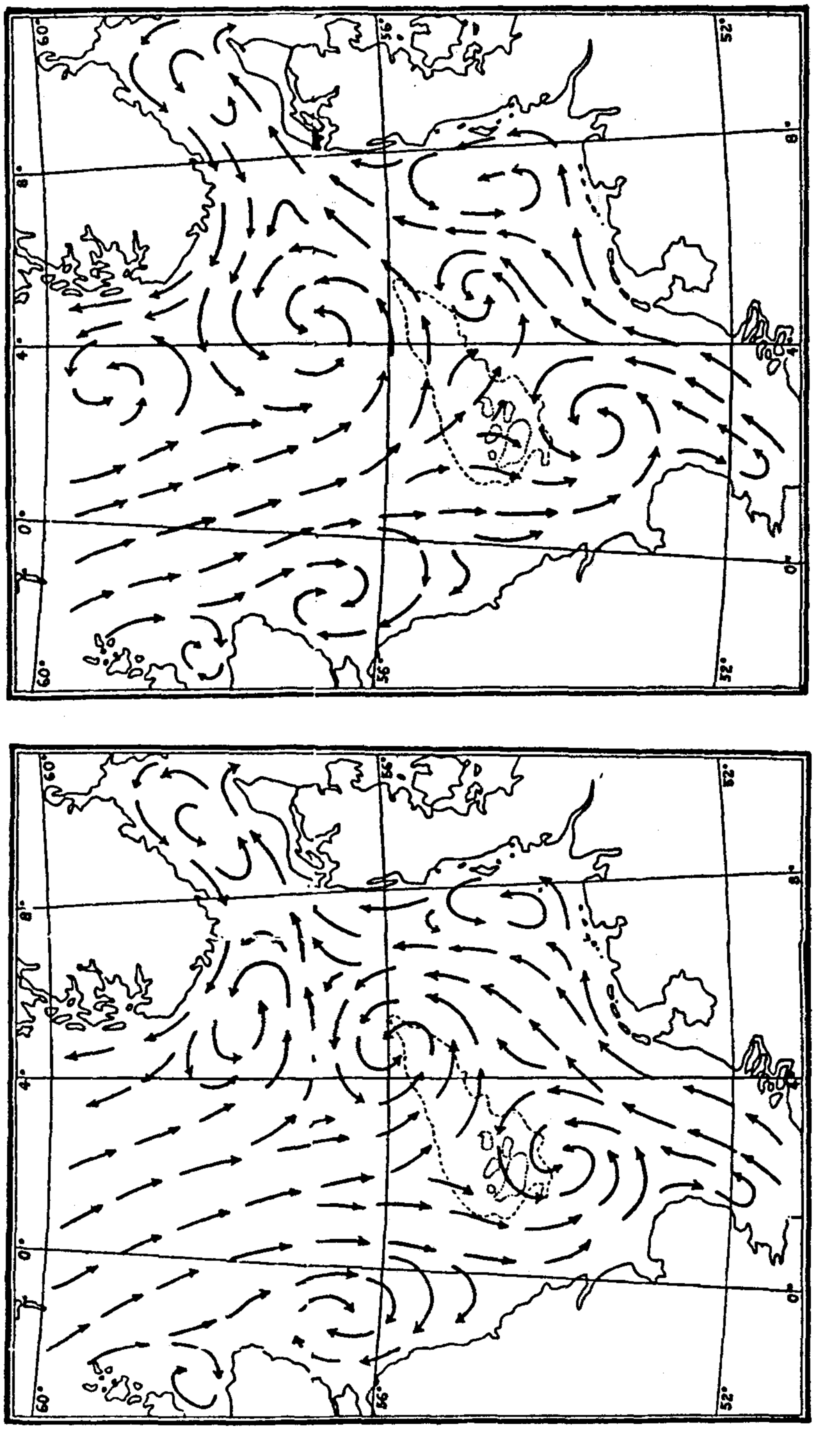

Fig. 28. Schematic diagrams of the mean surface currents of the North Sea during February (left) and August (right). From Böhnecke (1922)

which along with the organic material are transported to deeper layers in a cyclic way and are finally deposited on the sea floor. These pollutants may originate from mixing processes with pure North Sea water, from the atmosphere, or from the mixed coastal and Atlantic water, which comes from the Irish Sea.

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