Some observations on the plankton of the north Irish Sea.

Thesis submitted in accordance with the requirements of Liverpool University for the degree of Doctor in Philosophy.

By

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To my family

Abstract

Seasonal changes of the dominant phyto-, micro- and macrozooplankton species composition, abundance and distribution were studied along a transect of 6 stations to the east and west of the Isle of Man between March 1986 and October 1987. The stations to the east are characterized by strong tidal currents and can be considered representative of permanently well-mixed waters. The stations to the west, due to their greater depth and to lower tidal currents can be considered as representative of more stable conditions.

At each station surface and bottom temperatures were measured and composite whole water samples were obtained by pooling together subsamples collected from different depths. These were later studied for total and fractionated (< 20 μm) chlorophyll *a*, size-fractionating experiments, nitrate and phosphate determinations and phyto- and microzooplankton counts. At each station 10 minute oblique hauls were made with nets of 140 and 350 μm mesh to collect the macrozooplankton. All the da collected during the study period are presented as the mean for the transect to the west (station 1-2-3) and to the east (4-5-6).

In terms of production timing the overall seasonal cycle of all plankton groups was characterized by a clear single peak centered on early summer. Size-fractionation experiments show that potential primary production is almost entirely due to phytoplankters > 5.0 μm. Cell counts showed that the phytoplankton assemblage was dominated by chain-forming diatoms and microflagellates approximately 8 μm in diameter. Dinoflagellates were never important. The protozoan plankton was dominated by oligotrichous ciliates. Tintinnids were never important. A more detailed study of the ciliates in Port Erin Bay showed a similar seasonal cycle with the summer maxima constituted by short-lived peaks by different species. The aberrant photosynthetic ciliate species *Myrionecta rubra* (ex *Mesodinium rubrum*) accounted for a considerable proportion of total ciliate numbers. The mesozooplankton was characterized by the dominance of a few copepod species which accounted for most of total zooplankton numbers throughout the year. The presence of high numbers of nauplii during a short period suggests that breeding is mostly limited to the short phytoplankton summer maximum.

No differences were observed in the species composition and the dominance of species between the different transects, however, some showed consistently higher values of abundance along the west rather than the east transect. No differences were observed in the total numbers of diatoms but higher numbers were observed for the microflagellates. Higher values were observed for the the microzooplankton (ciliates and nauplii) and for some adult copepod species.

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SECTION ONE

GENERAL INTRODUCTION

In the temperate shelf waters around the British Isles plankton distributions are determined directly by water movements (Southward 1962; Fraser 1965) and indirectly by the effects of tidal mixing and seasonal stratification (Pingree & Griffiths 1978) on species succession and survival (Pingree 1978; Pingree *et al.* 1976; Holligan 1981). By determining the availability of light and/or nutrients to phytoplankton, mixing modulates primary production and thus the abundance and distribution of higher trophic levels.

In the English Channel Holligan *et al.* (1984) demonstrated that different types of food web develop each year in response to different conditions of vertical (tidal) mixing. In mixed waters where net phytoplankton production is restricted by the low photosynthesis to respiration ratio the food chain is characterized by the classical pyramidal structure where a higher biomass of phytoplankton supports successively smaller biomasses of herbivores and carnivores. In contrast, in stratified waters where the thermocline creates a more favorable light regime for the phytoplankton higher biomasses of zooplankton are supported by a smaller biomass of fast growing photoautotrophs.

Situations comparable to that in stratified waters in the English Channel are not uncommon and indeed are thought to be generally typical of stratified conditions (Raymont 1980). [For example, Mullin & Brooks (1970) showed that zooplankton to phytoplankton carbon ratios changed from 0.3 in April / May to 2.1 in May / June and 1 to 2 between July and August in the coastal waters off California]. There is increasing evidence that dominance by heterotrophs in stratified waters indicates a more efficient utilization of the plankton carbon, with relatively small losses to the benthic community (Holligan *et al.* 1984).

In the Irish Sea (Fig.1), tides produce changes from well-stratified to

well-mixed conditions within a few kilometers (Simpson 1971) (Fig. 2). In most areas of the Irish Sea, tides are sufficiently energetic to mix in the density deficit and create a vertically homogeneous water column throughout the year (Pingree & Griffiths 1978). The main exception is the area south west of the Isle of Man where increased water depth and weak tidal streaming prevent the generation of sufficient turbulent energy to maintain vertical mixing against the vertical surface buoyancy flux in summer and a seasonal thermocline is established to a depth to 20-30 m between April and October. The horizontal transition between stratified and mixed waters occurs over a frontal zone some 5-10 km wide, the location of which extends from approximately the southern tip of the Isle of Man to the Irish coast near Dublin. Stratified water to the NW of the front is usually separated from cooler well mixed water to the SE by a region of strong horizontal temperature gradients up to 1° C/km which is clearly visible in satellite infra-red images. A frontal system also exists in the shallow Cardigan Bay area in summer but is highly susceptible to destruction by wind mixing. The eastern Irish Sea forms the second main area of significant stratification. In this case the haline contribution is the more important, so that the stratification is most marked in winter and spring, especially near the main rivers entering along the Lancashire and Cumbrian coasts. Thermal stratification may also develop in Liverpool Bay but the frontal position is greatly affected by wind stress.

The importance of tidal mixing as a major factor in control of plankton production in the Irish Sea was first suggested by Herdman and his various co-workers (1908-1921), who pioneered the study of the plankton in this area. The impact of tidal mixing in different areas of the Irish Sea was later clearly demonstrated by Williamson (1952, 1956a, b) with his extensive sampling programme covering most of the Irish Sea. Although he attempted no detailed analysis of the phytoplankton, and only the dominant forms and approximate estimates of the density of total phytoplankton were recorded, he found that phytoplankton biomass was clearly consistently higher in the more stable water masses of the western Irish Sea, particularly to the west and south west of the Isle of Man, than in the mixed waters of

the eastern half of the entrance from St. George's Channel, between Anglesey and the Isle of Man and to the south east of the Isle of Man.

Since these earlier studies the most comprehensive work on the plankton of the Irish Sea is the study by Fogg *et al.* (1985a, b) on the thermal front separating stratified from mixed waters in the western Irish Sea. By combining the expertise of a number of authors their multidisciplinary study showed statistically that surface and bottom stratified waters and mixed waters in the Irish Sea are distinct, though seasonal ecosystems. Conclusions similar to those reached by Holligan *et al.* (1984) in the English Channel were also reached for these waters; the stratified waters quickly pass from an initial phase of unrestricted phototrophic growth to one in which biomass is fixed by nutrient limitation and populations of phytoplankton, bacteria and zooplankton show a considerable degree of homeostasis. These populations show a close interdependent association, with a high level of heterotrophic activity and associated high rate of nutrient turnover. This balanced community is destroyed when the water column becomes destabilized in autumn. In contrast, in mixed waters where the phytoplankton becomes light- rather than nutrient-limited, heterotrophic activity is lower and interdependence of the trophic levels is less tightly organized (Fogg *et al.* 1985b).

The higher biological activity of stratified waters in the Irish Sea compared to the mixed waters is clearly reflected by the consistently higher biomass of heterotrophs in stratified waters (Williamson 1952, 1956a,b). The very fine scale correlation between water column stability and zooplankton production was demonstrated by Scrope-Howe & Jones (1985a) who showed that zooplankton biomass decreased by as much as 64 % along a transect from stratified to mixed waters in the western Irish Sea.

Brander & Dickson (1984) identified low recruitment as the main factor responsible for the low fish production of the Irish Sea. Although the link between fish recruitment and plankton production is still unclear they suggested that the main factor responsible for such a difference was the consistently different phytoplankton

production cycle of the mixed waters that make up most of the Irish Sea at large. Comparison of Continous Plankton Recorder data on phytoplankton production timing and zooplankton abundance show that the phytoplankton is characterized by a short, late phytoplankton season centered on early summer and that copepod numbers are less than one third than in neighbouring areas of shelf (Colebrook 1979). Since the Continous Plankton Recorder route for the Irish Sea (from Liverpool to Dublin) can be considered as approximately representative of mixed waters these findings show that tidal mixing is clearly a major factor in control of plankton production and greatly influences the distribution of all other marine life, including benthos, fish, sea birds, marine mammals and even fishermen (Dickson 1987).

Despite the fact that mixed waters are the main feature of the Irish Sea at large detailed studies on plankton species composition, abundance and distribution have been mostly carried out in limited areas of stratified waters (Voltolina, 1970; Foster *et al.* 1982) or in frontal waters (e.g. Foster *et al.* 1976; Savidge 1976; Beardall *et al.* 1982; Savidge *et al.* 1984; Fogg *et al.* 1985a, b; Richardson *et al.* 1985; Scrope-Howe & Jones 1985a). Few workers have focussed on mixed waters and most of the information on these waters has been obtained in the western Irish Sea near the frontal discontinuity (e.g.Fogg *et al.* 1985a,b). Also, no studies have ever considered all the major planktonic components together. Even in their comprehensive work Fogg *et al.* (1985a,b) did not study the species composition of the microplankton. To date, no studies, have ever been carried out on the ecology of ciliated protozoans or the microzooplankton in general.

The waters around the Isle of Man are characterized by a complex hydrography but except for the deep waters to the west of its southern end they can be considered as representative of a range of mixed conditions.

The aim of this work was therefore to study the seasonal cycle of the most important species of each plankton level in an hydrographic environment that might be representative of that of the Irish Sea at large.

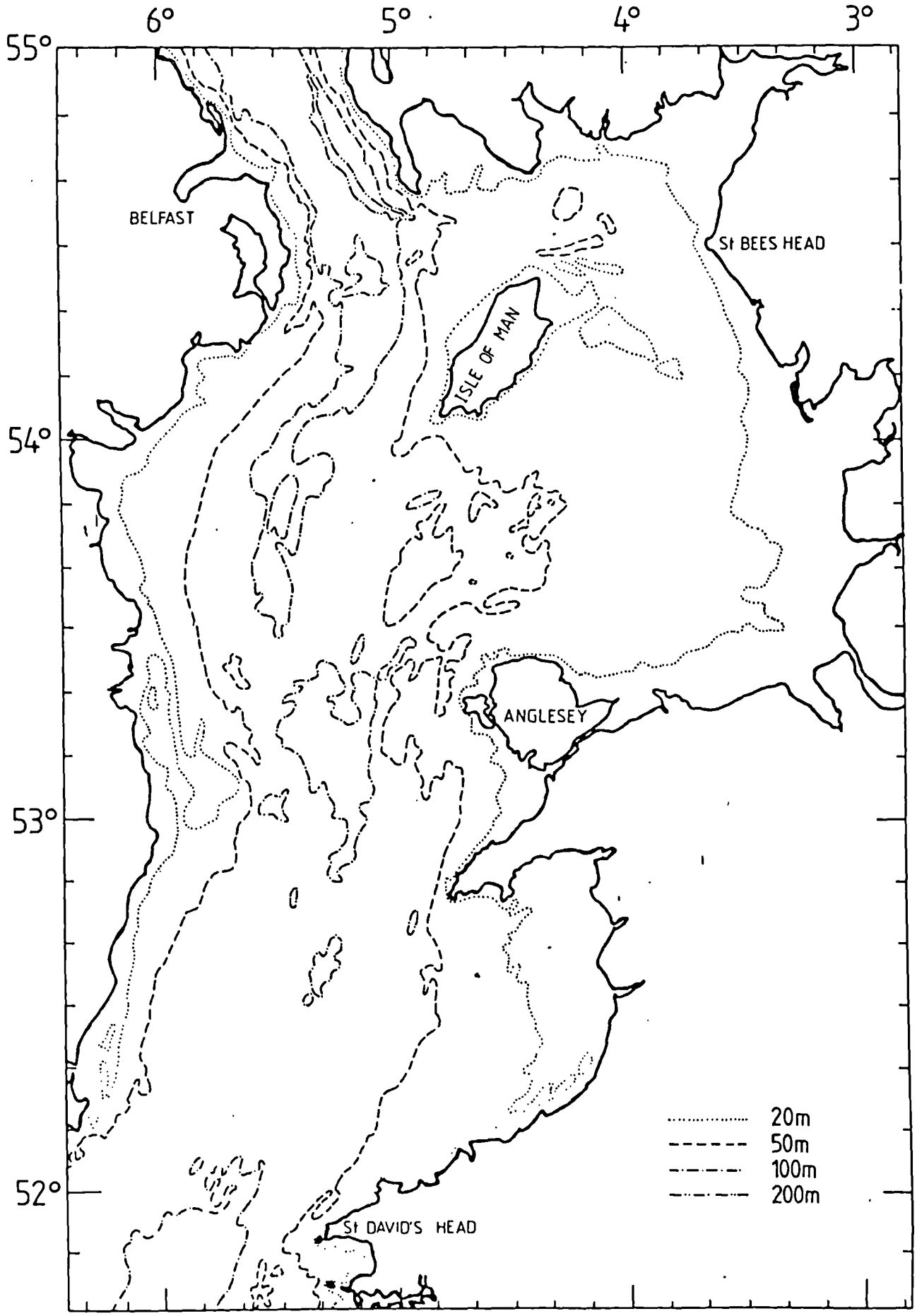


Fig. 1. Bathymetry of the Irish Sea

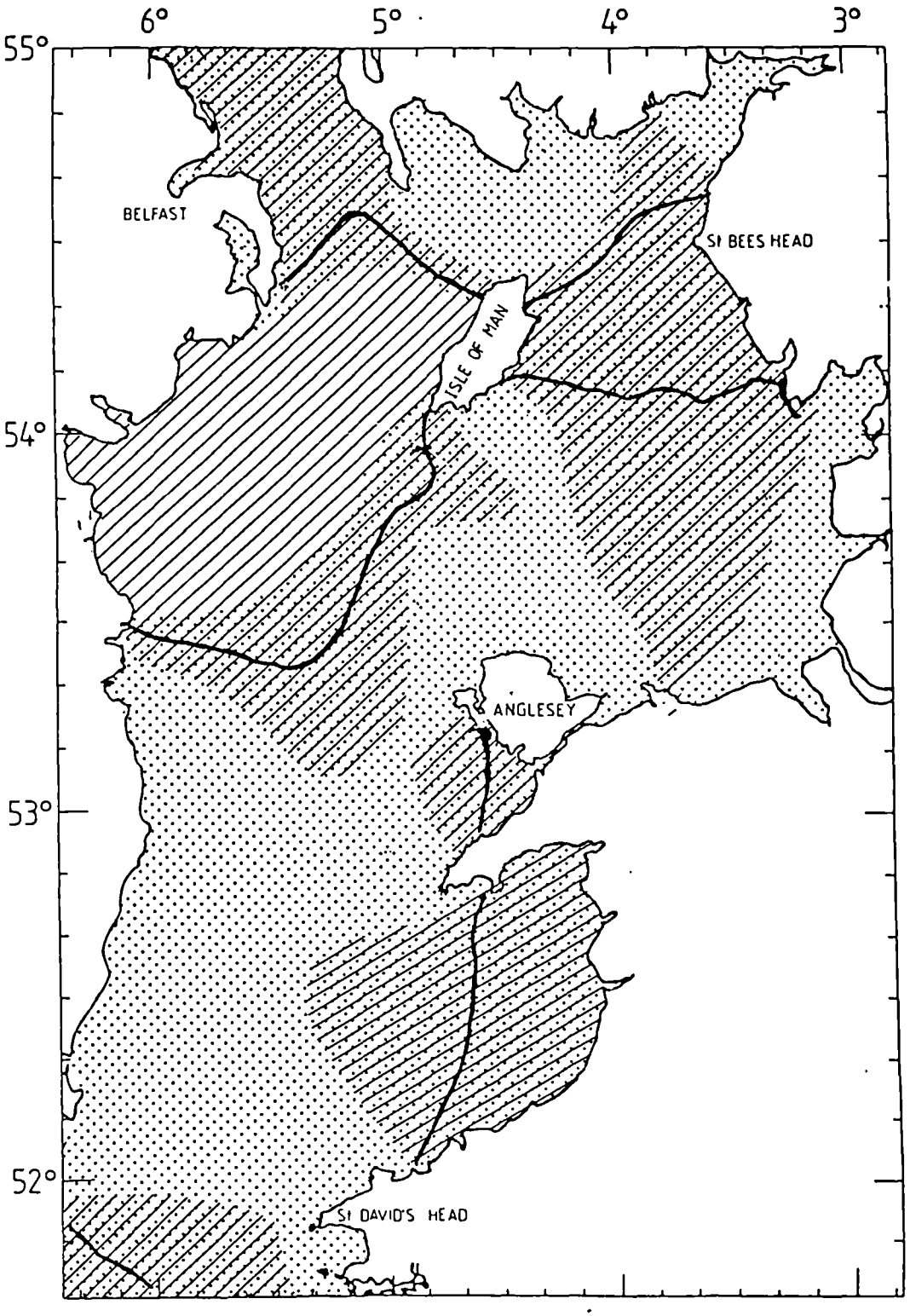


Fig. 2. Summer hydrographic conditions in the Irish Sea as predicted from the numerical model of Pingree & Griffiths (1978). Hatched areas indicate stratified waters; stippled, mixed areas; both, transitional waters.

SECTION TWO

OBSERVATIONS ON THE PHYTOPLANKTON CYCLE

2.1. INTRODUCTION

Since the turn of the century a considerable number of studies have been carried out on the physical and chemical hydrography of the north Irish Sea (e.g. Slinn 1974; Slinn & Eastham 1984 and ref. therein) and on the abundance and distribution of zooplankton taxa (for ref. see Chapter 3). In contrast, scant attention has been given, to date, to the distribution and succession of phytoplankton populations in the area. The limited data available are concerned mainly with the distribution of chlorophyll *a* (Slinn 1974; Slinn & Eastham 1984) or the occurrence of large species such as *Biddulphia* spp., *Coscinodiscus* spp. and *Ceratium* spp. in tow nets (e.g.Williamson 1952, 1956a, b; Lee 1971).

Long term hydrographical observations at a site 5 km off the south coast of the Isle of Man (Slinn & Eastham 1984) suggest a seasonal cycle of phytoplankton development similar to the one suggested by Colebrook (1979) for the approximately well mixed waters that characterize the Irish Sea route from Liverpool to Dublin. At this station mean levels of oxygen (in % saturation) and chlorophyll *a* increase on average around late April and reach a maximum in May. As these measures also coincide with the rapid fall in nutrient concentration they are clearly representative of the spring phytoplankton outburst. The lateness of this single summer bloom is clearly in contrast with the published data on production timing from the summer stratified areas (Burrows & Sharples 1973; Slinn 1974; Richardson *et al.* 1985) where the phytoplankton is characterized by the bimodal spring and autumn bloom seasonal model used to describe temperate coastal waters (Cushing 1959).

Studies on the seasonal qualitative and quantitative composition of the phytoplankton are mainly limited to the observations by Herdman *et al.* (1908-1921) on the net-collected phytoplankton of Port Erin Bay. Other data on phytoplankton include a floristic study by Marasigan (1986) of the net-collected phytoplankton of Port Erin Bay during 1983 and of the phytoplankton in surface whole water samples collected at a number of stations between the Isle of Man and Liverpool Bay during the

period March to July 1984.

The intensive study of the seasonal cycle of phytoplankton in Port Erin Bay by Herdman and his various co-workers (1908-1921) was summarized as follows by Johnstone *et al.* (1924) : "*The great event of the year occurs in March and April. The temperature is now rising and the intensity of sunlight is rapidly increasing. Some chemical substances have been accumulating in solution in the water during the cold and dark months. In March the diatoms begin very actively to reproduce and from then to the middle of June they attain their maxima of occurrence* ". - "*From June to the beginning of August the diatoms rapidly decrease. The physical conditions are, to all appearance still favorable, but something in the sea that is essential for further reproduction and growth of these organisms, has been used up. During July and August, the diatoms are less abundant than at any other time in the year. But the peridinians increase just as the diatoms are beginning to decrease and their maximal period is June and July* ". - "*Sometime around the end of August, or even in September and October, the diatoms again increase in number so that we have a secondary autumnal maximum as well as the principal vernal one*". According to such findings one might expect the seasonal cycle of phytoplankton species succession in these waters to be characterized by the same "classical" pattern formulated by Maddock *et al.* (1981) to decribe the typical phytoplankton cycle of most stratified areas of shelf in northern Europe: a bloom of diatoms in spring followed by a peak of dinoflagellates in summer and a further diatom peak in autumn; the relatively small winter population consisting mainly of diatoms. However, since the conclusions by Herdman *et al.* (1908-1921) are entirely based on phytoplankters collected by nets with mesh size 50 µm, their results are obviously only representative of the largest fraction of phytoplankton species. The problems concerned with sampling phytoplankton with nets have been reviewed by Tangen (1978) who concluded that because of their selective and non-predictable filtering properties they should not be employed in quantitative phytoplankton sampling. As for their use in qualitative studies he observed that while sampling with very small fine-mesh (5 or 10 µm) monofilament

nylon nets in the Oslo Fjord and other inshore waters has provided phytoplankton material of high quality, comparison with results from quantitative water samples collected simultaneously has made quite clear that a large number of small cells still escaped from these nets.

Given this limited background of data there appears to be, therefore, plenty of scope for a more detailed of the phytoplankton study in this area of the Irish Sea.

2.2. MATERIAL & METHODS

2.2.1. The study area

The location of the sampling stations are indicated in Fig.3 and their physical characteristics are summarized in Table I. The tidal currents given are the maximum surface values at spring tides and not the actual values at times of sampling. They show however, that the stations to the east are subject to much more tidal mixing than the stations to the west. The latter are also considerably deeper. Whereas the stations to the east can therefore be considered representative of very well mixed hydrographic conditions the stations to the west are characterized by more stable conditions during summer (J. D. Slinn, pers. comm.). Reference to Slinn (1974) shows that in the north Irish Sea, north of the 54° parallel, surface-bottom temperature differences rare exceed 3.0° C even where the water column reaches its greatest depths (≈ 100 m). Station 3 concided with a site where long term hydrographic observations have been carried out at approximately weekly intervals since 1942 (Slinn & Eastham 1984). Such data from Slinn & Eastham (1984) show that although a surface bottom temperature layering of up to 2.0°C can occur during summer complete mixing of the water column often takes place even during these months.

2.2.2. Sampling and field methods

Monthly cruises to the stations to the east and to the west were usually separated by one day but several times by slightly longer intervals. Sampling dates are given in Table II.

At each station surface and bottom temperatures were measured and whole water samples were collected from 5 and 15 m. These were pooled together to give composite water samples and subsamples were taken for later analysis of total and fractionated (< 20 μm) chlorophyll *a*, phytoplankton cell counts, size-fractionating experiments and nitrate and phosphate measurements.

Immediately upon collection subsamples for phytoplankton counts were fixed

with a 0.5 % solution of Lugols iodine (Holligan & Harbour 1977); subsamples for chlorophyll *a* (2-4 l) and incubation experiments (1 l) were gently screened through a 350 μm mesh to remove large zooplankters and kept in plastic containers in a shaded waterbath with running seawater at sea-surface temperature until arrival at the laboratory (approximately within 6 hrs of collection).

2.2.3. Laboratory methods

a. Estimation of chlorophyll *a*

Chlorophyll *a* was estimated by filtering approximately 2-4 l sea-water samples through 90 mm Whatman GF/C filters, the retentivity of which had been improved with a suspension of powdered carbonate magnesium. [Takahashi *et al.* (1985) have shown that the retention of particles on glass fiber filters coated with carbonate magnesium is as good as that retained on membrane filters (Millipore GS, 0.22 μm pore size)]. The filters were macerated in 90 % acetone, centrifuged and the extinction of the supernatant liquid measured spectrophotometrically at 750, 663, 645 and 630 nm. Calculations were based upon the equations given in the Scor-Unesco (1964) report.

Size fractionation was carried out by reverse-flow filtration (Dodson & Thomas 1964) using a fractionating unit consisting of a 20 μm mesh mounted on a flanged plastic cylinder 25 cm in diameter. This was allowed to sink by gravity. Fractionated seawater was siphoned from inside the fractionator into flasks, where samples were temporarily stored before filtration.

b. Size fractionation experiments

The incubator experiments were designed to assess the potential contribution to primary production of different size fractions of phytoplankton. Duplicate 500 ml subsamples from each station were inoculated with a known amount of ^{14}C and kept overnight in an incubator consisting of a Gallenkamp shaking waterbath fitted with 2 lamps with a photon fluence rate of approximately 100 μmoles m^{-2} s^{-1}. Except for

temperature, which was kept at ambient sea surface values as recorded in Port Erin Bay, experimental conditions remained the same throughout the study period. At the end of the incubation period samples were size-fractionated by passing different aliquots (some prescreened through a 20 μm nylon mesh) through a cascade of two 47 mm diameter Whatman membrane filters of pore size 5.0 and 0.2 μm, each filter being held in a separate filter holder. Samples were filtered through the 5.0 μm filters by gravity only and no vacuum was applied; small pressure differences were required for the 0.2 μm filters but never greater than 100 mm Hg. The wet filters were placed in liquid scintillation vials and transferred to a desiccator with active silica-gel. The filters dried in 1 h and 10 ml of Aquasol (L. S. C.) were then added. Liquid scintillation counting usually took place within 2 weeks and until then all vials were stored in the dark. Before counting all vials were thoroughly shaken (Niemi *et al.* 1983). Counting efficiency was determined by the internal standard method. The netplankton (> 20 μm) and the nanoplankton (> 5-< 20 μm) size fractions were obtained by subtraction.

c. Phytoplankton counts

Phytoplankters in whole water samples were concentrated by settling of a 500 or 50 ml sample, according to overall phytoplankton abundance, in graduated cylinders, and by siphoning the supernatant to a final volume of 5 ml. Samples were usually counted within one month to avoid deterioration. Diatoms, dinoflagellates and other large flagellates were enumerated in a Sedgwick-Rafter cell (Ricker 1937). Microflagellates and other small cells were counted in a Fuchs-Rosenthal haemocytometer (Reynolds 1973). This category includes all cells that had recognizable flagella and/or plastids (excluding diatoms and dinoflagellates) and was dominated by forms with a mean diameter of ≈ 8 μm. A minimum of 100 cells were enumerated for total diatoms and dinoflagellates together and total microflagellates for each sample; therefore, 95 % confidence limits for single counts were always < 20 % or less.

The greatest axial linear dimensions, excluding appendages, were measured for the most abundant diatom taxa examined and their volume calculated by approximating the cells or the colonies to some of the most simple geometric forms of Kovala & Larrance (1966). Measurements were made of 25-100 individuals of each taxon from samples taken throughout the season. No attempt was made to correct for cell vacuoles or wall thickness.

The Wilcoxon rank test (Zar, 1984) was used to compare the total abundance of phytoplankton groups of species on the west and east side.

d. Phytoplankton Identification

For identification purposes raw material in water mounts, dried material and cleaned material were observed. Preparation of cleaned specimens is following the procedure outlined by Hendey (1964).

Nomenclature is after Hendey (1974) for diatoms, Dodge (1982) for dinoflagellates and Parke & Dixon (1976) for other groups.

e. Nutrient analysis

Upon returning to the laboratory samples for nutrient analysis were immediately filtered through Whatman GF/C filters and frozen in polythene bottles. Later analyses were performed in accordance with the standard methods used by Slinn for his long term hydrographical observations in the north Irish Sea (e. g. Slinn & Eastham, 1984). Nutrients are expressed as mmol m^{-3} (= μg-at l^{-1}).

2.3. RESULTS

2.3.1. Temperature

On an annual basis, temperature values along the transect varied from a late winter minimum of 5.7 ° C to a maximum of 14.5 ° C in late summer. While during winter conditions were fairly uniform throughout the water column, during summer mean values at the surface were always equal to or higher than at the bottom (Table 3).

At the deepest station surface-bottom temperature differences (Δt) both years exceeded 1.0° C only in June and 3.0° C in July. By September Δt values were already < 0.5° C. At station 2 a similar pattern was observed, but temperature differences were nearly always lower. At station 3, where a more detailed set of data was made available by the routine measurements carried out by the Port Erin Marine Laboratory Δt never exceeded 1.9° C (Fig. 4). During late spring and summer of 19 Δt first exceeded 1.0 C on the 16th of May. Less than a week later temperature differences were < 0.2° C and < 0.5° C until the end of June. By early July values ranged between 0.8 and 1.1° C. During the whole of July temperature differences were never higher than 1.0 C. The highest temperature differences in August did not exceed 0.5° C. During 1987 Δt higher than 1.0° C were only reached by the second half of June but values remained above 1.0° C until the end of July. Highest temperature difference of 1.9° C was measured in the second week of July. Throughout August values ranged between 0.2 and 0.7° C.

At the eastern stations Δt were always < 1.0° C with maximum values in June. Over the whole study period Δt values at the westernmost stations 1 were significantl higher (Wilcoxon paired test) than values at station 3 ($p < 0.001$), station 4 ($p < 0.001$) and stations 5 and 6 ($p < 0.005$). Values at station 2 were also significantly higher than at station 3 ($p < 0.005$), station 4 ($p < 0.02$), station 5 ($p < 0.02$) and station 6 ($p < 0.05$). No statistically significant differences were observed between stations 3, 4, 5 and 6.

2.3.2. Chlorophyll *a*

Total chlorophyll *a* values during the study period ranged from approx. 0.09 mg m^{-3} in November to 13.86 mg m^{-3} in June during 1986, and from 0.13 mg m^{-3} n October to 8.41 mg m^{-3} in late May in 1987 (Table 4a,b). As clearly shown in Fig. 5a, for both years the seasonal cycle of total chlorophyll *a* was characterized by a single peak centered on early summer. During the winter months chlorophyll *a* values were always < 0.5 mg m^{-3}. Concentrations started to increase in March but were below 1.0 mg m^{-3} until late April. Chlorophyll *a* values exceeded 1.0 mg m^{-3} only from late April to October in 1986 and from May to July in 1987. During the summer maximum in 1986 the distribution of chlorophyll *a* along the transect was considerably patchy and characterized by intermittent blooms. More homogeneous conditions were found in August. A slightly longer phytoplankton growth season was observed at the western rather than the eastern stations. During the growth season in 1987 the distribution of chlorophyll *a* was very similar at all stations. Differences in chlorophyll *a* concentrations were observed only in early May, as chlorophyll *a* values at the offshore stations 5 and 6 were only reached in late May. From late May until August, with only a few exceptions, values for each station were always within 1.0 mg m^{-3} of the mean value for the whole transect. Higher values were found in June and July at the western transect. Values declined to < 0.5 mg m^{-3} at all stations by October.

Although with lower values, the seasonal cycle of fractionated chlorophyll *a* (approx. < 20 μm) showed a similar distribution to that of total chlorophyll *a* (Fig. 5b). During 1986 concentrations exceeded 2.0 mg m^{-3} only in early July at station 1 and were generally between 0.5 and 1.0 mg m^{-3}, although occasionally other values were also observed. During 1987 considerably higher values were observed at the stations to the west where chlorophyll *a* remained > 0.5 mg m^{-3} until August. At station 6 nanophytoplankton chlorophyll *a* concentrations > 0.5 mg m^{-3} were observed only in the second half of May and in June. At station 5 nanophytoplankton chlorophyll *a* exceeded 0.5 mg m^{-3} only in May.

2.3.3. Nitrate and phosphate

The seasonal cycles of phosphate (Fig. 6) and nitrate (Fig. 7) were very similar to each other. Concentrations were highest during the winter months, reaching a peak in February - March (between 5 and 6 mmol m^{-3} nitrate; between 0.7 and 0.8 mmol m^{-3} phosphate). Values started to decline slowly in April and sharply in May. As a consequence of the different timing of the bloom at the different stations in 1987 considerable differences in the concentration of both nutrients could be observed along the transect. Highest concentrations were always observed at station 6.

By June whereas nitrate was at some stations almost undetectable, phosphate concentration was below 0.1 mmol m^{-3} only very seldom. Little change was observed from June until August in the NO3 values. In September, however, nitrate concentrations were already above 1.0 mmol m^{-3} and phosphate values between 0.2 and 0.3 mmol m^{-3} all along the transect.

2.3.4. Phytoplankton cell counts

Data on the seasonal cycle of phytoplankton groups are presented as the means for the three east and the three west stations respectively.

The seasonal cycle of mean diatom abundance (Fig. 8) was characterized by a minimum in winter when total numbers ranged from 10^6-10^7 cells m^{-3}, to a single summer maximum with highest values (> 10^9 cells m^{-3} in 1987) during the period May -June. [During June 1986 values lower than 10^6 cells m^{-3} were observed in discrete samples at both the stations to the east and the stations to the west].

No significant difference was observed in mean total diatom abundance between the western and the eastern transect.

Whereas diatoms were characterized by an approximate 10^3-fold variation throughout the year microflagellates showed a much smaller variation with only about a 10-fold difference between winter and bloom concentrations (Fig. 8). Highest

numbers were always found to coincide with highest numbers of total phytoplankton. Between September and April concentrations were always < 10^9 cells m^{-3} and minimum values were always above 10^8 cells m^{-3}. Significantly ($p < 0.001$) higher numbers of microflagellates were found on the western rather than the eastern transect of stations.

Dinoflagellates were never important and highest abundance in discrete samples never exceeded 2 x 10^7cells m^{-3}. Lowest concentrations were observed in July of 1987 (Fig. 8) when these organisms were practically absent from the samples. Highest abundance was recorded in May in 1987 and coincided with highest numbers of diatoms and microflagellates. Significantly ($p < 0.05$) higher numbers of microflagellates were found on the western rather than the eastern transect of stations.

Silicoflagellates were never important and their maximum abundance in discrete samples never exceed 10^6 cells m^{-3}. Blue-green filamentous algae were occasionally found during winter but their numbers were never high.

2.3.5. Phytoplankton species composition

The flora was mainly neritic. A complete list of the species identified during the whole study period and their maximum abundance in discrete samples for each month is given in Table 5. Combining the percentages from stations 1,2,3 and 4,5,6 the percentage composition in terms of abundance and biomass for the dominant species or groups of species (excluding the microflagellates), for each month, were obtained for the east and west transect. Groups of species were created so that all phytoplankton species present at a given time of year were represented. Also, all figures have been arranged to show the progression to the spring and summer composition and the following regression to the autumn and winter state.

Fig. 9a,b illustrate those species that account for over 5 % of the total phytoplankton numbers at the western and eastern transect respectively. Fig.10a,b illustrates the 5 dominant diatom species in terms of biomass [calculated from numbers x external cell volume excluding appendages; no correction was applied to correct for

vacuole space in diatoms, although this can be a considerable source of error (Dr. Savidge, pers. comm.)] at the western and eastern transect respectively. The numerically dominant species or group of species generally accounted for more than 30 % of the total and the most abundant two species for usually over 50 % of the total numerical abundance. No single dinoflagellate species ever accounted for more than 5 % of the total so they were listed as total.

Two very distinctive assemblages can be distinguished during autumn-winter and the late-spring summer period. In terms of numerical abundance the autumn-winter period was characterized by the dominance of large benthic chain-forming species such as *Paralia sulcata* and *Bacillaria paxillifer*, and by small pennate diatoms such as small *Nitzschia* spp, (*N. delicatissima* and *N. closterium*) and naviculoid species such as *Navicula* spp. and *Thalassionema nitzschioides*. In terms of biomass dominant species were different species of the family Coscinodiscaceae (e.g. *Coscinodiscus radiatus, C. eccentricus, Podosira stelliger, Actynopthicus senarius*), *Biddulphia* spp. (mainly *B. sinensis* and *B. mobiliensis*), *Bacillaria paxillifer* and *Thalassiosira* spp. (mainly *T. decipiens*). The early stage of the late spring-summer period was characterized by blooms of *Thalassiosira* spp. in 1986 at the inshore stations followed by the overwhelming dominance of *Rhizosolenia delicatula* from June onwards. Early May of 1987 was dominated by the dominance of *Nitzschia seriata* in terms of cell numbers and by the overwhelming dominance of *Coscinodiscus concinnus* in terms of biomass. From late May throughout summer *R. delicatula* was again a dominant species in terms of numbers and biomass. The period July to August of both years was dominated by the very large chain forming species *Rhizosolenia stolterfothii, Guinardia flaccida* and *Stauroneis membranacea.*

The silicoflagellate *Dictyocha fibula* occurred throughout the year but although it often reached concentrations as high as 10^6 cells m^{-3} it only seldom accounted for more than 5 % of total phytoplankton numbers.

The contribution of some of the larger phytoplankton species at different times of the year might have been greatly underestimated because of their very low numbers

counted in the whole-water samples. Whereas in net samples (140 µm mesh) collected at the same stations (see section three) large species such as the diatoms *Biddulphia* spp., *Bacillaria paxillifer* and *Coscinodiscus* spp., or the dinoflagellates *Ceratium* spp. were often very abundant they were often not observed in the whole water samples. *Coscinodiscus concinnus* generally appeared in the plankton in January and its abundance gradually increased until May when the annual maximum of phytoplankton abundance was reached. At this time of the year all the zooplankton samples were green in coloration as this phytoplankton species accounted for most of the catch. Abundance then rapidly fell and from June until September it was only recorded very seldom. Other large phytoplankters, with a similar seasonal cycle, abundantly collected in the net samples were *Biddulphia* species, particularly *B. sinensis* and *B. mobiliensis*. Maximum numbers occurred in April and entire absence or extremely small numbers were observed from June to August. *Ceratium* species were the most common phytoplankters in zooplankton collections. The most abundant species was *C. tripos*, in contrast with the whole water samples where *C. furca* was the overwhelmingly dominant species.

Fig. 11a,b shows the species that account for over 5 % of total dinoflagellate numbers. Because very few species contributed for more than 5 % of total dinoflagellates, major groups had to be created, pooling together not only single species but also organisms phylogenetically very far apart as in the case of the Gyro- and the Gymnodiales. As for the diatoms no apparent differences in species composition were observed between the east and the west side. In contrast no distinct seasonal cycle was observed in the succession of species. Small peridinians and *Ceratium* species were the dominant species (*C. furca, C. lineatum* and *C. fusus*) but species of all other groups occurred in different proportions throughout the year. During May and July 19871987, the only occasion when dinoflagellate numbers exceeded 10^7 cells m^{-3} and reached a maximum of 2.2 x 10^7 cells m^{-3} *Scripsiella* spp. and *Heterocapsa triquetra* were the overwhelmingly dominant species with small peridiniales such as *Protoperidinium bipes* and *Protoperidinium* spp. following in

importance.

2.3.6. Size-fractionation experiments

The results here presented rely on the fractionation of particles according to their size and the conclusions reached depend on the ability of the filters to separate different sized particles in a reproducible way. Membrane filters behave as screens (Sheldon 1972) but they may still retain particles smaller than the rated pore size and this may influence the interpretation of the results. The seasonal cycle of size-fractionated potential primary production from September 1986 to September 1987 is presented in Fig. 12. On a year basis the nanophytoplankton size fraction (>5-<20 μm) was the overwelmighly dominant one accounting for approximately 65 and 60 % of total potential primary productivity at the western and eastern transect respectively. On a year basis the netphytoplankton size fraction accounted for a significantly ($p < 0.01$) higher (approximately 38 and 32 % of total production respectively) at the eastern rather than the western transect respectively. Whereas at the eastern stations the netplankton was the most important size fraction throughout the summer maxima from May to August, at the western stations, except for the month of May, the nanophytoplankton was always the most important size-fraction. A noteworthy feature of the incubation experiments was the absence of any significant contribution to potential primary production by phytoplankton organisms < 5.0 μm. During summer, this size-class repeatedly contributed as much as 10% of total production at different stations but as this never resulted in a consistent pattern along the transect mean values along the transect were always very low.

2.4. DISCUSSION

2.4.1. Production timing

In terms of production timing the results from this study compare well with the seasonal cycle suggested by the I. M. E. R. Continuous Plankton Recorder data (Colebrook 1979) for the Irish Sea route from Liverpool to Dublin. Comparison with data from other Continous Plankton Recorder routes (e.g. Colebrook 1979; Reid 1978) show clearly that along the Irish Sea route the spring bloom is about a month later and the autumn decline nearly two months earlier than in most areas of neighbouring shelf. The lateness of this single summer maximum, in contrast to the spring peak within the restricted stratified zones, appears to be due to the intensity of tidal streaming (Sager & Sammler 1968) in keeping with the observations of Pingree *et al.* (1976) that in the Celtic Sea, production begins earlier where the weakest tides permit the earliest development of stable stratification. A clear example of the influence of tidal mixing on such a plankton production cycle is given by the C. P. R. data for the North Irish Sea (Reid 1978) which show that in this area, the tendency towards a summer phytoplankton maxima increases proceding from north to south, i. e., from summer stratified to permanently well mixed waters, the most typical condition of the hydrographical regime of the Irish Sea at large (Pingree & Griffiths 1978). Although summer phytoplankton maxima have been described by a number of authors (Colebrook & Robinson 1965; 1979; Boalch *et al.* 1978; Maddock *et al.* 1981; Cadee 1986) in no other area of shelf in northern Europe is the bloom so well organized into a single summer peak as in the Irish Sea.

The main factor controlling phytoplankton growth in mixed waters is generally believed to be the mean level of light energy (Sverdrup 1953). Studies of the global radiation at different northern latitudes and the available information on phytoplankton cycles in Norwegian waters led Smayda (1959) to present the theory that the spring bloom will not start until the surface radiation has surpassed $\approx$ 10 - 12 mol m^{-2} day^{-1} photon irradiance. Further investigations in Norwegian waters have supported this

provided that the thickness of the homogeneous surface layer does not exceed a certain depth.

In the north Irish Sea the mean surface radiation surpasses 10-12 mol m^{-2} day^{-1} already by February and by the end of March is > 40 mol m^{-2} day^{-1} (Kain *et al.* 1976). The development of the bloom as late as May or even June (this study; Slinn & Eastham 1974) falls clearly in phase with the highest values in surface irradiance in these months (Fig. 13). Despite surface irradiance values > 25 mol m^{-2} day^{-1} photon irradiance until the end of October no bloom can be observed during these autumn months.

Besides delaying the onset of the phytoplankton bloom in mixed waters, light limitation is probably also the most important factor in control of phytoplankton production. Studying photosynthesis and respiration rates of phytoplankton populations in stratified, frontal and mixed waters in the English Channel during summer Holligan *et al.* (1984) reported that due to the combined effects of low mean light levels in the whole water column and respiration, the growth rates of diatoms in mixed waters were low and probably positive only on sunny days. In this situation diatoms appear to survive through resuspension by mixing and fluctuations in production are likely to occur over times scales comparable to those in surface irradiance (i.e. sunny versus cloudy weather patterns). In mixed waters in the western Irish Sea, where nitrate concentrations remain high, Fogg *et al.* (1985) suggested that phytoplankton production might be light-limited. The findings by Turley (1985) of consistently lower rates of urea uptake in mixed rather than stratified waters in the western Irish Sea might support the hypothesis of light limitation to be higher in mixed waters.

In the present study nitrate concentrations during summer were < 1.0 mmol m^{-3}. all along the transect. Although at the eastern stations nitrate values were always well above detection levels, in contrast to the stations to the west, such values are low compared to those reported by Fogg *et al.* (1985a) in mixed waters. Nutrients can, therefore, be an important limiting factor during summer (Dr. Savidge, pers. comm.).

The importance of light limitation on phytoplankton production, however, is clearly suggested by the absence of an autumn bloom although the main nutrients are at this time high all along the transect [$NO^3 > 1.0$ mmol m^{-3}; $PO^4 > 0.3$ mmol m^{-3}; $SiO^3 > 3$ mmol m^{-3} (see also Slinn & Eastham 1984)]. Futhermore, the presence of high numbers of empty or bleached phytoplankton cells in August during 1987 (pers. observations) which is a clear indication of a stressed physiological state, clearly suggest that because of strong turbulence phytoplankton might be carried at a greater depth where light limitation might occur. Although the importance of storms and winds decreases from winter to summer, the weak stratification of the water column due to tidal mixing can make their action very significant even at this time of the year. The faster increase in production at the two coastal stations 3 and 4 compared to the deeper but more stable stations to the west (1 and 2) and those within the same range of depths to the east (5 and 6) could be attributed to their shallower depth and more sheltered position which makes them less liable to wind stress. The intermittent phytoplankton blooms that characterized the summer maximum during 1986 could also be explained as the result of stabilization of the relatively shallow water column following previous destabilization by strong winds. In this study the instability of the water column is clearly illustrated by the small surface-bottom temperature differences at station 3. The impact of such instability on phytoplankton production is clearly shown by the long term hydrographical measurements which have been carried out at station 3 (Slinn & Eastham 1984). Chlorophyll *a* data show that great differences in phytoplankton production occur from one year to the other (Slinn & Eastham, 1984 and ref. therein). Whereas in some years (e.g. 1970) monthly chlorophyll *a* mean concentrations exceeded 1.0 mg m^{-3} only during one months and were never higher than 1.5 mg m^{-3} in other years concentrations exceeded 1.0 mg m^{-3} for several months.

2.4.2. The phytoplankton assemblage.

Differences in the ability of phytoplankton species to reach their maximum growth rates under various conditions of light and nutrient limitation have been suggested by Dugdale (1967) and Eppley *et al.* (1969) as important factors in causing species succession in phytoplankton blooms. The clear relationship between the relative dominance of certain phytoplankton taxa and the stability of the water column has been recognized for some time. For example Grøntved (1952) noted that in the North Sea the diatom dominated community in spring was rapidly succeeded by dinoflagellate species as the water stability increased, whereas near Roscoff, where the water did not become stratified, Grall & Jacques (1964) noted that diatoms were dominant throughout the summer. Holligan & Harbour (1977) showed that in the western English Channel the establishment of the seasonal thermocline in early summer was characterized by a successional series from diatoms to dinoflagellates to microflagellates and then in reversed order as the thermocline was eroded in late summer.

One of the most distinctive features of the phytoplankton species succession in most shelf waters of the temperate area is a peak of dinoflagellates in summer (Maddock et al. 1981). Holligan *et al.* (1980) showed that dinoflagellate communities in summer were dominated by different species according to the temperature and stability of the water column. From data on the distribution of dinoflagellates in the surface waters around the British Isles (including the Irish Sea) in 1977, Holligan *et al.* (1980) identified four dinoflagellate groups to describe the successional series of dinoflagellate communities from well-mixed to well-stratified conditions. In the Irish Sea, where samples were taken in mixed waters as well as the well stratified waters to the south west of the Isle of Man (Slinn 1974) he found only two of such communities: a *Scrisiella* group, clearly representative of well mixed conditions and a less well defined *Prorocentrum micans* group, representative of intermediate environmemtal conditions. Although in this study the relatively low counts of dinoflagellates species do not allow an accurate comparison with the results of

Holligan *et al.* (1980), most of the species found during summer fall in these two groups. The absence of a dinoflagellate community representative of well stratified conditions in the study by Holligan *et al.* (1980) and in the present investigation poses some questions as to the applicability of dinoflagellates communities as indicators of water column stability in the Irish Sea. On the other hand, the significantly higher abundances of dinoflagellates along the western transect might be interpreted as a biological indication of higher water column stability, following the suggestions of Holligan *et al.* (1980) that hydrographic importance can be attached to the presence of dinoflagellates during summer. Clearly a more detailed study is required to understand the hydrophical importance that can be attached to dinoflagellate communities in the Irish Sea.

In the present work the dominance of diatoms is clearly shown. Although no apparent difference was observed in the species composition and abundance of the diatom population all along the transect, microflagellate and dinoflagellate numbers were considerable higher, especially in 1987, at the western rather than the eastern stations.

The finding that microflagellate numbers were significantly higher at the western stations is in accordance with the findings of Beardall *et al.* (1982) who observed that in the western Irish Sea the contribution of microflagellates to total phytoplankton numbers were consistently higher in stratified rather than in mixed waters.

In both years a very distinctive feature of the phytoplankton cycle was the dominance of *Rhizosolenia delicatula*. The dominance of this species has been reported for other well mixed waters on the northwest European continental shelf (e.g. Pingree *et al.* 1986; Cadee 1986). In the permanently well mixed waters off Roscoff (western English Channel) blooms of *R. delicatula* are a regular event of the phytoplankton cycle and their dynamics have been the object of a considerable number of studies (e.g. Grall & Jacques 1964; Grall 1972 a, b; Wafar *et al.* 1983; Sournia *et al.* 1987; Klein & Sournia 1987).

By comparing the seasonal cycle of this species at Roscoff and in the area

covered by this investigation no apparent differences can be observed in its dynamics in the two areas. As at Roscoff, in the north Irish Sea cell concentrations of *R. delicatula* higher than 10^6 m^{-3} were generally observed in the second half of May and high abundance observed until late June. Maximum concentration of 4.69 x 10^8 cells m^{-3} found at Roscoff in 1964 is in the same order of magnitude as highest abundance in the Irish Sea (8.0 x 10^8 cells m^{-3}).

Although the dominance and recurrence of this species in the mixed waters off Roscoff suggests that it might be considered as a biological indicator of mixed waters, monospecific populations of this species were found all along the transect. Similar results were reached by Richardson *et al.* (1985) and Beardall *et al.* (1982) who reported that monospecific populations of *R. delicatula* characterized the spring bloom both in mixed and stratified waters in the western Irish Sea.

More work is clearly needed to define the potential hydrographic importance of this species in the Irish Sea. However, the findings from the present study and the observations of Richardson *et al.* (1985) and Beardall *et al.* (1982), clearly show that this species has a definite place in both the hydrographical and the plankton cycle in the Irish Sea.

2.4.3. Size fractionated phytoplankton production

Since the first reports of very small unicellular photosynthetic organisms in the sea (Johnson & Sieburth 1979; Waterbury *et al.* 1979) there have been many reports which have shown the quantitative importance of small phytoplankton cells (< 5 μm) in various marine provinces, from the polar seas to the tropics (e.g. Gieskes *et al.* 1979; Krempin & Sullival 1981). Studies in oceanic waters have shown that the < 1 and < 3 μm size fractions may represent more than 50 % of the total phytoplankton biomass in terms of either chlorophyll *a* (Bienfang & Szyper 1981; Bienfang & Takahashi 1983; Herbland *et al.* 1985), carbon (Herbland & Lebouteiller 1981; Furuya & Marumo 1983; Takahashi *et al.* 1985) or cell concentrations (Waterbury *et al.* 1979;

Murphy & Haugen 1985). Small phytoplankton can be responsible for the majority of primary production in tropical oceanic waters (Gieskes *et al.* 1979; Li *et al.* 1983; Platt *et al.* 1983; Takahashi & Bienfang 1983). Recent investigations, however, have revealed significant abundance and production of phytoplankton < 5.0 μm in temperate waters as well as in the North Atlantic (Joint & Pomroy 1983; Joint *et al.* 1986). Although little is still known about the factors controlling the distribution or the seasonal significance of these organisms it is clear that their importance decreases in proportion to the total as waters become more eutrophic. Mommaerts (1973) and Reid (1983) have found that the smaller forms make up a greater proportion of the total phytoplankton as one moves from coastal to offshore and oceanic waters. Studying nitrogen assimilation by size-fractionated phytoplankton along a shelf-break-coastal bay transect in the English Channel, Owens (1986) found that in coastal waters, throughout the growth season, nitrogen assimilation was predominantly carried out by organisms > 5 μm. In contrast, offshore, as the season progressed and nutrients became depleted, up to 60 % of the nitrogen was assimilated by the < 5 μm size fraction. He suggested that the increased importance of organisms < 5 μm offshore, where nutrients became limiting, was due to their ability to assimilate nitrogen, particularly NH_4, more efficiently than larger phytoplankters.

In the present study small nanoplankton (<5 μm) made a negligible contribution to primary production potential; a result which clearly suggests that the importance of this phytoplankton component in the north Irish Sea is very small.

These findings would appear to clash with the work of El Hag (1984) who observed that minute chroococcoid cyanobacteria contribute a very significant proportion (up to 50 %) of chlorophyll *a* to the waters in the western Irish Sea; similar conclusions have been reached by Boyden (pers. comm.) who observed that the production by small nanoplankton (< 1.0 μm) at a coastal station on the eastern coast of Ireland at approximately the same latitude as the stations in this study was very small and that highest peaks up to 20 % of total production were found only occasionally in the summer months of June and July.

It may be suggested that intense mixing, might be a limiting factor for the development of this small size fraction. In the western Irish Sea, Lochte (1985), studying bacterial productivity in waters close to a front, observed that during summer the uptake of ^{14}C-glucose was consistently several fold higher in surface stratified waters (SSW) than in mixed waters (MW) although bacterial numbers were only higher by a factor between two and three (Egan & Floodgate 1985). This has lead to the hypothesis that bacterial production is higher in the SSW than in MW and is rapidly removed by grazing (Lochte 1985). In experiments carried out *in situ* in dialysis bags in the stratified area near the western Irish Sea front Lochte & Turley (1985) found that in water filtered free of predators, bacterial production near the surface equalled that of phytoplankton. Growth rates were considerably higher near the surface waters than at depth. Similar results, suggesting a potential control by mixing (mediated by its effects on nutrient and/or light availability) was also observed by Magazzu *et al.* (1987). Studying phytoplankton production in the Strait of Messina (Central Mediterranean) they found that although picoplankton chlorophyll *a* accounted for 56 to 63 % of total phytoplankton chlorophyll *a*, picoplankton (defined as photosynthetic organisms < 1 μm) carbon fixation accounted for only 24 to 43% of total primary production. They attributed such a relatively low photosynthetic potential (compared with the larger size fractions) to the very strong turbulence of the environment.

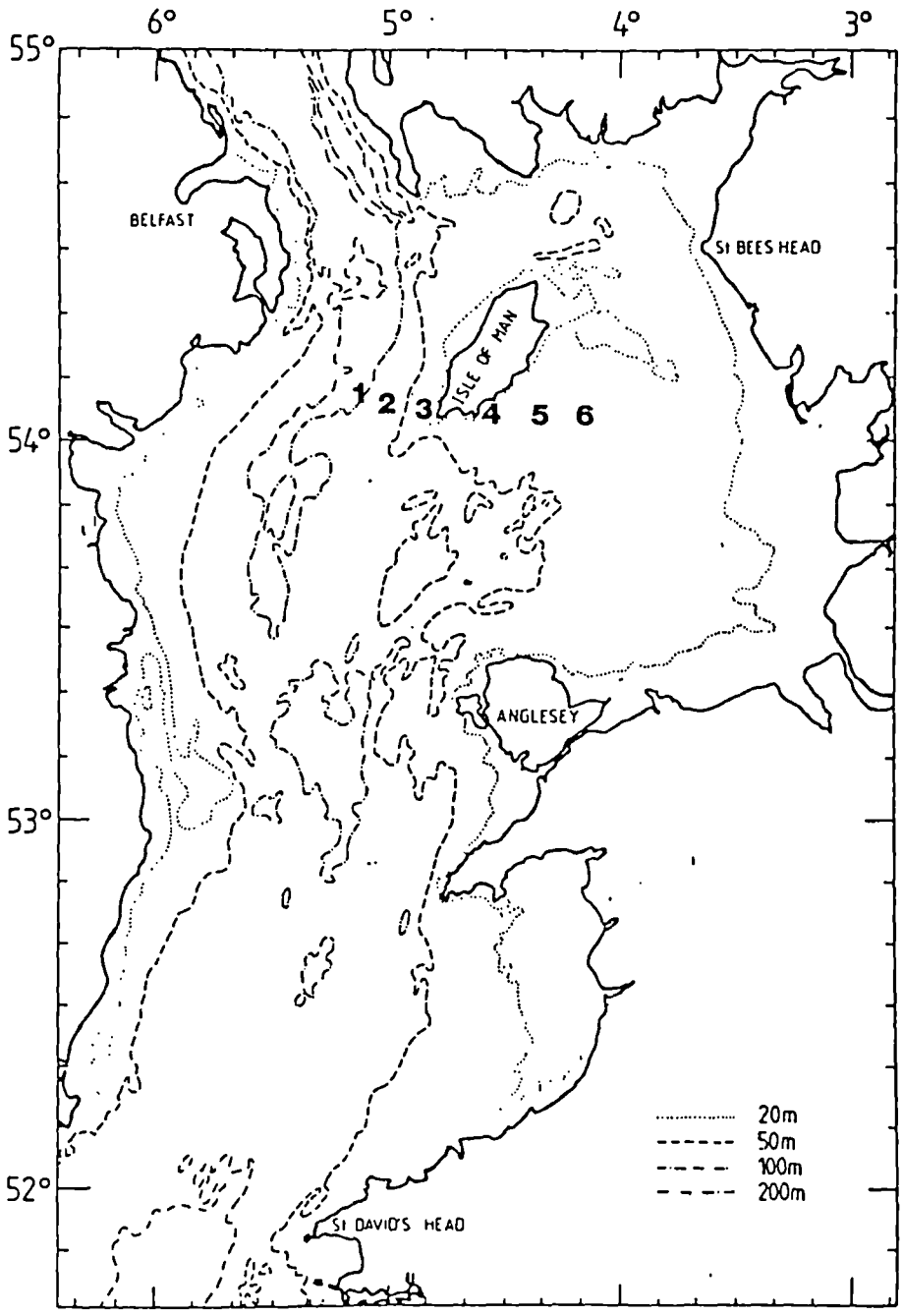


Fig. 3. Approximate position of sampling stations.

station	latitude	longitude	approximate distance from the coast / km	depth/m	max. tidal current/km
1	54 04'N	4 4930'W	18	100	0.5
2	54 065'N	4 36'W	9	60	1.0
3	54 05'N	4 50'W	5	40	1.8
4	54 03'N	4 40'W	1	30	3.5
5	54 03'N	4 2510'W	11	45	3.0
6	54 03'N	4 13'30W	23	40	3.0

Table 1. Position of the sampling stations and their physical characters.

Cruise	Date	Stations sampled
	1986	
1	13 March	1-2-3
2	11 April	1-2-3
3	18 April	4-5-6
4	29 April	1-2-3
5	14 May	4-5-6
6	20 May	1-2-3
7	2 June	4-5-6
8	3 June	1-2-3
9	23 June	4-5-6
10	25 June	1-2-3
11	14 July	4-5-6
12	18 July	1-2-3
13	29 July	4-5-6
14	30 July	1-2-3
15	6 August	1-2-3
16	18 August	4-5-6
17	10 September	4-5-6
18	12 September	1-2-3
19	13 October	4-5-6
20	15 October	1-2-3
21	19 November	4-5-6
22	21 November	1-2-3
	1987	
23	16 January	1-2-3
24	20 January	4-5-6
25	16 February	4-5-6
26	19 February	1-2-3
27	29 March	1-2-3
28	30 March	4-5-6
29	13 April	1-2-3
30	16 April	4-5-6
31	6 May	4-5-6
32	8 May	1-2-3
33	20 May	1-2-3
34	22 May	4-5-6
35	8 June	1-2-3
36	12 June	4-5-6
37	13 July	4-5-6
38	15 July	1-2-3
39	3 August	4-5-6
40	5 August	1-2-3
41	17 September	4-5-6
42	19 September	1-2-3
43	15 October	4-5-6
44	18 October	1-2-3

Table 2. List of cruises during the survey.

station	1	2	3	4	5	6
1986						
April	6.3	6.3	6.3	6.1	5.9	6.3
	6.3	6.3	6.3	5.9	5.5	5.8
May	8.7	8.6	8.5	7.5	7.8	7.7
	8.0	8.4	8.5	7.5	7.6	7.5
June I	9.5	9.5	9.8	10.5	10.0	9.8
	8.1	9.0	9.4	9.6	9.6	9.1
June II	11.1	11.0	10.0	10.5	10.5	10.5
	8.6	9.3	9.8	10.5	10.3	10.3
July I	11.1	12.9	12.9	12.2	12.4	12.8
	9.0	9.5	12.0	12.2	12.2	12.2
July II	13.2	13.0	13.0	12.2	13.0	13.2
	9.3	9.6	12.4	12.2	12.5	12.6
August	13.2	13.0	13.0	12.9	13.3	13.0
	11.9	12.6	13.0	12.9	13.0	12.8
September	13.4	13.1	13.5	13.4	13.6	14.5
	12.9	13.1	13.1	13.1	13.0	13.8
October	12.7	13.1	12.8	13.0	13.3	13.7
	12.4	12.6	12.6	13.0	13.2	14.4
1987						
April	7.5	8.0	6.95	7.0	7.0	7.0
	7.0	7.0	7.8	6.9	6.9	6.8
May I	8.6	8.7	8.5	8.8	8.8	8.7
	7.5	8.4	8.4	8.6	8.6	8.5
May II	8.9	8.7	9.0	8.8	9.2	9.3
	7.6	8.4	8.5	8.6	8.8	8.8
June	10.5	10.4	10.5	10.4	10.3	10.3
	8.5	9.5	10.0	10.0	9.8	9.8
July	12.7	14.0	12.8	13.0	12.9	12.8
	10.2	11.1	12.2	13.0	12.8	12.6
August	12.5	12.1	13.8	14.0	14.0	14.0
	11.0	11.1	13.1	14.0	14.0	14.0
September	12.7	13.0	12.8	14.0	14.5	14.0
	10.2	11.1	12.2	14.0	14.1	13.7
October	12.5	12.5	13.0	12.7	13.0	13.2
	12.5	12.5	13.0	12.7	12.9	12.9

Table 3. Surface bottom temperatures

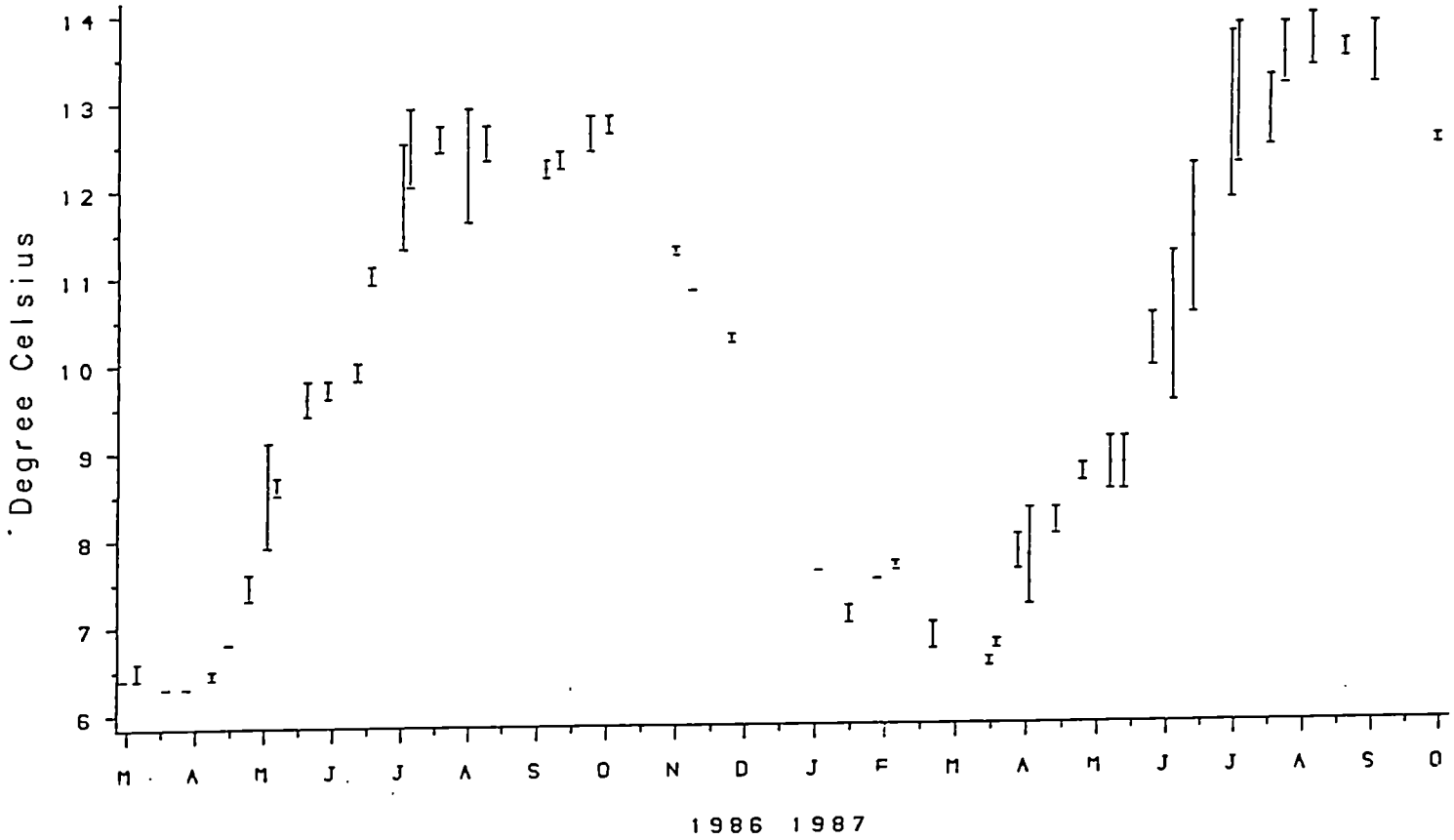


Fig. 4. Seasonal cycle of surface-bottom temperature differences at station 3.

Chlorophyll *a* (mg m^{-3}) 1986

station	1	2	3	4	5	6
March	0.72	0.58	0.65	n.s.	n.s.	n.s.
	0.39	0.25	0.35	n.s.	n.s.	n.s.
April	0.65	0.54	0.90	0.63	0.88	0.56
	0.33	0.33	0.39	0.47	0.34	0.40
April	0.74	0.65	0.92	n.s.	n.s.	n.s.
	0.32	0.55	0.41	n.s.	n.s.	n.s.
May	0.91	1.42	6.40	4.70	1.26	0.92
	0.47	0.97	0.81	0.84	0.73	0.52
June 1	0.43	3.12	0.35	0.44	0.425	1.31
	0.33	0.21	0.28	0.35	0.28	0.29
June 2	2.04	2.85	2.57	1.35	1.45	13.86
	0.596	0.57	0.44	0.79	1.61	1.64
July 1	2.85	1.05	0.76	0.49	0.29	0.84
	2.93	0.53	0.56	0.25	0.25	0.31
July 2	1.16	1.63	0.95	0.84	0.88	0.28
	0.70	1.33	0.71	0.53	0.66	0.40
August	1.72	1.93	1.51	1.00	1.25	0.92
	1.06	0.96	1.16	0.50	0.56	0.43
September	1.21	0.77	1.26	0.66	0.72	0.54
	1.00	0.55	0.43	0.53	0.58	0.34
October	0.73	0.79	0.66	0.54	0.11	0.14
	0.49	0.82	0.06	0.12	0.08	0.08
November	0.20	0.09	0.09	0.52	0.45	0.43
	0.08	0.06	0.01	0.43	0.29	0.29
December	n.s.	n.s.	0 .47	n.s.	n.s.	n.s.
	n.s.	n.s.	0.27	n.s.	n.s.	n.s.

Table 4a. Chlorophyll *a* values at the open water stations during 1986.

Chlorophyll *a* (mg m^{-3}) 1986

station	1	2	3	4	5	6
March	0.72	0.58	0.65	n.s.	n.s.	n.s.
	0.39	0.25	0.35	n.s.	n.s.	n.s.
April	0.65	0.54	0.90	0.63	0.88	0.56
	0.33	0.33	0.39	0.47	0.34	0.40
April	0.74	0.65	0.92	n.s.	n.s.	n.s.
	0.32	0.55	0.41	n.s.	n.s.	n.s.
May	0.91	1.42	6.40	4.70	1.26	0.92
	0.47	0.97	0.81	0.84	0.73	0.52
June 1	0.43	3.12	0.35	0.44	0.425	1.31
	0.33	0.21	0.28	0.35	0.28	0.29
June 2	2.04	2.85	2.57	1.35	1.45	13.86
	0.596	0.57	0.44	0.79	1.61	1.64
July 1	2.85	1.05	0.76	0.49	0.29	0.84
	2.93	0.53	0.56	0.25	0.25	0.31
July 2	1.16	1.63	0.95	0.84	0.88	0.28
	0.70	1.33	0.71	0.53	0.66	0.40
August	1.72	1.93	1.51	1.00	1.25	0.92
	1.06	0.96	1.16	0.50	0.56	0.43
September	1.21	0.77	1.26	0.66	0.72	0.54
	1.00	0.55	0.43	0.53	0.58	0.34
October	0.73	0.79	0.66	0.54	0.11	0.14
	0.49	0.82	0.06	0.12	0.08	0.08
November	0.20	0.09	0.09	0.52	0.45	0.43
	0.08	0.06	0.01	0.43	0.29	0.29
December	n.s.	n.s.	0 .47	n.s.	n.s.	n.s.
	n.s.	n.s.	0.27	n.s.	n.s.	n.s.

Table 4a. Chlorophyll *a* values at the open water stations during 1986.

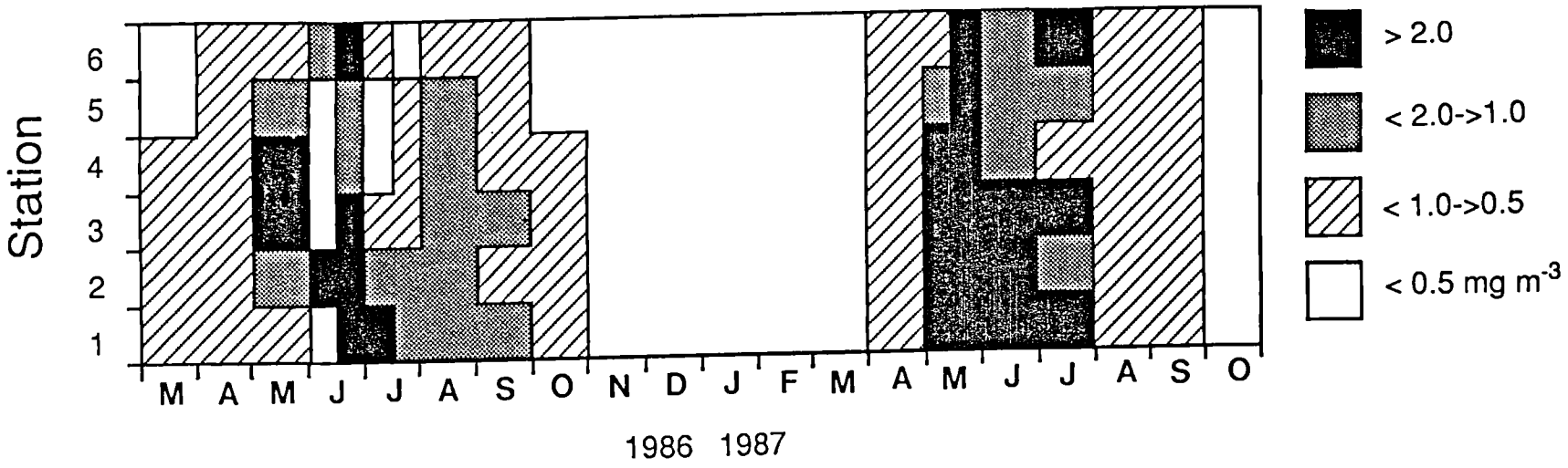


Fig. 5a. Seasonal cycle of total chlorophyll *a* along the transect.

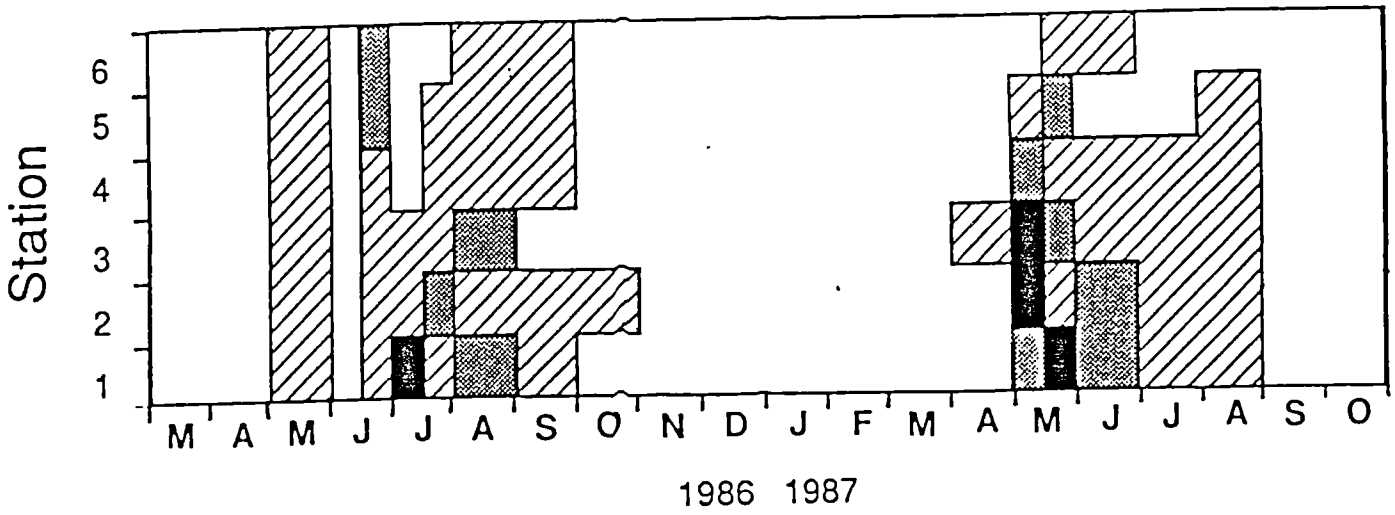


Fig. 5b. Seasonal cycle of nano chlorophyll *a* along the transect. Scale as in Fig. 5a.

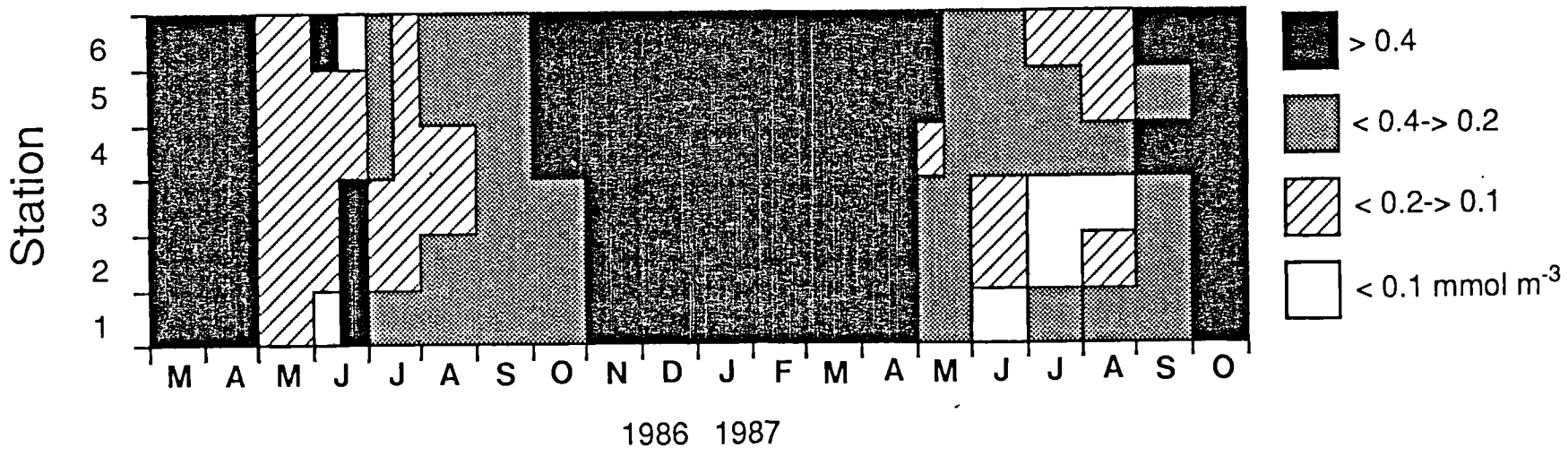


Fig. 6. Seasonal cycle of phosphate along the transect.

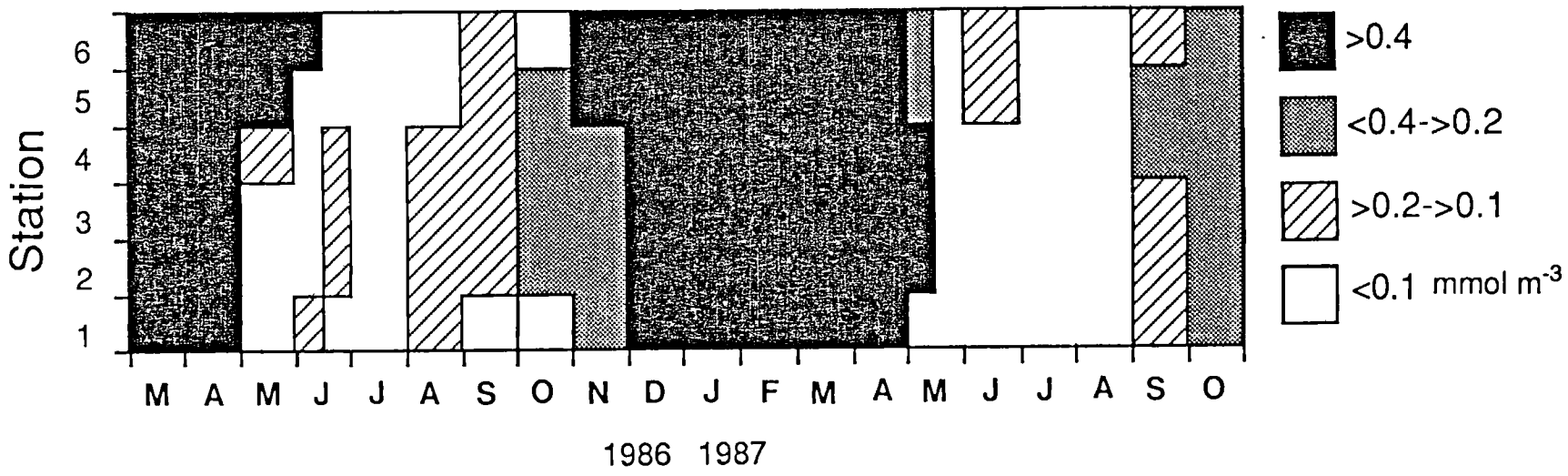


Fig. 7. Seasonal cycle of nitrate along the transect.

Fig. 8. The seasonal cycle of the dominant phytoplankton taxa at the open water stations. Filled in squares indicate the west stations, empty squares the east transect.

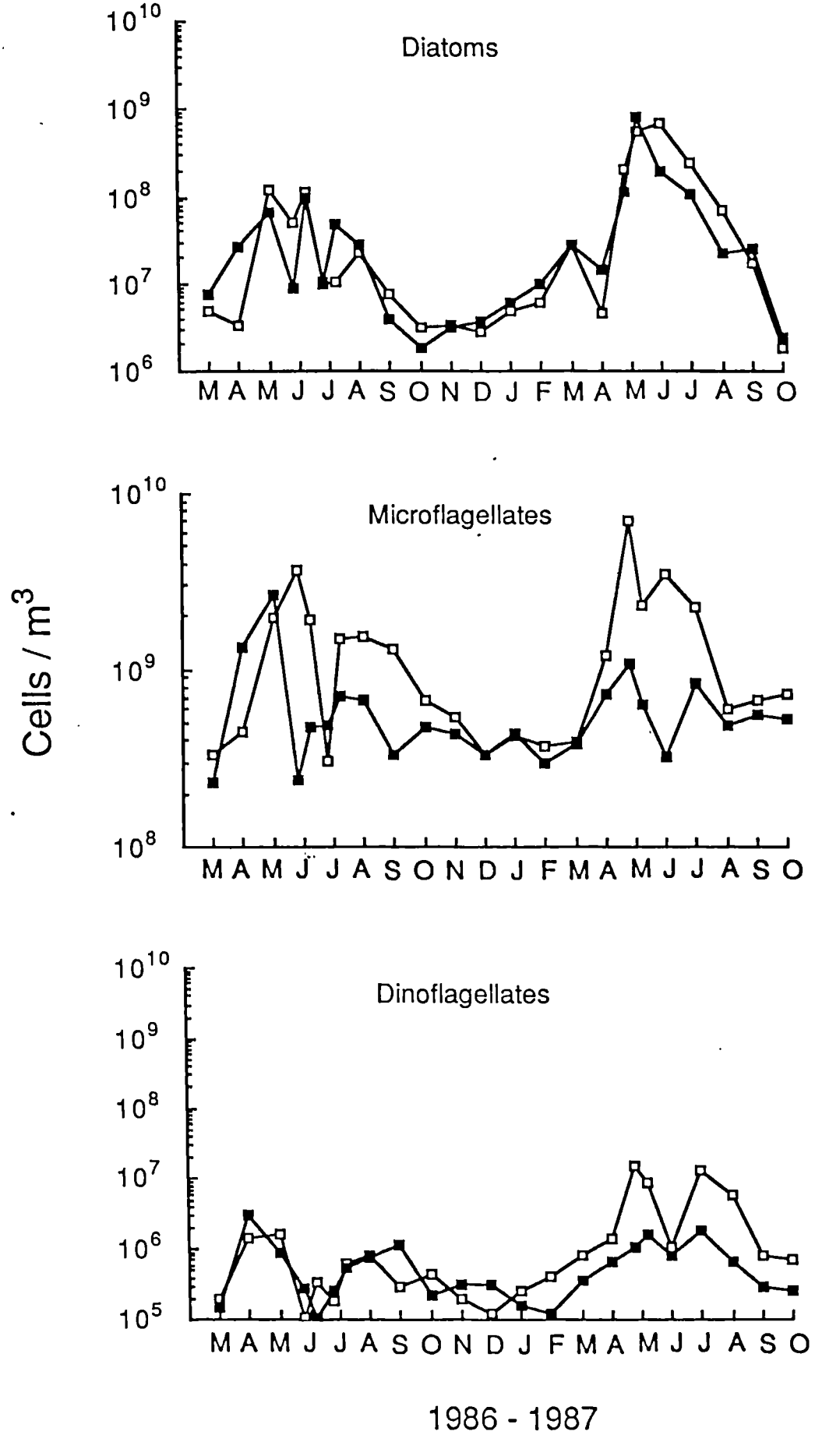

Diatoms
Microflagellates
Dinoflagellates
Cells / m3
10^10
10^9
10^8
10^7
10^6
10^5
M A M J J A S O N D J F M A M J J A S O
1986 - 1987

Table 3. List of phytoplankton species identified throughout the study period and their maximum abundance for any month of the year. Symbols indicate : +, $<10^5$; ++, $>10^5$-$<10^6$; +++, $>10^6$-$<10^7$; ++++, $>10^7$-$<10^8$; +++++, $>10^8$-$<10^9$; ++++++, $>10^9$

Diatoms			
Achnantes longipes	+	*N. closterium*	++++
Actinopthycus senarius	++	*N. seriata*	+++++
A. splendens	+	*Paralia sulcata*	+++
Asterionella glacialis	+++	*Peurosigma* spp.	++
Bacillaria paxillifer	++++	*Podosira stelliger*	+
Bacteriastrum hyalinum	+	*Rhizosolenia alata f. alata*	++
Biddulphia alternans	+	*Rhizosolenia delicatula*	++++++
B. aurita	+	*R. hebetata*	++
B. mobiliensis	++	*R. hebetata f. hemispina*	++
B. regia	+	*R. setigera*	+++
B. rhombus	+	*R. shrousbolei*	++
B. sinensis	++	*R. stolterfothii*	++++
Cerataulina pelagica	++++	*R. styliformis*	+
Cerataulus turgidus	+	*Skeletonema costatum*	++++
Chaetoceros affine	+++	*Stauroneis membranacea*	++++
C. boreale	++	*Stephanopyxis turris*	++
C. breve	+++	*Streptotheca thamesi*	+
C. compressum	++	*Striatella unipunctata*	+
C. constrictum	++	*Synedra* spp.	+
C. curvisetum	++++	*Thalassionema nitzschioides*	+++
C. danicum	++	*Thalassiosira decipiens*	++++
C. debile	++	*T. eccentrica*	++
C. decipiens	++	*T. gravida*	++
C. densum	++	*T. hyalina*	++
C. holsaticum	++	*T. nordenskioldii*	++++
C. teres	++	*T. subtile*	++++
C. sociale	++++		
C. tortissimum	++++	**Dinoflagellates**	
Corethron cryophilum	+	*Ceratium compressum*	+
Coscinodiscus concinnus	++	*C. extensum*	+
C. eccentricus	+	*C. arietinum*	+
C.granii	+	*C. furca*	++++
C. lineatus	+	*C. fusus*	+++
C. radiatus	++	*C. gravidum*	+
Coscinosira polychorda	+++	*C. hexacanthum*	+
Diploneis spp.	+	*C. horridum*	+
Dytilum brigwellii	+++	*C. lineatum*	+++
Euchampia zodiacus	++	*C. longipes*	++
Fragilaria spp.	++	*C. minutum*	+
Grammatophora marina	+	*C. tripos*	+++
G. serpentina	+	*Dinophysis acuminata*	+++
Guinardia flaccida	++++	*D. acuta*	++
Gyrosigma spp.	+	*D. caudata*	+
Lauderia borealis	++++	*D. recurva*	+
Leptocylindrus danicus	+++++	*D. rotundata*	+
L. minimus	++	*Gonyaulax digitata*	++
Licmophora flabellata	+	*Gonyaulax spinifera*	++
Melosira moniliformis	+	*Goniaulax* spp.	++
M. nummuloides	+	*Gyrodinium aureolum*	+
Navicula distans	++	*G. spirale*	++
Navicula spp.	++++	*Gyrodinium* spp.	+
Nitzschia delicatissima	++++	*Mesosporus perforatus*	+++

Noctiluca scintillans	++
Peridium curtipes	++
P. depressum	++
P. divergens	++
P. leonis	++
P. ovatum	++
P. pentagonum	++
P. steinii	++
Pyrocistis lunula	+
Prorocentrum micans	+++
Protoperidinium bipes	++
P. conicoides	+
Scripsiella trochoidea	++++
Silicoflagellates	
Dictyocha fibula	+++

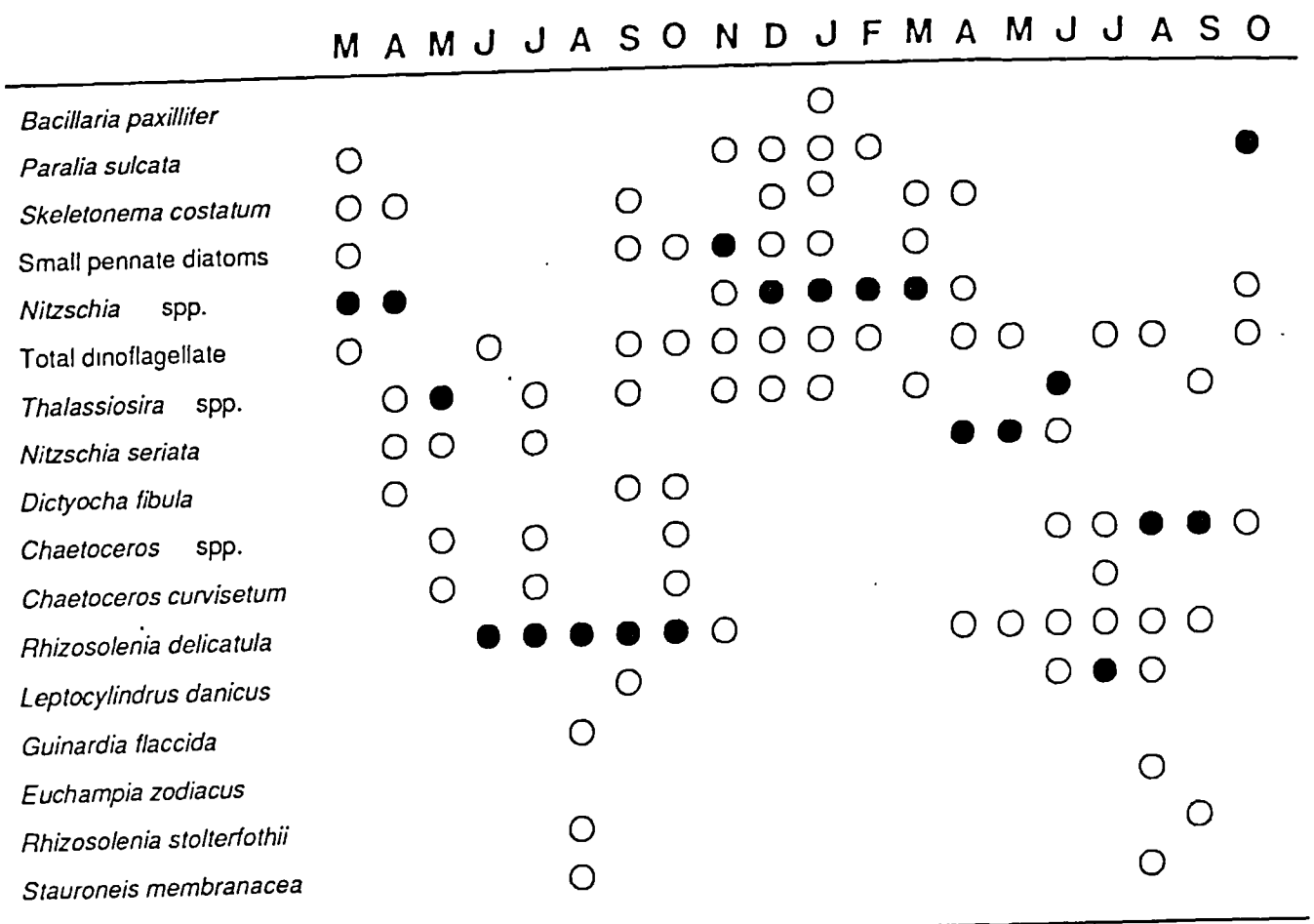


Fig. 9a. The succession of taxa which account for > 5 % of total phytoplankton abundance (excluding microflagellates). The filled in circles indicate the dominant species.

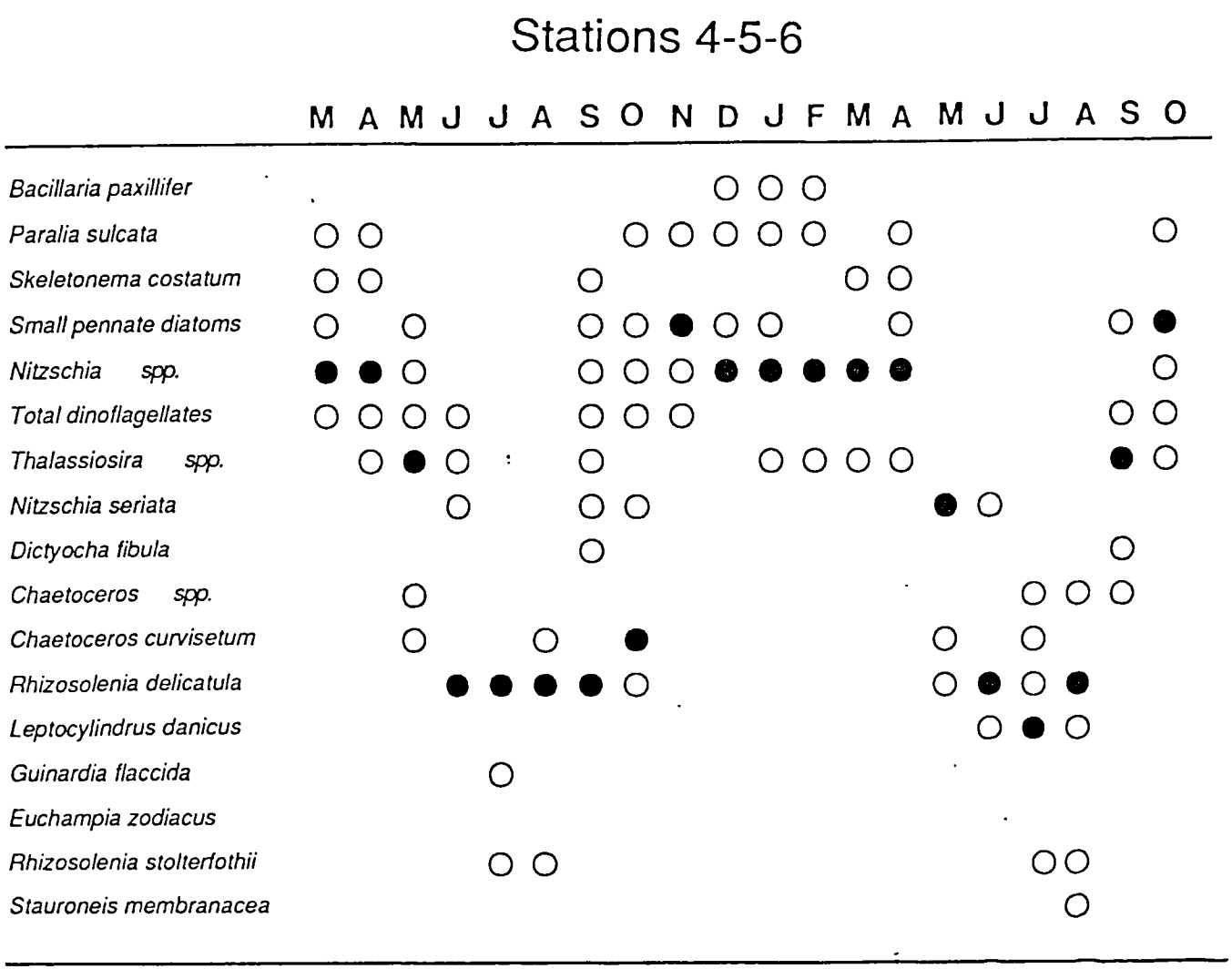


Fig. 9b. Legends as in Fig. 9a.

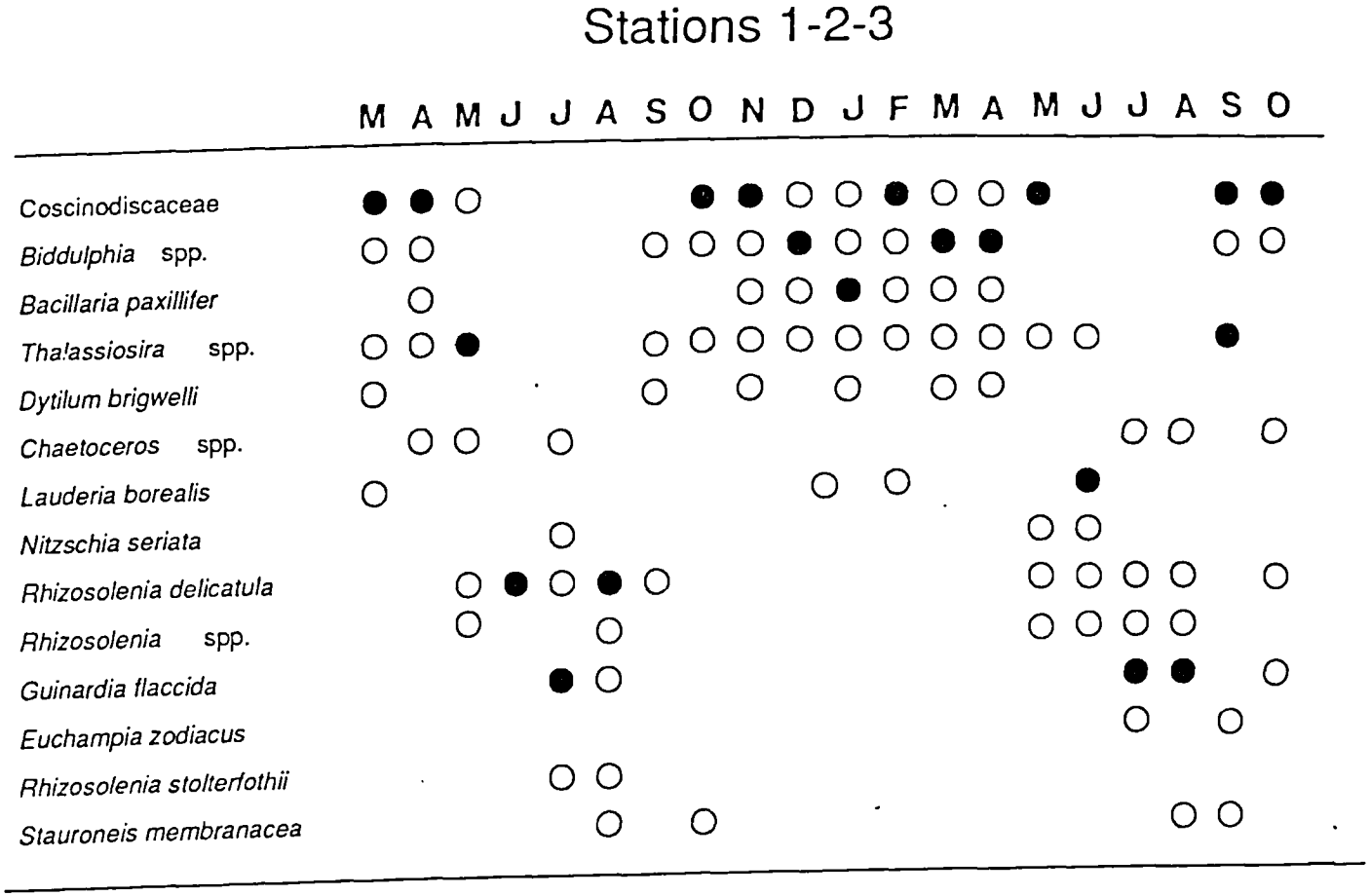


Fig. 10a. The succession of the 5 dominant diatom taxa in terms of their biomass. The filled in circles indicate the dominant species.

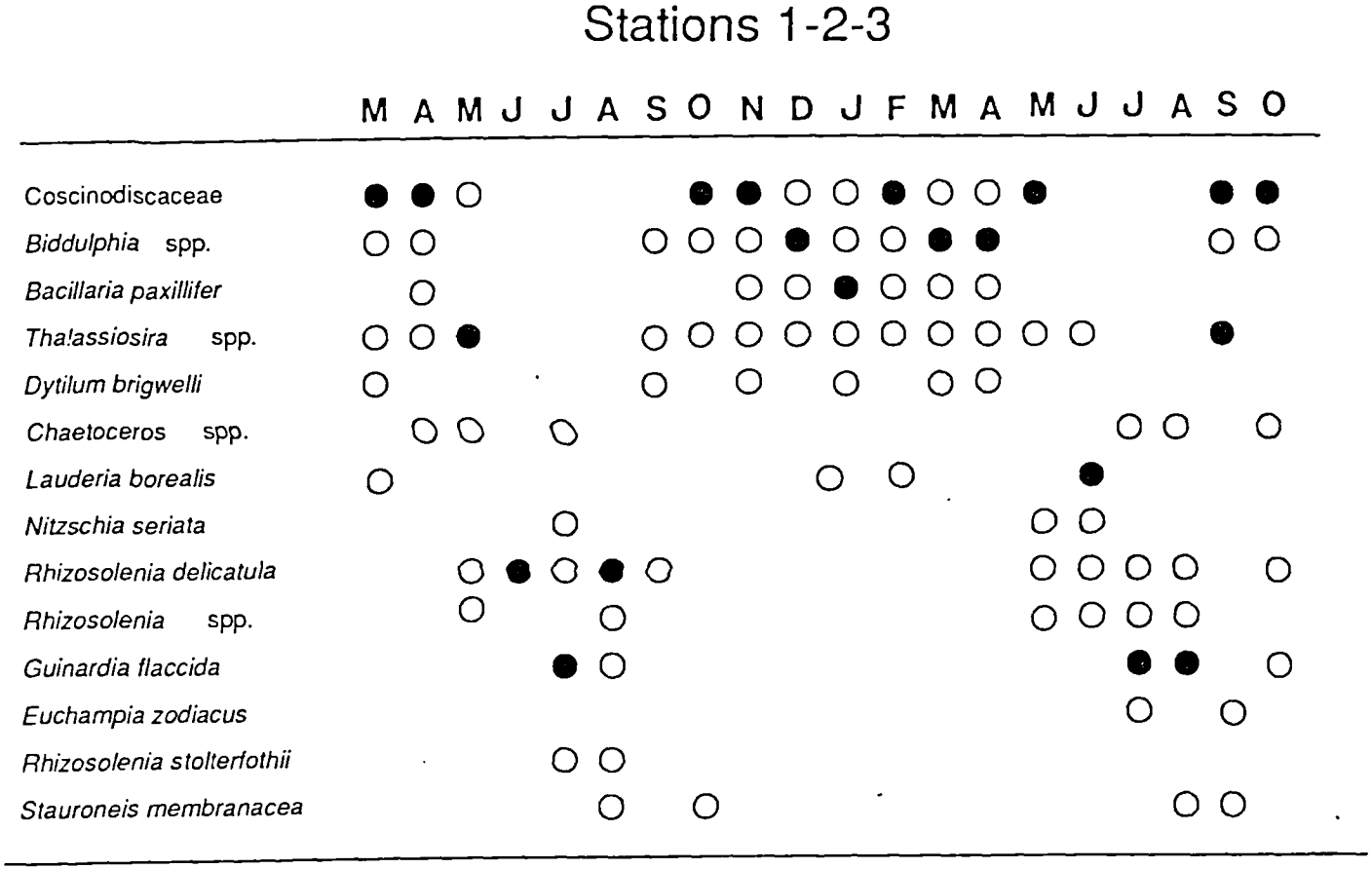


Fig. 10a. The succession of the 5 dominant diatom taxa in terms of their biomass. The filled in circles indicate the dominant species.

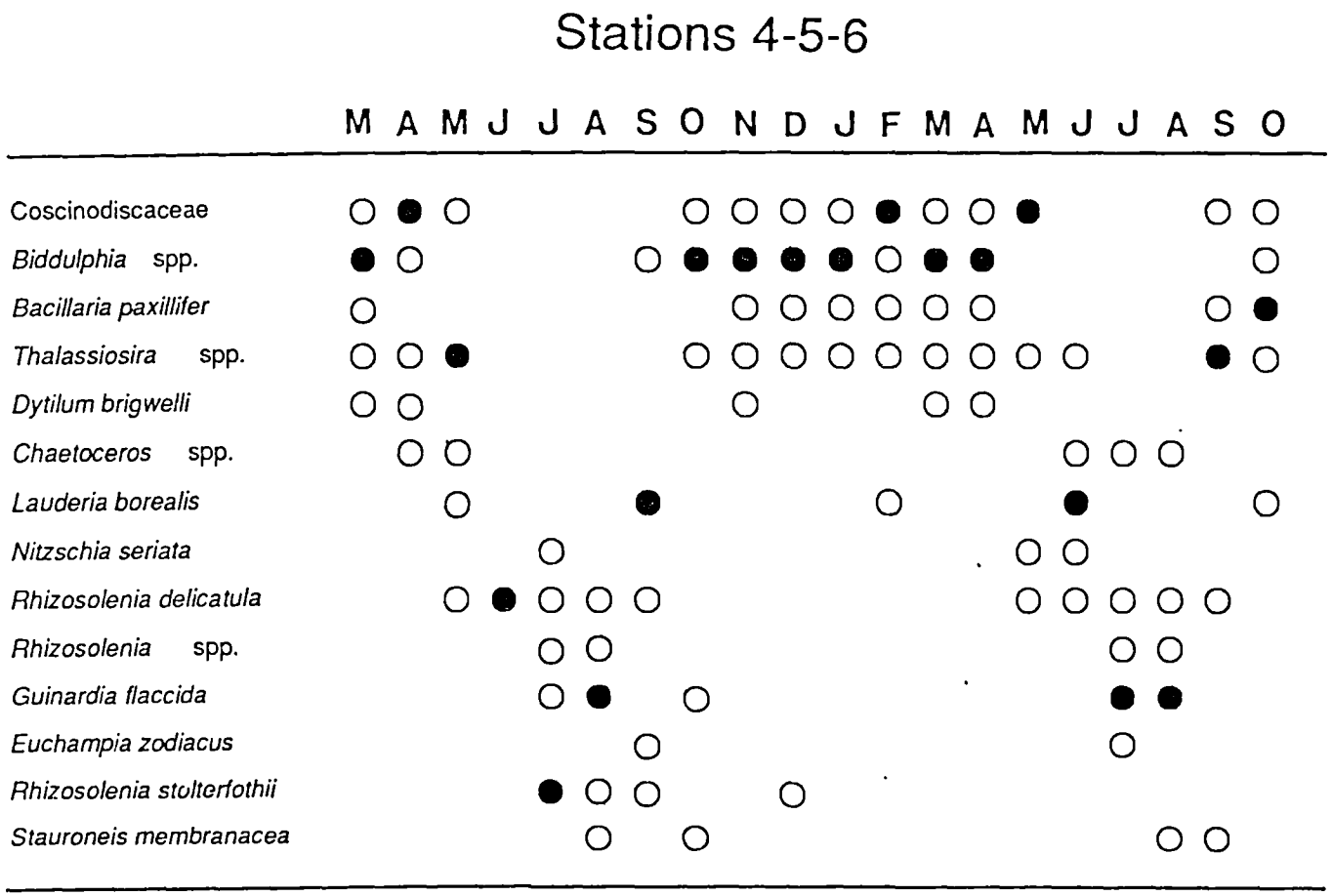


Fig. 10b. Legends as in Fig. 10a.

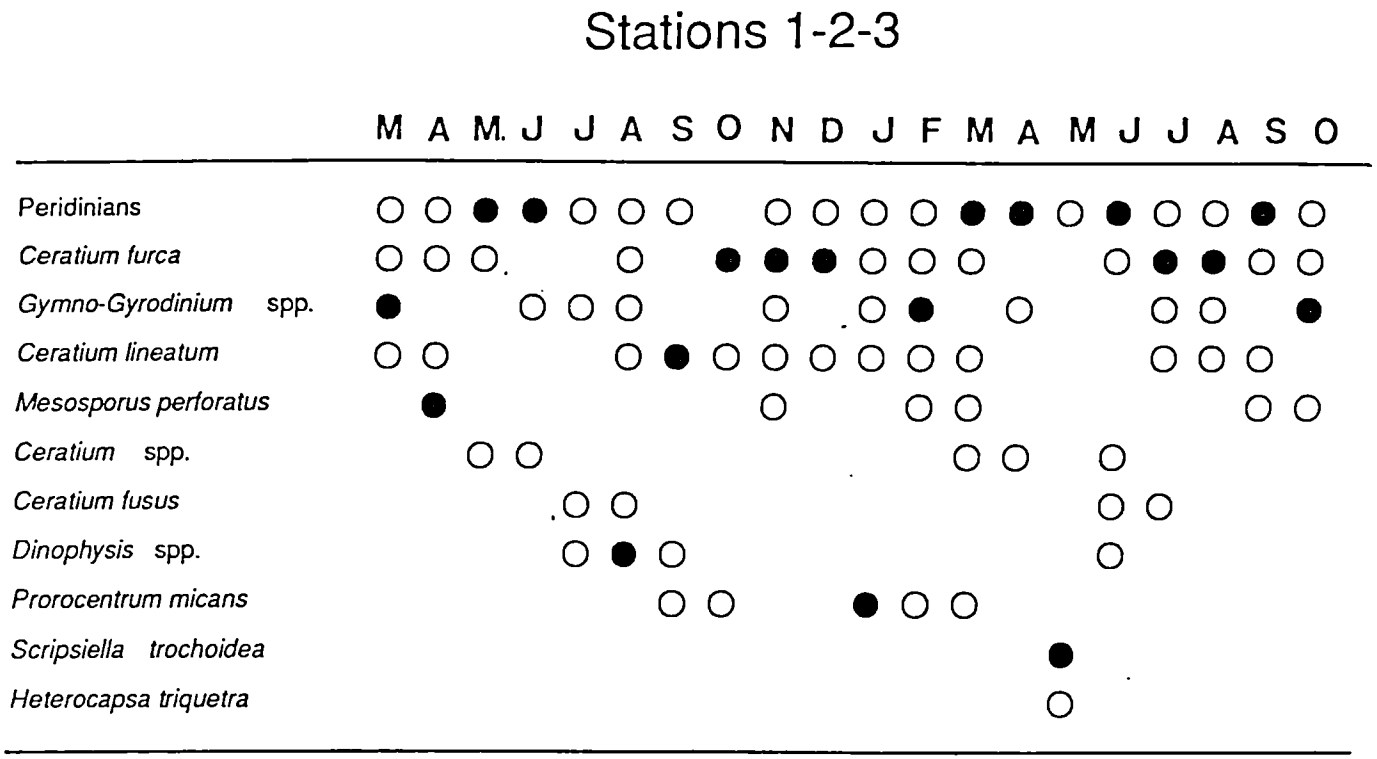


Fig. 11a. The succession of dinoflagellate taxa which account for > 5 % of total The filled in circles indicate the dominant species.

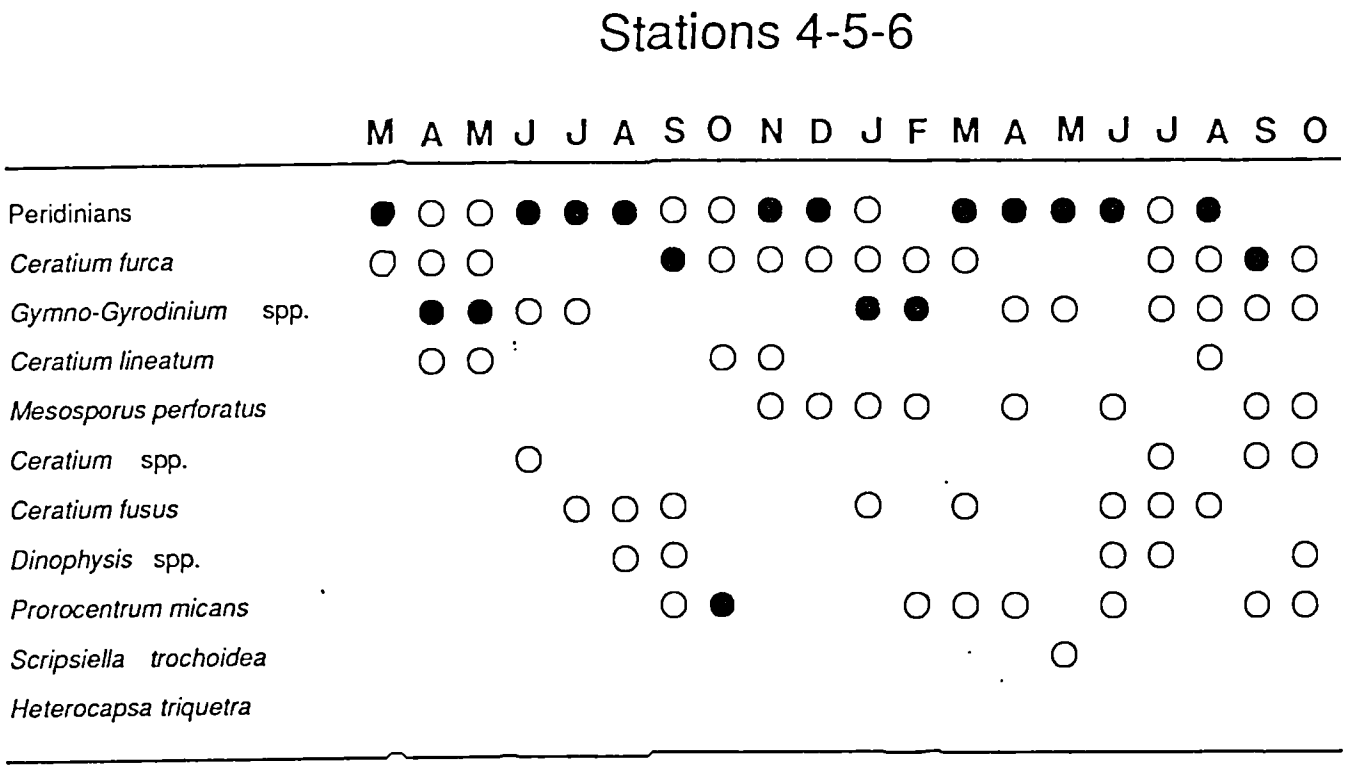
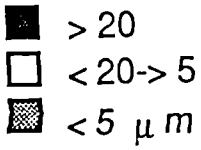
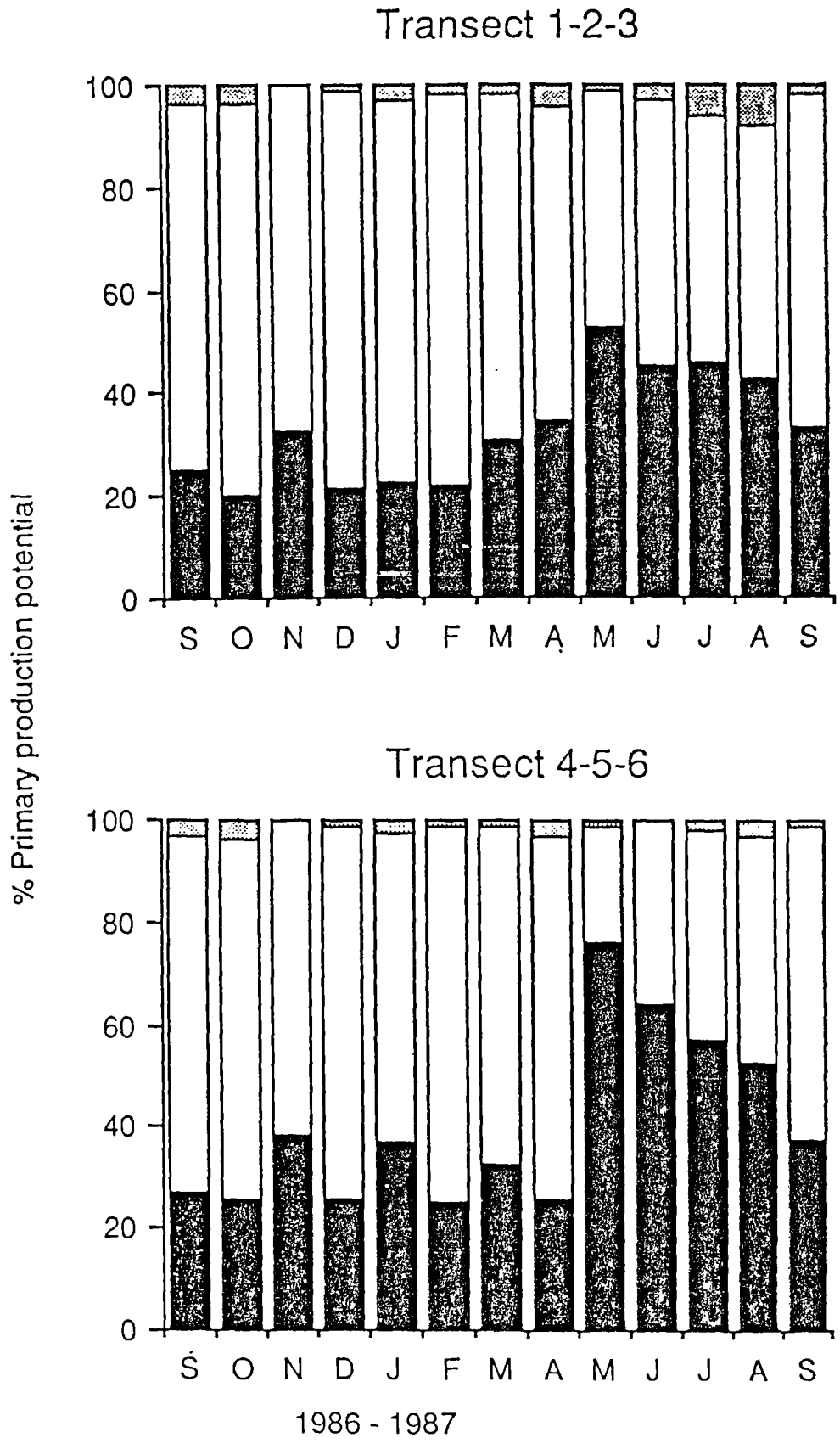


Fig. 11b. Legend as in Fig. 11a.

Fig. 12. Contribution of size fractionated phytoplankton populations to potential primary production.




Transect 1-2-3
100
80
60
40
20
0
S O N D J F M A M J J A S
Transect 4-5-6
100
80
60
40
20
0
S O N D J F M A M J J A S
% Primary production potential
1986 - 1987

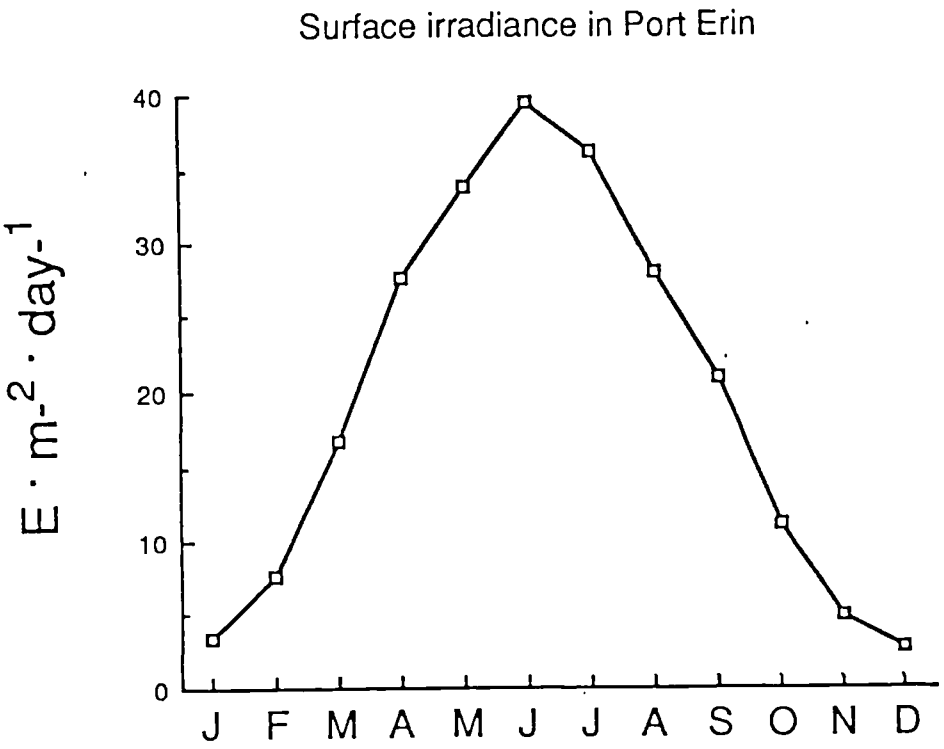


Fig. 13. Monthly means of surface irradiance at Port Erin Bay during the period May 1970 to April 1974. [Data replotted from Kain *et al.* (1974) after conversion from W · m-2 to E · m-2 · day-1]

SECTION THREE

OBSERVATIONS ON THE CILIATE PLANKTON CYCLE

3.1. INTRODUCTION

It has been increasingly apparent that very small organisms constitute an important role in marine pelagic food webs and that a substantial part of primary production in the water column is due to photoautotrophs less than 3 µm, including microflagellates and cyanobacteria (Johnson & Sieburth 1979, 1982; Murphy & Haugen 1985). Several studies also show that aquatic autotrophs release a significant proportion of photosynthate as Dissolved Organic Carbon (DOC) (see review by Larsson & Hagstrom 1982). The exudate release appears to be rapidly assimilated by bacterioplankton which reconvert this DOC fraction to particulate carbon, and recent studies reveal that bacterial production in the water column is greater than previously believed, that is, up to 5 to 20 % of primary production (Fuhrman & Azam 1982; Larsson & Hagstrom 1982). Thus the major part of particulate carbon production originates from organisms in the size range of a few µm or less. Food particles withir this size range are mostly unavailable to metazoan zooplankton, notably copepods (Nival & Nival 1976). This calls for a revision on our view on the lower trophic levels in the traditional pelagic food chain as consisting of large diatoms and dinoflagellates preyed upon by mesozooplankton, mainly copepods.

In the search for the 'missing links' in an extended food web, much interest has focussed on the assemblage of organisms operationally defined by Sieburth (1979) as nanozooplankton (2 to 20 µm) and microzooplankton (20 to 200 µm). In a series of papers Fenchel (1982 a, b, c, d) showed the importance of heterotrophic microflagellates, mainly 3 to 7 µm chrysomonads, as efficient predators on bacterioplankton. As an additional trophic level the significance of planktonic cilates as major predators on small autotrophic and heterotrophic flagellates has been proposed by a number of authors (e.g. Margalef 1967; Beers & Stewart 1969; Heinbokel & Beers 1979; Smetacek 1981; Jonsson 1986). Due to inappropiate sampling techniques, planktonic ciliates were almost overlooked in routine zooplankton samples until the early seventies. The few reliable estimates of ciliate

biomass, e.g. Rassoulzadegan (1977), Smetacek (1981) and Relevante & Gilmartin (1983, 1987), all indicate that planktonic ciliates make up a substantial part of zooplankton biomass. Considering the rapid metabolism per unit weight of ciliates (Klekoski 1981; Fenchel & Finlay 1983), these biomass assessments suggest a very important role for ciliates in the pelagic food web.

Ciliated protozoa are considered to be a significant food resource for fishes and zooplankton as Ryder (1881) and Hirano & Ohshima (1957) first suggested. More recently it has been shown that the ciliated protozoan *Uronema* is eaten by the copepod *Eurytemora* (Berk *et al.* 1977) and that *Daphnia* feed on *Paramecium* and *Cyclidium* (Porter *et al.* 1979). The feeding rate of *Acartia* was increased using tintinnids as food at a concentration of 10^3 l (Robertson 1983). Stoecker & Saunders (1985) found that *Acartia* preferred the tintinnid *Favella* to the dinoflagellate *Heterocapsa* as food when both food organisms were available. It is interesting that the copepod *Scottolana canadensis* was capable of producing eggs more frequently when ciliated protozoa were given as food than when only microalgae were available (Heinle *et al.* 1977). Thus many mesozooplankton feed on ciliates which appear to be important in the transfer of bacterial or detrital material to the larger animals, such as copepods and fish larvae.

Through active feeding, protozoa produce dissolved nutrients at a high rate. Johannes (1964) showed that as the excretion rate of phosphate increases with decreasing animal body size, protozoans can produce dissolved phosphate at a very high rate. Johannes (1965) also reported that organic phosphate was mineralized more quickly in the presence of bacteria, ciliates and flagellates than in the presence of bacteria alone. The feeding activity of the protozoa reduces bacterial numbers to a low level, at which the bacterial population is nurtured in a state of high metabolic activity (Maeda 1986). Fenchel and Harrison (1976) have shown that detrital material is broken down more quickly in the presence of mixed populations of heterotrophic protozoa with bacteria. There are also several reports of recycling of nutrients by protozoa. The ciliated protozoa, *Strombidium viride,* excreted phosphate after feeding

on bacteria (Taylor & Lean 1981) and *Paraunema acutum* produced guanine and hypoxanthin in a soluble fraction (Soldo *et al.* 1978). Microzooplankton in a size class less than 200 μm have been shown to be responsible for the regenerating of ammonium ions in seawater (Harrison 1978; Paasche and Kristiansen 1982; Gast & Horstmann 1983).

There are many solid surfaces in the aquatic environment which provide favoured biological niches for microbial colonization because dissolved organic materials are concentrated on them (ZoBell 1943; ZoBell & Grant 1943). Bacteria, microalgae and protozoa attach to them soon after substrata are immersed in the water. In the first stage, bacteria appear on the surface excreting a polysaccharide "glycocalyx" with which they attach (Costerton *et al.* 1978). Small rod shape bacteria preferentially adhere to the surfaces (Marshall *et al.* 1971). Then the attached bacteria grow and form colonies. The numbers of colonies increase with time and their shapes are diversified (Jordan & Staley 1976). After a few days, when the bacterial thin films have developed, protozoa, ciliates and heterotrophic flagellates appear on the surfaces and destroy the bacterial communities by feeding. This allows microalgae to adhere to the surface in place of the bacterial populations (Marszalek *et al.* 1979). Thus the protozoa assist the microbial successions on solid surfaces as well as in or on suspended particles in the water column.

Among planktonic ciliates, the Oligotrichina (oligotrichs) and the Tintinnina (tintinnids), contain the most abundant species. Whereas the latter are a well studied group (e.g. Verity, 1987 and ref. therein), the oligotrichs (generally grouped as "naked ciliates"), although more abundant in cases where both groups have been enumerated (e.g. Beers & Stewart 1967; 1970; Beers *et al.* 1971; Johansen 1976; Rassoulzadegan & Gostan 1976; Smetacek 1981; Endo *et al.* 1983), because of their fragility and the difficulties involved in their examination, identification, and culturing, have largely been ignored.

Although better methods of culturing, preservation, enumeration and identification (Dale & Burkill 1982; Corliss 1979 ; Paranjape & Gold 1982; Maeda &

Carey 1985; Montagnes & Lynn 1987), herald a new understanding of the role of oligotrichs in the dynamics of the planktonic food web, at present, only a few quantitative studies have been performed on their ecology (e.g. Rassoulzadegan 1977; Smetacek 1981; Revelante & Gilmartin 1983, 1987). As for coastal waters around the British Isles, ciliates have been the object of very few studies. By concentrating plankton with a 45 μm net Burkill (1978) studied the seasonal cycle of the larger ciliates at a shallow, eutrophic site, in southern England. In his study he found that naked ciliates were an order of magnitude less abundant than tintinnids. However, since it has been clearly shown (e.g. Revelante & Gilmartin 1983; Gifford 1985) that the impact of collection and concentration methods by the use of nets on oligotrichs is extremely severe and leads to a clear underestimation of ciliate abundance, his results can only be taken as a minimum estimate. Except for some observations on the relative abundance and vertical distribution of ciliates at a station off Plymouth (western English Channel) by Reid (1987), no other studies have taken naked ciliate protozoans into consideration in waters around the British Isles.

In comparison with the non-loricate species, the tintinnids have received considerably more attention. Because the sturdiness of their loricas provides a convenient basis for identification (Kofoid & Campbell 1929) they have been served by major, although dated, revisions. Because methods for their culture are well-developed (e.g. Gold 1971, 1973; Verity 1985), a considerable number of studies have been carried out on their role as grazers (Capriulo & Carpenter 1980), in regenerating nutrients (Johansen 1976; Verity 1985) and as food for higher trophic levels (Robertson 1983). However, although a considerable amount of information has now accumulated on their significance in marine habitats and pelagic food chains as compared to other marine protozoa, data on their ecology are still rare in comparison to other plankton taxa and factors controlling their spatial and temporal distributions are still unclear.

Only a few quantitative seasonal studies have been performed in the North Sea (Hensen 1887; Gillbricht 1954; Hedin 1975; Admiraal & Venekamp 1986) and in the

North Atlantic (Halldal 1953; Zeitschel 1967). As for coastal waters around the British Isles, except for the work of Diwan (1978) and Burkill (1978) at the site in southern England, no other quantitative papers on tintinnids have been published. With his concentrating technique Burkill (1978) found twelve species of tintinnids and maximum abundance of 1.5 x 10^6 organisms m^{-3}. Since Revelante & Gilmartin (1983) have shown that in the north Adriatic approximately 40 % of the tintinnids were smaller than 30 µm the concentrating procedure by Burkill (1978) might have also lead to an underestimation of tintinnid abundance and also composition. Other references to tintinnids in studies around the British Isles include the observations by Reid (1987) that the only tintinnid found during an approximately annual cycle in the waters off Plymouth, was *Tintinnopsis* sp., which was also never abundant. Some qualitative information on the distribution of tintinnid species around the British Isles can be inferred from the work of Lindley (1975) who studied the distribution of such organisms along the Continous Plankton Recorder routes in the North Sea and North Atlantic.

A number of studies (for Ref. see chapter 3) have shown that mesozooplankton abundance in mixed waters in the Irish Sea is considerably lower than in stratified waters of the Irish Sea itself and of most neighbouring areas of shelf. No comparable data exist for ciliated protozoans and/or microzooplankton in general. Since besides short taxonomical lists (e.g. Bruce *et al.* 1963), practically no other work has ever been carried out on the ecology of these groups in the Irish Sea, there appears to be plenty of scope for a study of their seasonal cycle of abundance and distribution. The aim of this work was therefore to assess quantitatively the importance of the principal ciliated protistan groups so to provide a basis for further investigations aimed at a better understanding of their dynamics in the food web.

3.2. MATERIAL & METHODS

3.2.1. Sampling and field methods

Samples for ciliate counts were obtained from April 1986 to October 1987 at the six open water stations described in the phytoplankton chapter and from January 1987 to October 1988 from the ruined breakwater in Port Erin Bay. While sampling frequency at the open water stations was monthly to bimonthly, in Port Erin Bay samples were collected at daily to weekly intervals. Sampling frequency was always higher at times of rapid population growth. At the open water stations water samples were taken with a 5-l Nansen Peterson water bottle from 4 to 5 depths (1, 5, 15, 20 and 30 m) and pooled together in a plastic container to give a final 10-l composite sample of the water column. In Port Erin Bay 10-l surface samples were collected with a plastic bucket. Whenever possible, samples were taken at high water to minimize contamination by benthic species.

Between early May until the end of June samples for total chlorophyll *a* were also collected in Port Erin Bay to study the dynamics of the ciliates during the "spring" bloom. A total of 27 samples were collected. Methods for chlorophyll determination were as in chapter 1.

3.2.2 Fixation and concentration

All samples were immediately fixed with a 1 % solution of Rhode's acid version (Lovergrove 1960) of Lugols iodine solution. Revelante & Gilmartin (1983) found this to preserve the non-loricate ciliates better than buffered formaldehyde which caused a loss of 30 to 70 % of the non-loricate ciliate densities. Similar observations were also reported by Pace & Orcutt (1981). A number of authors have recently began to utilize Bouin's solution as an alternative to Lugols (e. g. Lee *et al.* 1985; Montagnes *et al.* 1988). For comparative purposes only, during 1988, replicate whole water samples were fixed with a 5 % final solution of Bouin's. No significant differences were observed in the abundance and state of preservation of ciliates with these two

fixatives.

Whole water samples were concentrated by a three step settling process (Revelante & Gilmartin 1983); an initial 72-hr settling in a cylindrical plastic bucket (bucket height 30 cm) reduced the volume from 10 to approximately 1 l; a second 72-hr period in graduated cylinders (cylinder height 25 cm) reduced the volume from 1 l to 100 ml; and a third 72-hr period (cylinder height 20 cm) reduced the volume from 100 to 10 ml. The supernatant was removed by siphoning. Prior to counting the fixed samples were stored for no longer than 1 month.

3.2.3. Enumeration

In samples collected at the open water stations only the tintinnids were identified to species level. All other ciliated protozoans were simply enumerated for total ciliate abundance. Whereas samples collected in Port Erin Bay from March to August 1987 were studied only for tintinnids, samples collected from September 1987 to September 1988 were analysed for both tintinnids and naked ciliates. The latter also were identified to species level.

As preliminary observations of whole water samples concentrated to a few ml for phytoplankton counts had shown naked ciliates to be present in much higher abundance than tintinnids, naked ciliates were counted in samples concentrated 100-fold, tintinnids and large naked ciliates such as *Strombidium strobilum* in samples concentrated 1000-fold. The concentrated sample was stained with Rose Bengal to identify protoplasm and 1 ml subsample was examined and counted in a Sedgwick-Rafter cell at 160 or 200 X magnification using a Zeiss Universal microscope. According to overall abundance counting was repeated once or twice more. Total ciliate counts generally exceeded 100 individuals for each sample; therefore, 95 % confidence limits for single counts were± 20 % or less. For closer examination, specimens were picked out from the counting slide with a micropipette and viewed at higher magnification. All morphologically similar species were differentiated in relevant groups such as *Strombidium "conicum"*, *Strombidium*

"delicatissimum", and *Strombidium* spp. Where identification was uncertain or impossible, as is often the case with "naked" organisms that generally alter their shape on fixation, groups according to size and shape were constructed within the lowest recognizable systematic category and sketches were made of all different organisms. Unidentifiable ciliates were counted as rounded, conical or oval ciliates. In addition all ciliated protozoans were coarsely grouped in two size classes (smaller or larger than 40 µm). Population abundances are expressed as organisms m^{-3}. Because losses of ciliates can occur due to fixation (e.g. Dale & Burkill 1982) the numbers reported here should be considered as minimum estimates. Data collected at the open water stations are presented as monthly means for the three east and the three west stations; the data from Port Erin Bay (n=101 samples) are presented as weekly means. Numbers are plotted on a logarithmic scale: records of 1 organisms m^{-3} include those counts where the organisms was just present.

The Wilcoxon rank test (Zar, 1984) was used to compare the abundance of ciliate species or groups of species on the west and east side.

3.2.4. Identification of tintinnids

Tintinnids were identified according to lorica structure. Marshall (1969) and Kofoid & Campbell (1929) served as main references for general identification and the recommendations of Bakker & Phaff (1976) were followed for some species of the genus *Tintinnopsis*. Hedin (1974), and Faure-Fremiet (1924) were also helpful for the identification of some species. Nomenclature is according to Marshall (1969).

During 1987 and 1988 enrichment experiments were frequently carried out in an attempt to isolate tintinnid species for culturing purposes. Approximately 10 l water-samples, were taken from the water reservoirs of the Marine Biological Station or the jetty in Port Erin Bay, prescreened through a 140 µm mesh to remove large predators, concentrated 10-fold by slow reverse-flow filtration (See chapter 1) and incubated in situ with the addition of a suspension of the haptophycean *Isochrysis* sp. Samples were inspected a week later and when tintinnid growth had occurred

individual specimens were isolated with a micropipette, inocululated in 100 ml containers with *Isochrysis* as their only food, and cultured in a costant temperature room at 15 °C on a 12 hours light cycle. By this technique a culture of *Tintinnopsis beroidea* was obtained which lasted for several months.

3.2.5. Identification of naked ciliates

During 1988, concentrated water samples were fixed at approximately monthly intervals with a 2 % osmium tetraoxide solution in a 0.1 M Cacodylate buffer containing 0.01 % calcium chloride made up in 27 % sucrose (Dr. Carey, pers. comm.) for identification of naked ciliates. Sea water samples for such observations were taken from the jetty in Port Erin Bay, or from plastic enclosures (1-10 m^3) held in the sea water reservoirs of the Marine Biological Stations (These were designed to stimulate plankton growth and nitrate and phosphate were periodically added to them). According to the abundance of ciliates in these samples or in Port Erin samples, of various size (1-10 l) were immediately concentrated to a few ml by gentle slow reverse filtration (Dodson & Thomas, 1964) using fractionating screens consisting of a nylon mesh (5 or 20 µm) mounted on plastic cylinders 15 or 25 cm in diameter. N pressure was applied and the fractionator was allowed to sink by gravity. According to overall plankton abundance, concentration of a 10 l sample to approx. 10-20 ml took between 1 and 2 hrs. The whole procedure was carried out in a temperature controlled room. Fixative was added immediately after concentration had been achieved. The final concentration of fixative added to the concentrated sample did not appear to be critical. Two ml additions to 10 ml of sea water was the proportion most often used. In other cases cells were micropipetted directly from the sea water into the fixative. Longitudinally oriented specimens were examined under x 400 and x 1000 magnification using a Leitz Dialux 20 EB microscope. Diagnostic features for identification were: somatic length, somatic width, cell shape, the placement and kynetid structure of the girdle, the placement and length of the ventral kinety, the

position of trichites and when recognizable the shape and number of macro and micronuclei. Identification was according to Kahl (1935), Maeda & Carey (1985) and Maeda (1986). Other useful references were Faure'-Fremiet (1924), Corliss (1979), Lynn & Montagnes (1988) and Lee *et al.* (1985).

Replicate samples were always fixed with Lugol and comparison with the osmium fixed material was later used to identify the most abundant taxa in the preserved samples. As a permanent record slide photographs were taken of all the most abundant naked ciliate species in Osmium fixed samples and all tintinnid species were drawn using a camera lucida attached to a Zeiss model D-7082 microscope.

3.3. RESULTS

3.3.1. Ciliate dynamics at the open water stations

a. The naked ciliates

The seasonal distribution of total ciliate abundance along the transect for the period 1986-1987 is presented in Fig. 14. The winter months were characterized by very low ciliate abundances. Average ciliate numbers were always lower than 10^6 organisms m^{-3}. In late April 1986 ciliate numbers rapidly increased and by early May peaks of more than 2×10^7 organisms m^{-3} were often observed. Such high numbers were observed throughout the summer, until August-September. During this period however, minimum values as low as 10^6 organisms m^{-3} were also observed. Abundances lower than 10^6 organisms m^{-3} were observed throughout late autumn and early winter. Highest values in 1986 were observed in June, highest values in 1987 in July. Significantly ($p < 0.001$) higher numbers of ciliates were observed at the western rather than the eastern transect of stations. Whereas at the latter mean concentrations never exceeded 5×10^6 organisms m^{-3}, during the summer mean values at the western transect were always higher than 5×10^6 organisms m^{-3} and peaks as high as 10^7 were not infrequent.

b. The Tintinnids

The seasonal cycle of tintinnids at the open water stations is presented in Fig.15a. No statistically significant difference was observed in the abundance of total tintinnids between the western and the eastern side. Except for a very clear minimum in June and July, the seasonal cycle of total tintinnids did not show any consistent pattern. Monthly means never exceeded 2×10^5 organisms m^{-3}. Highest concentration in discrete samples was 2.5×10^5 organisms m^{-3} in March 1988. In total, concentrations exceeded 2×10^5 organisms m^{-3} on only three occasions.

The tintinnid fauna was typically neritic. In all seventeen species, representing

10, genera were identified (Table 6). Of these, seven were recorded only once or twice: *Favella ehrenbergii, Favella serrata, Helicostomella subulata, Salpingella acuminata, Tintinnopsis baltica, Tintinnopsis* spp. and *Xystonellopsis* sp.; another, *Tintinnopsis campanula,* was found less than 10 times. *Stenosomella nivalis* was the overwhelmingly dominant taxon and usually accounted for over 90 % of total tintinnid numbers (Fig.15b). For most of the year monthly means of abundance ranged between 1 and 5 x 10^4 organisms m^{-3} and only during autumn and spring values were higher than 5 and occasionally 10 x 10^4 organisms m^{-3}. As for the seasonal cycle of total tintinnids lowest densities were found in summer when values of abundance were lower than 10^4 organisms m^{-3} or totally absent.

Table 7 shows the tintinnid species composition at each station during the whole study period. Because the species composition and the seasonal cycle of abundance of tintinnid species did not differ between the open water stations and Port Erin Bay the seasonal cycle of other species is described for Port Erin where a more detailed set of data was available.

3.3.2. Ciliate dynamics in Port Erin Bay.

In this study, a more detailed account of the dynamics of ciliates was obtained by identifying to species or genus level all the most abundant organisms and by taking daily to weekly samples.

a. The naked ciliates

Dominant naked ciliate taxa

Although all species of naked ciliates are distorted to a lesser or greater degree in fixed samples most specimens retain certain characters by which it is possible to identify them, in some cases even down to species level. For example even the smallest specimens of *Myrionecta rubra*, which are so delicate that the simple pressure of a coverslip can destroy them (Dale & Burkill 1982), retain their equatorial ciliary

fringe when their body shape is very poorly preserved. By utilizing such characters and by comparing samples fixed with Lugols and Osmium tetroxide it was possible to describe the seasonal cycle for some of the dominant species or groups of planktonic oligotrichs ciliates. The following species or groups of species were used to characterize the seasonal cycle of naked ciliates in Port Erin Bay;

Family Strobilidiidae

***Lohmaniella* spp.** - In this group there was an overwhelming dominance of *Lohmaniella oviformis* (diameter approx. 30 µm). Observed in all samples studied, this species was often very well preserved in the Lugols iodine fixed samples. This group also included some *Lohmaniella spiralis* (dia. approx. 50 µm) but this species was only very seldom recorded and always in low abundances. This larger species also was fairly easily recognizable in the Lugols fixed samples. Its abundance, however, was never very high.

Family Strombidiidae

Strombidium "conicum" - This group includes all species of *Strombidium* larger than 40 µm with a distinct conical shape. Osmium samples always showed that *S. conicum* (max. length 60 µm; max. width 30 µm) was the overwhelmingly dominant species but from March to May approximately equal numbers of *Strombidium reticulatum* (max length 60 µm; max. width 45 µm) were also observed.

Strombidium "delicatissimum" - This small *Strombidium* species was present in every month. Because the difference between *S. delicatissimum* and *S. vestitum* rests on size only, a poor parameter to distinguish between different ciliate species (Dr. Carey, pers. comm.), this taxon groups all small species of *Strombidium* whose size ranged between max. length 35 µm and max.width 20 µm and might possibly include both species. In fixed samples such organisms were characterized by the

clearly visible polysaccharide platelets.

Strombidium strobilum - Because of its size (max. length 140 μm) this species is probably the best studied ciliate organisms in the literature (Rassoulzadegan 1977). In this study this species was nearly always easily recognizable.

***Strombidium* spp.** - This group includes species of *Strombidium* which were not possible to identify or which were present in low concentrations. A species always observed in Osmium-fixed samples was *Strombidium sulcatum* (max. length 50 μm) but its numbers were always extremely low. In fixed samples this species wa distorted in a very distinctive manner and it was therefore possible to obtain an approximate idea of its concentration which never exceeded 5×10^5 organisms m^{-3}. Other identified species occasionally observed or present in low concentrations were *Strombidium cornucopiae* (Dr. Carey, pers. comm.), *Strombidium crassulum, Strombidium opisthostomum* (recorded only in May) *Strombidium conicoides* (observed only in samples from the sea water storage ponds during summer).

Family Mesodiniidae.

Myrionecta rubra (Dr. Carey pers. comm.). - As already reported by a number of authors (Leegard 1920; Michanek 1965; Lindholm 1981) a great variability was observed in the size of this photosynthetic ciliate (formerly *Mesodinium rubrum*). In order to distinguish between forms two size classes were considered: organisms < 30 μm were referred to as *M. rubra* forma minor; organisms > 30 μm as *M. rubra* forma major. This species was fairly distinguishable in preserved samples because of the presence of the equatorial ciliary fring. Even organisms in very poor condition could generally be described.

Hypotrich ciliates Hypotrich species such as *Lachrymaria* spp., *Tiarina meunieri,* and others were often recorded but their abundance was always very low. These species

were classified as "Other ciliates" but because of their very low abundance they do not appear in any of the graphs or tables.

Seasonal dynamics

As shown in Fig.16 non-loricate species made by far the most important contribution to total ciliate numbers for most of the year.

In terms of abundance their seasonal cycle was characterized by highest abundances in summer with mean weekly abundances never exceeding 2 x 10^7 organisms m^{-3} (Fig. 17). Concentrations started to increase in late February and were higher than 10^6 organisms m^{-3} until the end of September. Highest mean values were 1.7 x 10^7 organisms m^{-3} in June but discrete samples reached concentrations as high as 3 x 10^7. Although from October onwards concentrations declined to less than 10^6 organisms m^{-3} isolated peaks could be observed until late December. Lowest concentrations were reached during the period from January to March when abundance were always lower than 5 x 10^5 organisms m^{-3}. Significantly ($p < 0.001$) higher numbers of total ciliates were observed at the western rather than the eastern stations.

In terms of species composition the seasonal cycle of ciliates was characterized by the overwhelming dominance of the genus *Strombidium* followed by the genus *Myrionecta* and the genus *Lohmaniella* (Fig. 16). All three of these genus were present almost at any time of year. The seasonal cycle for some of the species belonging to these genera are shown in Fig. 18 and 19. For most of the year the genus *Strombidium* was the overwhelmingly dominant taxon. The genus *Myrionecta* was most important during the summer months when it accounted for between 25 and 60 % of total ciliate abundance. The contribution of the genus *Lohmaniella* did not show any particular pattern but highest numbers were observed during late spring. Lowest % contribution to total ciliates was observed in late autumn (< 4 %) and highest in January, April and May (31 to 36 % of total). The summer maximum was characterized by a succession of peaks of different species. The first in earlyMay was

due to a bloom of the small *Lohmaniella oviformis* and *Myrionecta rubra* which in weekly means of abundance reached approximately 5 x 10^7 organisms m^{-3} and in discrete samples (see appendix) approximately 10^7 organisms m^{-3}. This peak was followed by a smaller one due again to a second peak of *Lohmaniella oviformis* and to the increase in numbers of *Myrionecta rubra* and *Strombidium "conicum"*. The following was centered in the second half of June and was mainly due to a bloom of the small *Strombidium "delicatissimum"* which reached a maximum concentration of 10^7 organisms m^{-3}. The successive peak in the first half of July was mostly due to *Myrionecta rubra* (in particular *Myrionecta rubra* forma major reaching concentrations as high as 6 x 10^6 organisms m^{-3}. Minor peaks of less than 2 x 10^6 organisms m^{-3} by *Strombidium "delicatissimum"* and *Strombidium* spp. also contributed to this peak. August and September were characterized by high numbers of all species of *Strombidium,* and *Strombidium* spp. and *Strombidium "conicum"* in particular reached at this time their highest annual concentrations.

Despite the fact that the highest peaks in abundance were due to small ciliate species (approx. < 40 μm) on an annual base the percentage contribution of large species (approx. > 40 μm) was significantly higher ($p < 0.02$) than that of smaller species. Although such a result might be due to the fact that small organisms might be more easily overlooked than the larger specimens, observations at magnifications higher than those usually used for routine counting (600-400 X instead of 150-200 X) no evidence was ever observed of small species being underestimated.

b. The tintinnids

Values of abundance in Port Erin Bay (Fig. 21a) did not differ from those observed at the open water stations. As for the offshore stations minimum values were observed during summer, especially in August, when tintinnids were almost completely absent from the samples. Except for the presence of *Tintinnus inquilinum* no differences were observed in terms of tintinnid fauna. *Stenosomella nivalis* was again the overwhelmingly dominant species and it frequently accounted for 90 % of

total tintinnid numbers. Its seasonal cycle is shown in Fig.21b). As for the open water stations no apparent differences were observed with the seasonal cycle of total tintinnids. Lowest concentrations were also found during summer when it was often completely absent in discrete samples. The exceptionally high peak in August 1988 (1.5×10^6 organisms m^{-3}) was almost entirely due to this species. Only three species other than *Stenosomella nivalis* ever exceeded 5×10^4 organisms m^{-3} in discrete samples; *Tintinnopsis nana, Leprotintinnus pellucidus* and *Stenosomella ventricosa.*

Tintinnopsis nana was the second most abundant species and although in very low numbers, it occurred in every month of the year (Fig. 22a). Bakker & Phaff (1976) consider the existence of this species to be problematic and suggest it should be considered a form of *Tintinnopsis beroidea.* In this study, however, due to the large size difference of lorica as well as ecological characteristics it is considered a distinct species. Except for March and April 1988 when its abundances in discrete samples from Port Erin Bay frequently exceeded 2×10^5 organisms m^{-3}, weekly means throughout the rest of the study period were always $< 10^5$ organisms m^{-3} with peaks $> 5 \times 10^4$ organisms m^{-3} only occasionally observed. In both years *Leprotintinnus pellucidus* was recorded only between January and March (Fig.22b). During these months weekly means of abundance were always $< 5 \times 10^4$ organisms m^{-3} with just one peak of approximately 10^5 organisms m^{-3}. On three occasions densities $> 2 \times 10^5$ organisms m^{-3} were recorded in discrete samples. *Stenosomella ventricosa* was rarely recorded during the first six months of the year but it gradually became more abundant from July until November when it occurred in almost every sample (Fig.22c). Weekly means exceeded 5×10^4 organisms m^{-3} only on one occasion. Discrete samples contained more than 5×10^4 organisms m^{-3} only on three occasions. All the other species recorded occurred only during restricted periods of time and when present were usually rare. Table 3 shows any month when they were found and their highest concentration in any one discrete sample. *Codonellopsis lusitanica* was recorded only during 1986 and except for a peak of approx. 3×10^4 organisms m^{-3} in September,

abundances were always < 10^4 organisms m^{-3}. *Codonellopsis pusilla* was only recorded in the open water stations and never exceeded 10^4 organisms m^{-3}. *Ptychocylis* sp. was frequently recorded but except for a peak of approx. 4 x 10^4 organisms m^{-3} in May 1987, its values of abundance were always very low. *Tintinnidium mucicola* was only seldom observed and only in very low numbers. Always present in very low numbers *Tintinnus inquilinum* was only occasionally observed in samples collected in Port Erin Bay. In the storage ponds, however, this species was found throughout the year and it occasionally exceeded 10^5 organisms m^{-3}.

Whereas in samples collected along the transect and in Port Erin Bay *Tintinnopsis beroidea* was always present in very low numbers, it was generally the dominant species in samples collected from the storage ponds of the Marine Biological Station. In these enclosed systems total tintinnid abundances of > 10^6 organisms m^{-3} were repeatedly observed during the summer. Maximum abundance ever recorded was 2.5 x10^6 organisms m^{-3} and *Tintinnopsis beroidea* accounted for 80 % of the total number of tintinnids.

Of all species *T. beroidea* exhibited the highest degree of morphological variability. The most common appearance was specimen d of fig. 2 from Bakker & Phaff (1975) but specimen c, f and h of the same series were also frequently observed. Contrary to the "wild" specimens which were characterized by the presence of agglutinated particles and by pointed aboral ends cultured specimens had completely hyaline loricas, rounded aboral ends and displayed great variability of lorica length (40-110 µm in length). These specimens were very similar in appearance to specime a, c and e of fig. 3 of Bakker & Phaff (1975). Other species characterized by a large variability in the shape of the lorica were *Pthycocylis minor* and although only very seldom observed *T. campanula*. All other species, however, showed some degree of variations in lorica size and shape.

3.4. DISCUSSION

Because few quantitative studies have been conducted on the ecology of naked ciliates in marine ecosystems, comparison with other areas is not easy. In the Kiel Bight Smetacek (1981) found that total ciliate cell numbers ranged from 2 to 28 x 10^6 and 2 to 20 x 10^6 cells m^{-3}, respectively during the spring and the autumn maxima in 1973, and from 17 to 92 x 10^6 cells m^{-3} prior to the spring bloom in 1974; tintinnids were never important. In the northern Adriatic Sea Revelante & Gilmartin (1983) found abundances of non-tintinnid ciliates of 0.018 - 2.02 x 10^6 organisms m^{-3} during winter when primary production was low and the water column vertically mixed, and 0.097 - 39.28 x 10^6 organisms m^{-3} during summer when the water column was stratified and the phytoplankton biomass higher. In the north-west Mediterranean Rassoulzadegan (1977) reported maximum concentrations of 120 x 10^6 cells m^{-3}, with an annual mean estimated around 4.6 x 10^6 cells m^{-3}. Record numbers of ciliates were found by Dale & Dahl (1987) during a red tide in a bay in southern Norway where *Strombidium reticulatum* alone reached abundance values of 12.4 x 10^8 organisms m^{-3}.

Contrary to naked ciliates much more information is available for tintinnids. The range of tintinnid community abundance recorded in the literature is large and reflects the greater diversity of marine environments studied. At the lower end of this range, Hedin (1975) found between 5 and 40 x 10^3 tintinnids m^{-3} throughout the year on the Swedish west Coast. Abundances of the same order of magnitude have been reported from the Gulf of Panama (Smayda 1966), the Peru upwelling region (Beers *et al.* 1971), the Scotian shelf (Johansen 1976), the Adriatic Sea (Krisnic 1987a,b) and open waters (Beers & Stewart 1971; Taniguchi 1977). In comparison, maximum abundances above 10^7 organisms m^{-3} have been reported for the eastern Mediterranean (Vitiello 1964), the Sea of Azov (Zenkevitch 1963), Long Island Sound (Capriulo & Carpenter 1983), Bedford Basin (Paranjape 1980), Halifax Harbour, (Johansen

1976), southern California nearshore waters (Heinbokel & Beers 1979), and the sea of Japan (Sorokin 1977). In comparison, Verity (1987) recorded fluctuations between 10^5 and 10^8 organisms m^{-3} in Narragansett Bay, Rhode Island. Even higher populations have been reported by Dale & Dahl (1987) who found that during a "red tide" of oligotrichous ciliates in a bay in southern Norway, *Tintinnopsis beroidea* alone reached a maximum abundance of 7×10^8 organisms m^{-3}.

In the present study numbers of naked ciliates exceeded 10^7 organisms m^{-3} only during late spring and early summer, and highest density ever recorded in a discrete sample was 2.8×10^7 organisms m^{-3}. Tintinnids exceeded 5×10^5 organisms m^{-3} only on one isolated occasion. Although by comparison, such values fall at the lower end of the range of values mentioned above, the importance of ciliates in the study area might still be very important.

Grazing by microzooplankton in general has been proposed as a mechanism regulating nanoplankton populations in Canadians waters (Blackbourn 1974; Johansen 1976), but estimates of their grazing impact are indirect and range from < 10 to 100 % of net primary production. The only annual estimates suggest consumption of 60 % of total phytoplankton production in the Solent Estuary (Burkill 1982), 27 % of production in Long Island Sound (Capriulo & Carpenter 1983) and 62 % in Narragansett Bay (Verity 1986). The impact oligotrichous and tintinnid ciliates have on the pelagic food web can be understood by combining laboratory experiments with *in situ* population densities. Studying the clearing rates of oligotrichous ciliates Jonsson (1986) found that three common species (*Strombidium reticulatum, Strombidium vestitum* and *Lohmaniella spiralis*) fed on particles ranging from 1 to 15 µm. By multiplying the clearing rates found for these species by the densities of oligotrichous ciliates found in Rassoulzadegan (1977), Smetacek (1981) and his own observations, he estimated that roughly oligotrichous ciliates could remove 10 to 35 % of the phytoplankton biomass per day.

Reid (1987) demonstrated that cysts of oligotrichs appear to be present in the water column throughout the year. Given their fast developmental rates and the

presence of a seed for whenever conditions become favourable, ciliates can therefore respond extremely quickly to changes in the food environment and exert a considerable impact on phytoplankton standing stocks. An example of the potential importance of protozooplankton in pelagic ecosystems is given by Smetacek *et al.* (1980). Studying plankton dynamics in enclosed ecosystems they report that a population of the oligotrich ciliate *Lohmaniella* sp. by maintaining a cell division rate between 1.5 and 3 day^{-1} attained a biomass of 157 mg m^{-3} within 4 days, reducing the phytoplankton standing stock (in terms of chlorophyll *a*) from 6.6 to 2.2 mg m^{-3} in the process. After attaining its maximum, the ciliate population practically vanished in 3 days. Phytoplankton standing stock in the tank increased sharply to 6.0 mg m^{-3} immediately following the decline of the ciliate. Organisms with such potential filtration rates can clearly exert a profound impact on phytoplankton standing stock. Because these organisms can react much faster to any sudden increase in the food supply than the metazooplankton, given the "patchiness" in phytoplankton production in the north Irish Sea, naked ciliates, by reacting much faster to any sudden increase in the food supply than any other zooplankton group, might bypass copepods and ensure a link between the phytoplankton and higher trophic levels.

At present little is known about the factors that determine seasonal and regional changes in standing stock. Some authors have found significant correlations between ciliate abundance and several parameters such as food supply (Smetacek 1981; Verity 1987), physical factors (Kurahawa *et al.* 1975) and predation (Smetacek 1981). Conflicting evidence from several studies however does not yet allow any definite generalizations to be made and it is most likely that changes are due to a complex interplay of a great number of factors.

Without doubt food supply is a major factor in control of ciliate dynamics and recently a large number of studies have concentrated on this aspect, on the basis of laboratory breeding or the study of natural populations.

All studies on ciliate feeding have emphasized the importance of size. Spittler (1973), Heinbokel (1978b) and others have shown that tintinnids can only graze

particles approximately < 40-45 % of the oral lorica diameter. Since the oral diameter of most tintinnid species is between 10 and 50 μm these organisms are believed to graze mainly on nanoplankton size particles. Such laboratory findings have been supported by several authors, who have found significant correlations in the field between nanophytoplankton (< 20 μm) and ciliate abundance (e. g. Verity 1987). In contrast such a restriction in the size of food does not seem to apply so much to the larger non-loricate ciliates that can adapt their shape to that of the ingested particles. It is well known that naked ciliates are capable of ingesting cells their own size and even larger, and that for some species this is the rule rather than the exception (Kahl 1935; Mackinnon & Hawes 1961). The latter authors and Gifford (1985) also report that some ciliate species that are normally bacterivorous become cannibalistic when other food is scarce.

Since the oral diameters of the dominant tintinnid species in the study area, *Stenosomella nivalis* and *Tintinnopsis nana,* are respectively approximately 16-21 and 12-19 μm (Marshall 1969) these species would be limited to graze only particles w maximum diameter of 5 - 9 μm. Although size constraints would then limit these t species to microflagellates or to the smaller diatoms and dinoflagellates, the size of the phytoplankton particles that characterized the seasonal succession of species would not have been a limiting factor for larger tintinnid species such as for instance *Pthycocylis* sp., whose lorica diameter of 90 μm would have enabled it to graze on a wide size selection of phytoplankton species. Clearly factors other than size must be important.

Although diatoms made up most of phytoplankton standing stock it is unlikely, because of their size, that their contribution to the diets of tintinnids and oligotrichs in general was significant. Although this point has not been yet rigorously examined, little and conflicting evidence exists as to whether or not diatoms are a suitable food for oligotrichous ciliates in general. Blackbourn (1974) rarely observed diatoms in the gut contents of field collected specimens of tintinnids. Similarly Smetacek (1981) observed that naked ciliates were found only occasionally with ingested diatoms. Johansen (1976) reported that tintinnids could not be maintained on a pure culture of

diatoms. Gifford (1985) found that when the diatoms *Thalassiosira pseudonana* and *Thalassiosira weissflogii* were used as food, growth rates of naked ciliate species were either slight or negative. In contrast to these findings, Fenchel (1968) reported that interstitial oligotrich ciliates were commonly observed with pennate forms lacking spinose processes; Verity & Villareal (1986) found that for the two tintinnid species *Tintinnopsis acuminata* and *Tintinnopsis vasculum,* diatoms were a good food, provided that size was not a limiting factor. In their experiments neither species grew when fed thread or setae-bearing diatoms but grew well at rates similar to those for small prymnesiophytes when fed species lacking such projections. That size rather than nutritional inadequacy was responsible for the lack of growth on thread bearing diatoms was clearly shown by the fact that both tintinnids grew well when fed the same diatoms with threads reduced by culture on a shaker table.

The absence of any correlation between the abundance of heterotrophic ciliates and the abundance of diatoms is particularly clear on the occasion of the diatom bloom in May 1988 (Fig. 12), when, despite chlorophyll *a* values of 8 mg m^{-3}, and an initial high ciliate population that could have acted as a seed, no changes were observed in total ciliate abundance. The dominance of *Rhizosolenia delicatula* at this time and the dominance of diatoms throughout the phytoplankton succession strongly suggests that phytoplankters in this size class are not efficiently grazed by these organisms.

Although the relative plasticity of their mouth due to the absence of a lorica might be an important factor favouring the dominance of naked ciliates in the study area, the low abundance of tintinnids also during summer, when microflagellates were often present in high numbers (> 10^9 cells m^{-3}) cannot be attributed just to size and suggest that another factor must be important. In contrast to diatoms microflagellates are a very good food for tintinnids (Blackbourn 1974; Johansen 1976; Heinbokel 1978 a). Although in the present study during late spring-early summer such phytoplankters often reached concentrations of > 10^{10} cells m^{-3}, comparable to those found associated with much higher tintinnid numbers (Verity, 1987), they also failed to support higher tintinnid abundance. The absence of a tintinnid "bloom" in such conditions is quite

surprising, especially in consideration of the fact that at the same time the non-loricate species reached abundances well above 10^7 organisms m^{-3}. Also the importance of microflagellates for naked ciliates is shown by the consistently higher numbers to the west than to the east transect where these phytoplankters were more abundant. Since the nutritional value of different phytoplankton species can differ greatly it might be possible that the quality of such particles in the study

area, while suitable for non-loricate species, was not ideal for tintinnids. Blackbourn (1974), Johansen (1976) and Heinbokel (1978 a) reported that while the haptophytes *Isochrysis, Dicrateria* and *Pavlova* supported rapid growth rates for some tintinnids, other species such as *Dunaliella* were not equally good food items and other species such as chroococcoid cyanobacteria caused 100% mortality. Similarly Scott (1985) reported that while the naked ciliate *Strombidium* sp., isolated from a rock-pool, grew well on *Pavlova,* it would not grow on other rock-pool algae such as *Isochrysis* and *Dunaliella.* The lethal effects of the red tide flagellate *Olisthodiscus luteus* on the growth and abundance of tintinnids have been the object of detailed studies by Verity & Stoecker (1982).

The absence of a summer dinoflagellate-dominated phytoplankton assemblage might also be an important factor limiting the abundance of tintinnids. Hitchcock (1982), has clearly shown that diatoms and dinoflagellates differ greatly in their nutritional value : diatoms contain half the caloric value of a dinoflagellate on a per cell basis, and have less protein, carbohydrate and lipid on a per cell basis. Very specific dietary requirements have been shown for the tintinnid *Favella* which requires dinoflagellates for growth (Stoecker *et al.* 1981; Gold 1969,1970). Also fine scale spatial correlations have been found between planktonic ciliates and dinoflagellates (Stoecker *et al.* 1983). Tintinnids in the genus *Favella* are often associated with dinoflagellate blooms. In the Bay of Fundy, *Favella* sp. prey on the dinoflagellate *Gonyaulax tamarensis* (=*Gonyaulax excavata* of some authors) and coincide in abundance with dinoflagellates (Needler 1949; Prakash 1963; White 1979). Oligotrichs were reported to co-occur with large dinoflagellates by Johansen (1976),

Stoecker *et al.* (1984) and Gifford (1985). Blackbourn (1974) observed that *Favella serrata* was usually associated with high dinoflagellate numbers in British Columbia. Selective predation has been demonstrated for *Favella ehrenbergii* on and among dinoflagellates (Stoecker *et al.* 1981). Dinoflagellates might therefore be very important in the diet of tintinnids.

The fact that tintinnid species were limited to restricted periods of the year might be due to their adaptation to utilize certain types of food only.

Although little is known about the different nutritional value of different phytoplankton species recent studies strongly suggest that this might be important in determining the abundance of the ciliated protozoans. Many ciliate species, for instance, vary greatly in abundance over short periods of time. Their fast generation times (Gold 1970, 1971) and ability to encyst (Reid & John 1978; Paranjape 1980; Reid 1987) may be an evolutionary strategy to allow them to specialize on particular taxonomic group of algae.

From theoretical considerations of ciliate filtering capabilities as well as from results of laboratory feeding experiments (Fenchel 1980; Berk *et al.* 1976; Gast 1985; Jonsson 1986) pelagic ciliates have been characterized as inefficient grazers of picoplanktonic cells. Jonsson (1986) defined the range of particles for three common species as between 1 and 15 μm. In this study the absence of any significant contribution to potential primary production by the small nanoplankton (< 5 μm) suggests that also the smallest of the oligotrichs found in this study (15-20 μm) utilize larger particles.

As for predation, several studies suggest that this can have some impact on tintinnid dynamics. Although in this study it is difficult to assess its role, due to the absence of detailed quantitative data on zooplankton abundance, Robertson (1983) has shown that tintinnids were important contributors to the diet of *Acartia,* a very common species in the Irish Sea (e.g Williamson 1952), only if present at concentrations of > 10^6 organisms m^{-3} and small species in low concentration dominated the phytoplankton. Since neither of these two conditions ever occurred in

this study it might be concluded that predation did not affect significantly tintinnid abundance. However, throughout this study high numbers of loricas were often observed in copepod faecal pellets present in the same concentrated samples. On several occasions when numbers of tintinnids in the field were $< 10^5$ organisms m^{-3} as many as 10^4 empty loricas were observed in faecal pellets in the same concentrated samples. Since these observations were limited to the smallest faecal pellets, the width of which was only slightly larger than the loricas ($\approx$ 50 µm), which suggests that they belonged to nauplii or copeodite stages, numbers of ingested tintinnids could have been higher.

Studying the feeding behaviour of stage I specimens of *Sagitta elegans* and *Sagitta setosa* at the same stations as in this study, Alvares (pers. comm.) found that *Stenosomella ventricosa* was among the most important gut contents of stage I *Sagitta* spp. and larval *Clupea harengus*. As many as 50 empty loricas of this tintinnid species were repeatedly found among the gut contents of specimens of *Clupea harengus* < 10 mm. Stoecker & Sanders (1985) have shown that in laboratory experiments the copepod *Acartia tonsa* fed preferentially on the tintinnid *Favella* sp. rather than on the dinoflagellate *Heterocapsa triquetra*, even when the latter was more abundant in terms of carbon and nitrogen than the tintinnid. Korniyenko (1971), Heinle *et al.* (1977) and Houde & Schekter (1980) have demonstrated that even when tintinnids and other ciliates are not a major constituent of the diet of copepods and fish larvae in terms of carbon, their presence might enhance their survival and growth rates. Tintinnids are consumed by other tintinnids, ciliates, rotifers, polychaete larvae, euphasiids, mussels, pelagic shrimps, clams, tunicates, menhaden and larval fishes (Verity 1987 and references therein). Tintinnids might therefore be an important component of many zooplankton species, and selective predation might be responsible for the low tintinnid abundances in summer, when most zooplankton groups reach their highest abundance.

The impact of predation on the abundance of the naked ciliates is even more difficult to assess. Despite their abundance in the plankton few zooplankton species at

present have been shown to utilize them as a food source. It has been shown that the ciliated protozoan *Uronema* is eaten by the copepod *Eurytemora* (Berk *et al.* 1977) and that *Daphnia* feed on *Paramecium* and *Cyclidium* (Porter *et al.* 1979). Heinle *et al.* (1977) found that a diet of ciliates permitted production of eggs by the estuarine calanoid copepod, *Eurytemora affinis,* and that the magnitude of egg production was comparable to that obtained when the copepods fed on phytoplankton alone. The feeding rate of *Acartia* was increased using tintinnids as food at a concentration of 10^6 m^{-3} (Robertson 1983). The copepod *Scottolana canadensis* produced eggs more frequently when ciliated protozoa were given as food than when only microalgae were available (Heinle *et al.* 1977). These pioneering studies show that naked ciliates also can be very important in the diet of several zooplankton species. Given their abundance in the plankton in the study area it is thus very probable that their role in pelagic food webs as contributors to the diet of zooplankton species in the north Irish Sea is very important.

Several authors have tried to explain seasonal variations in standing stock by relating abundance to physical factors such as temperature or salinity. Although in some cases significant correlations have been found (Stoecker *et al.* 1984; Krisnic 1987; Sanders 1987), Hargraves (1981) suggested that the most direct effect of these factors on tintinnids was most likely to be exerted on annual faunal changes, biogeography and morphology rather than short term abundance changes. Krisnic (1987) reports that in the north Adriatic all the dominant species were present at a wide range of temperature and salinity; *Stenosomella nivalis* (the most abundant tintinnid species in this study) was found within the temperature and salinity ranges of 10.1-19.4° C and 29.3-38.5 ‰. On the Swedish west coast Hedin (1975) reported that *Stenosomella nivalis* was frequent throughout the year, also suggesting that this species can tolerate a wide range of variations. Temperature and salinity variations in the study area in the north Irish Sea are not great; the former varies between 6.5° and 14°C, the latter between 33.55 and 34.68 ‰ (Slinn & Eastham, 1984). Their importance in regulating ciliate dynamics might thus not be so important.

Many other factors are believed to be important in controlling ciliate dynamics but in many cases very little is known about them [e.g. interspecies competition, parasitism etc. (Stoecker & Evans 1985)]. Further studies are clearly required to understand better the factors that regulate the biology of protozoans in marine environments and improved techniques certainly herald a new understanding of their ecology (Gifford 1985). For instance, the recent discoveries of the phenomenon of ciliates functioning as autotrophs strongly suggests radical changes are required about our ideas about the role of protozoans in food chain dynamics. The most thoroughly investigated case of photosynthesis in a marine ciliate involves *Myrionecta rubra.*, and its cryptophyte endosymbiont has been the object of a number of studies (Hibberd 1977; Oakley & Taylor 1978). Photosynthetic chloroplasts, however, have also been reported by Burkholder *et al.* (1967) and Blackbourn *et al.* (1973) for several unidentified oligotrichs, by Faure-Fremiet (1969) for *Strombidium oculatum* and McManus & Fuhrman (1986) for *Strombidium strobilum* (ex *Laboea strobila*). Endosymbiont chloroplasts have also been found in tintinnids by May Silvers and co-workers (in McManus & Furhman 1986). In particular, ciliate photosynthesis has the effect of reducing the number of trophic transfers between primary producers and larger herbivores. This means that plankton surveys which divide microplankton into separate "phytoplankton" and "microzooplankton" categories for the purpose of creating budgets to account for the transfer of material through the planktonic food web may not be accurate if they assume that the ciliates are wholly heterotrophic.

Identification of the complex interplay of factors regulating the ecology of this group is clearly beyond the scope of this descriptive study. It is hoped, however, that the present study, by identifying the importance of this group in the Irish Sea, might provide a basis for future investigations. Several aspects of their ecology seem worth further studies; the absence of a distinctive seasonal pattern; the impact of predation as a possible factor responsible for the absence of tintinnids during early summer. Many factors pertaining to their biology are probably responsible for controlling their occurrence and such aspects cannot be revealed just by observations

of preserved field material. Direct observations of protozooplankton populations under controlled conditions would be necessary for this purpose. Given their potential importance it would certainly be desirable to learn more about the status of protozooplankton in the Irish Sea in relation to other pelagic components.

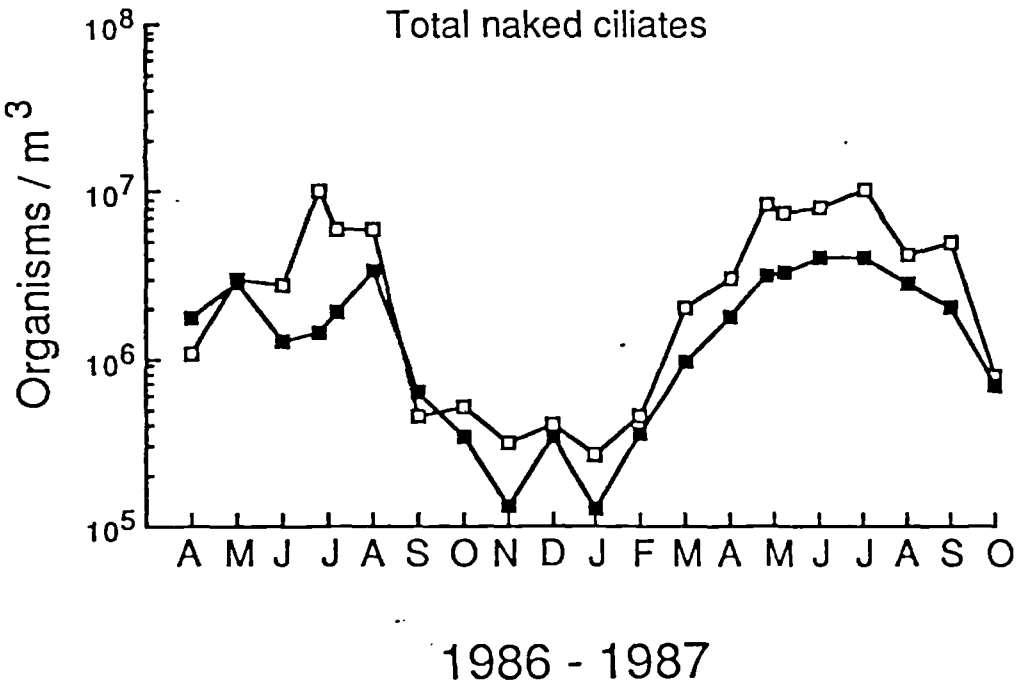


Fig. 14. Seasonal cycle of total naked ciliates at the open water stations. (Empty squares indicate the west transect, filled in squares the east transect.)

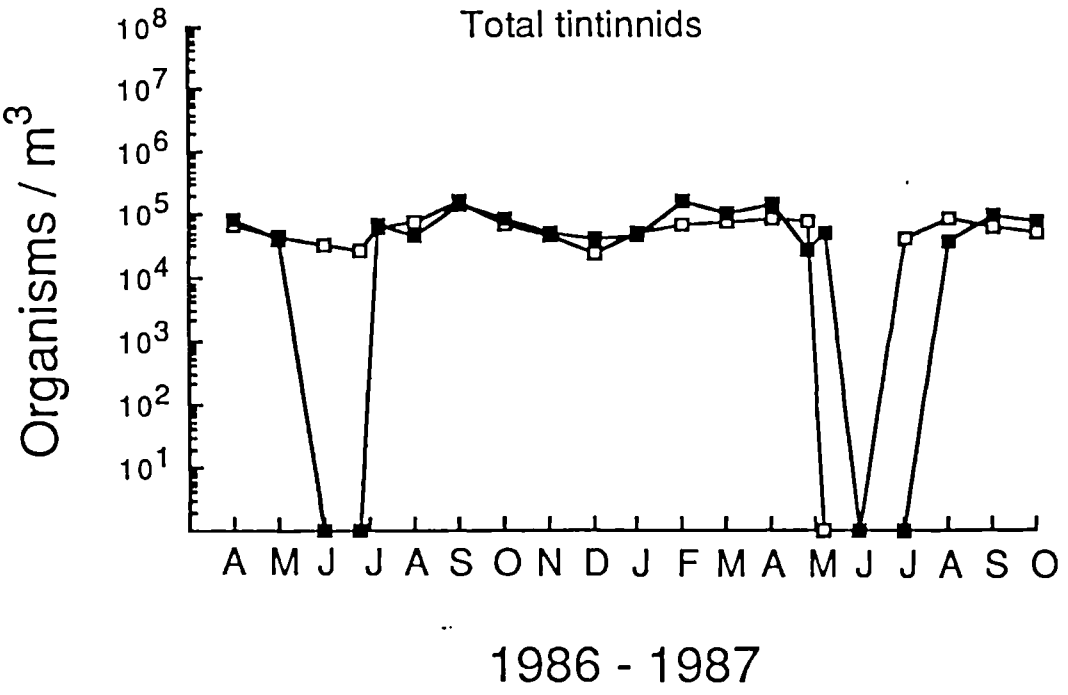


Fig. 15a. Seasonal cycle of total tintinnids at the open water stations. Empty squares indicate the west transect, filled in squares the east transect.)

Codonellopsis lusitanica	Jorgensen, 1924
C. pusilla	(Cleve, 1900)
*Favella ehrenbergii**	(Claparede & Lachman, 1858)
*F. serrata**	(Mobius, 1887)
*Helicostomella subulata**	(Ehrenberg, 1883)
Leprotintinnus pellucidus	(Cleve, 1889)
Pthychocylis sp.	Jorgensen, 1889
*Salpingella acuminata**	(Claparede & Lachman, 1858)
Stenosomella nivalis	(Meunier, 1919)
S. ventricosa	(Claparede & Lachman, 1858)
Tintinnidium mucicola	(Claparede & Lachman, 1858)
*Tintinnopsis baltica**	Brandt, 1896
T. beroidea	Stein, 1867
T. campanula	(Ehrenberg, 1840)
T. nana	Lohman, 1908
Tintinnopsis sp*.	Stein, 1867
Xystonellopsis sp.*	Jorgensen, 1924

Table 6. List of tintinnid species found throughout the study period at the open water stations (* species recorded only once or twice).

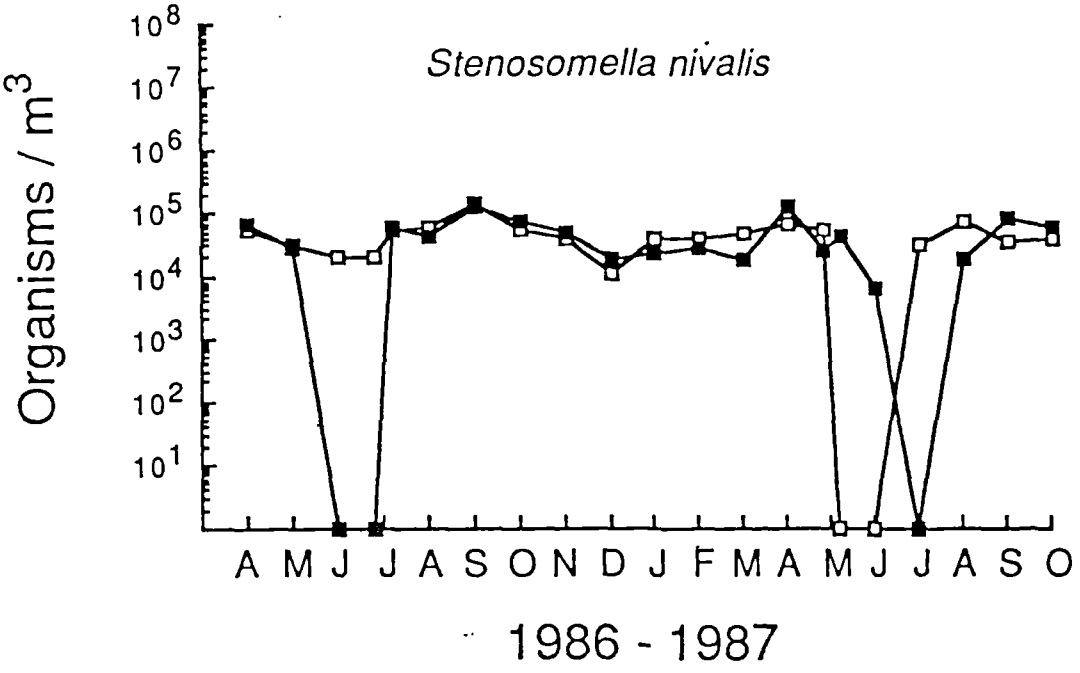


Fig. 15b. Seasonal cycle of *Stenosomella nivalis* at the open water stations. Empty squares indicate the west transect, filled in squares the east transect.)

	J	F	M	A	M	J	J	A	S	O	N	D
Codonellopsis lusitanica	n.s.	n.s.	-	-	-	-	-	-	14	1245	-	-
	-	-	-	-	-	-	-	-	-	15	n.s.	n.s
Codonellopsis pusilla	n.s.	n.s.	-	-	-	-	-	-	-	6	-	-
	-	-	4	25	-	-	-	-	-	-	n.s.	n.s.
Leprotintinnus pellucidus	n.s.	n.s.	123456	13456	-	-	-	-	-	-	-	-
	-	12346	123456	145	-	-	-	-	-	-	n.s.	n.s.
Pthycocylis sp.	n.s.	n.s.	-	-	-	-	-	136	26	-	-	-
	-	-	-	-	24	-	6	-	-	-	n.s.	n.s.
Stenosomella nivalis	n.s.	n.s.	123456	123456	123456	123456	123456	123456	123456	123456	123456	3
	123456	123456	123456	123456	123456	123456	123456	123456	123456	123456	n.s.	n.s.
Stenosomella ventricosa	n.s.	n.s.	256	16	3	-	1	345	123456	123456	123456	156
	4	13	4	2	1	-	3	123	123456	123456	n.s.	n s.
Tintinnidium mucicola	n.s.	n.s.	-	13456	12356	13	-	-	-	-	-	-
	-	-	-	-	1236	24	-	-	-	-	n.s	n.s.
Tintinnopsis beroidea	n.s.	n.s.	35	-	123456	-	-	-	-	-	-	-
	24	4	23456	123456	12356	-	-	3	-	-	n.s.	n.s.
Tintinnopsis nana	1246	123456	13456	123456	13	-	-	346	124	456	1235	4
	26	12345	126	12346	12356	26	-	-	-	123456	n.s.	n.s.
Total tintinnid species	n.s	n.s.	5	5	5	2	2	4	5	3	3	3
	4	5	6	6	6	3	3	3	2	4	n.s.	n.s.

Table 7. Tintinnid species present at each station along the transect during 1986 (above) and 1987 (below). Numbers indicate stations as in Fig. 3. - , absent at all stations; n.s., no samples taken for that month.

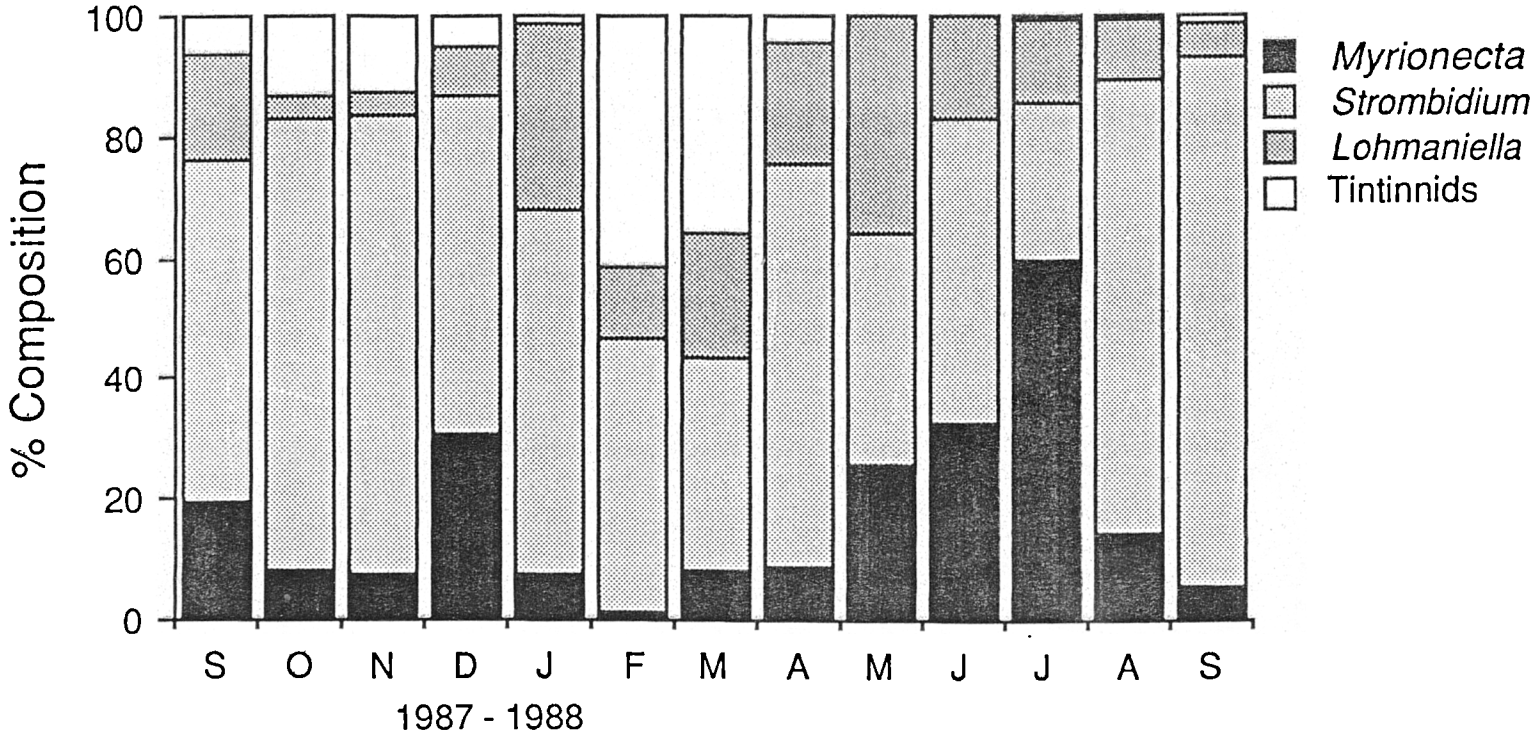


Fig. 16. Percentage contribution of dominant taxa to total ciliate abundance in Port Erin Bay.

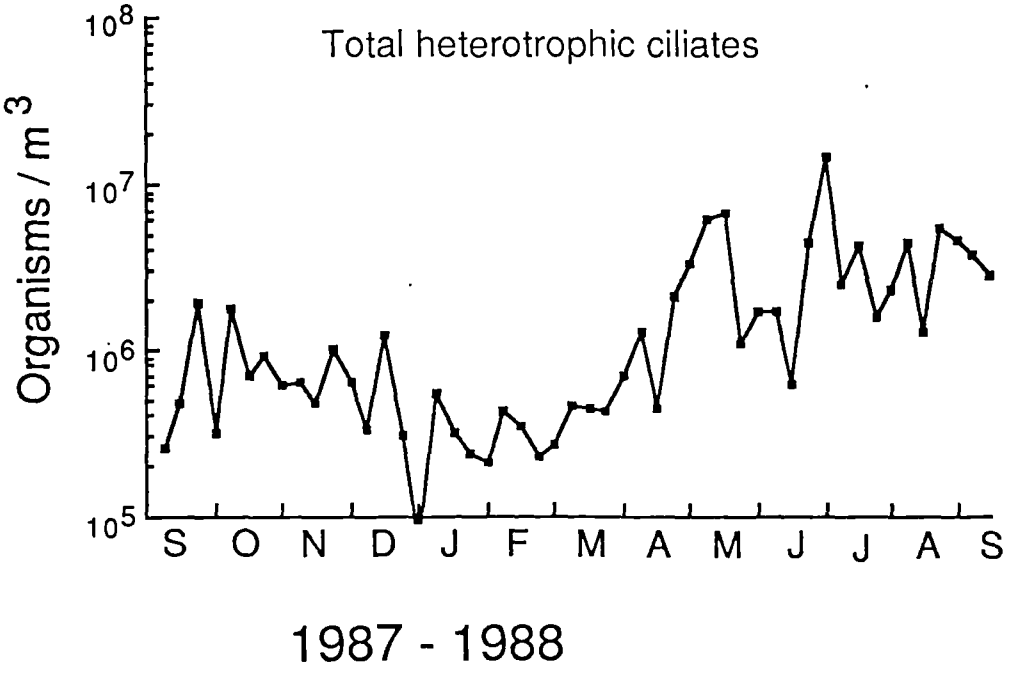


Fig. 17. Seasonal cycle of total heterotrophic ciliates in Port Erin bay.

Fig. 18. Seasonal cycle of major naked ciliate taxa in Port Erin Bay;
(a) *Lohmaniella oviformis*
(b) *Myrionecta rubra*
(c) *Strombidium "conicum"*

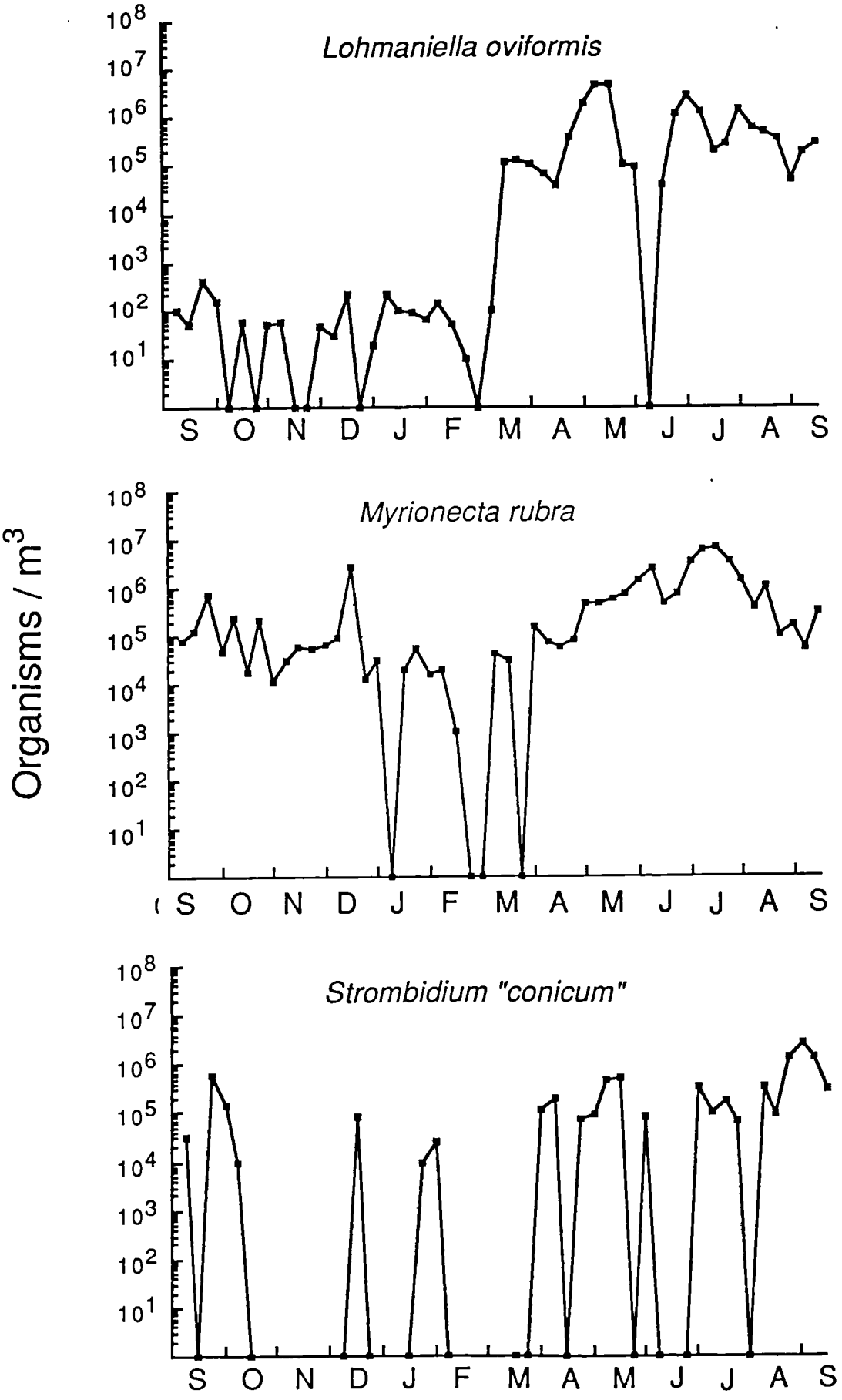
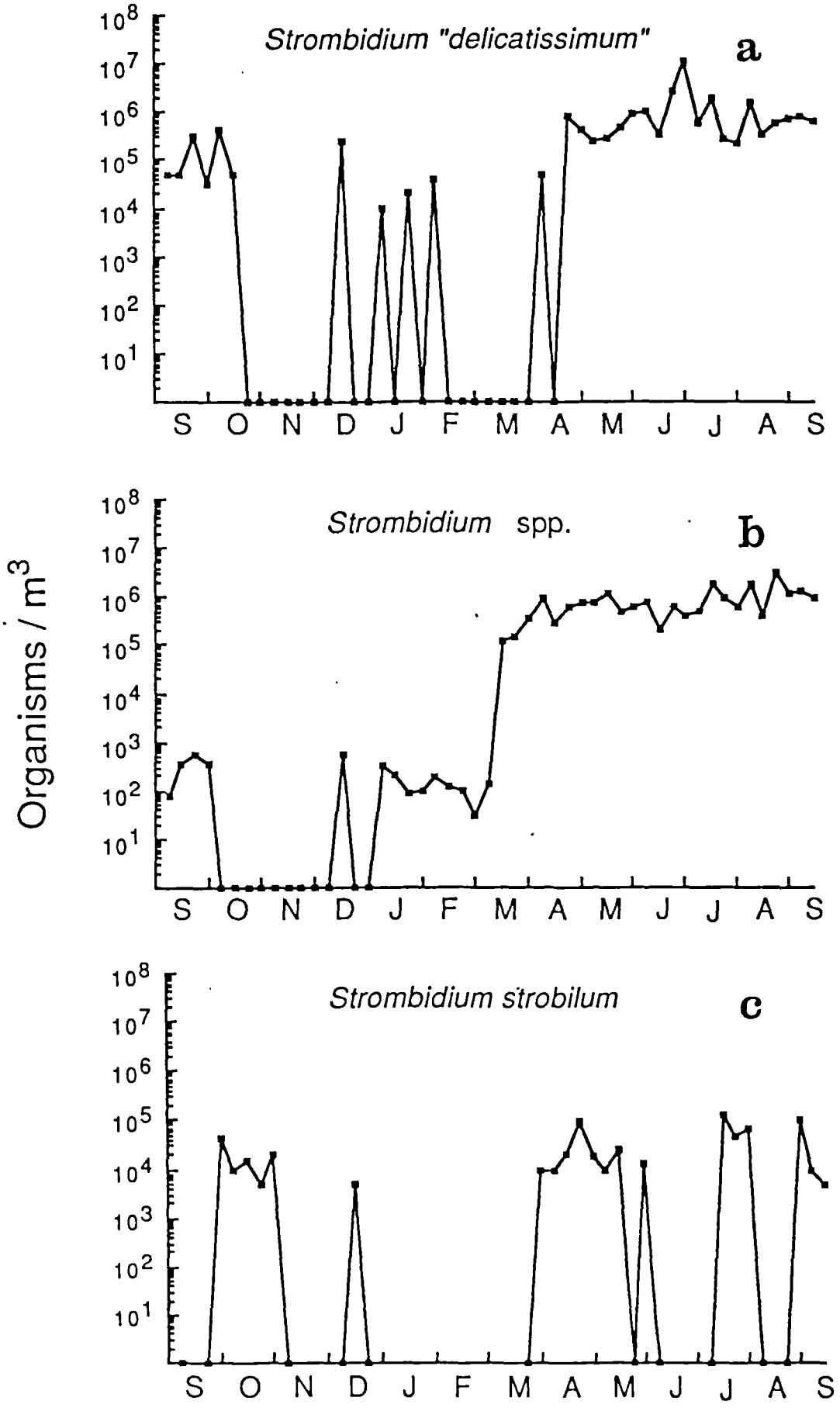

Lohmaniella oviformis
Myrionecta rubra
Strombidium "conicum"
Organisms / m3
10^8
10^7
10^6
10^5
10^4
10^3
10^2
10^1
S O N D J F M A M J J A S
1986 - 1987

Fig. 19. Seasonal cycle of major naked ciliate taxa in Port Erin Bay;
(a) *Strombidium "delicatissimum"*
(b) *Strombidium* spp.
(c) *Strombidium strobilum*


Strombidium "delicatissimum"
a
Strombidium spp.
b
Strombidium strobilum
c
Organisms / m3
10^8
10^7
10^6
10^5
10^4
10^3
10^2
10^1
S O N D J F M A M J J A S
1987 - 1988

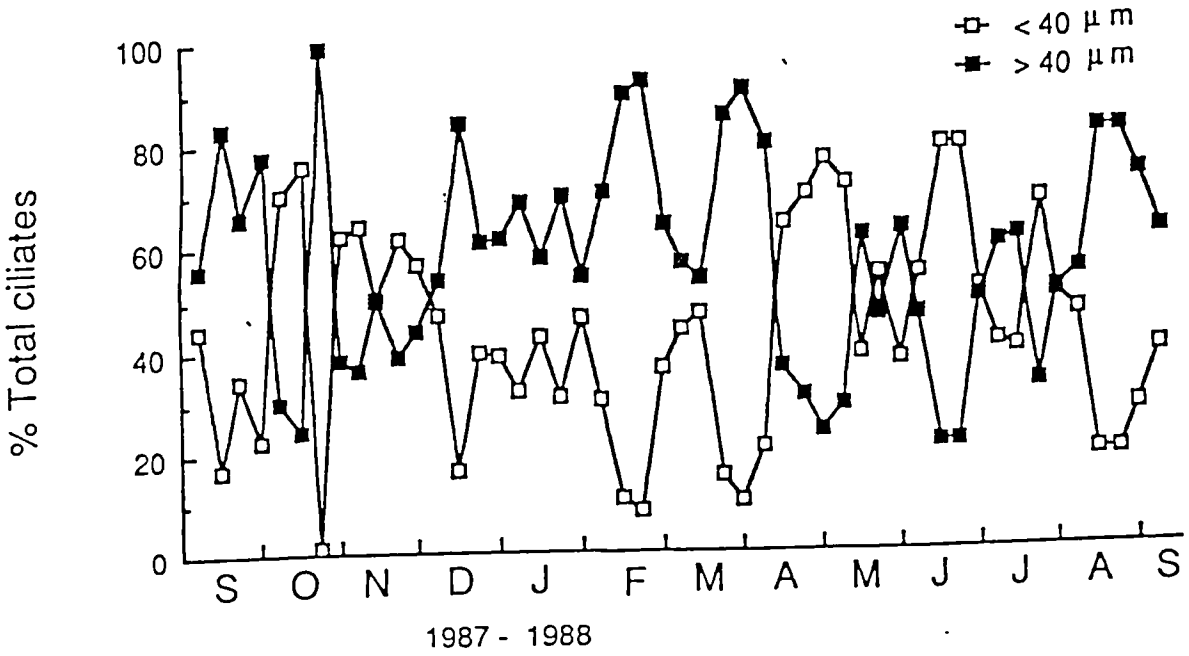


Fig. 20. Percentage contribution of two size fractions to total naked ciliate abundance.

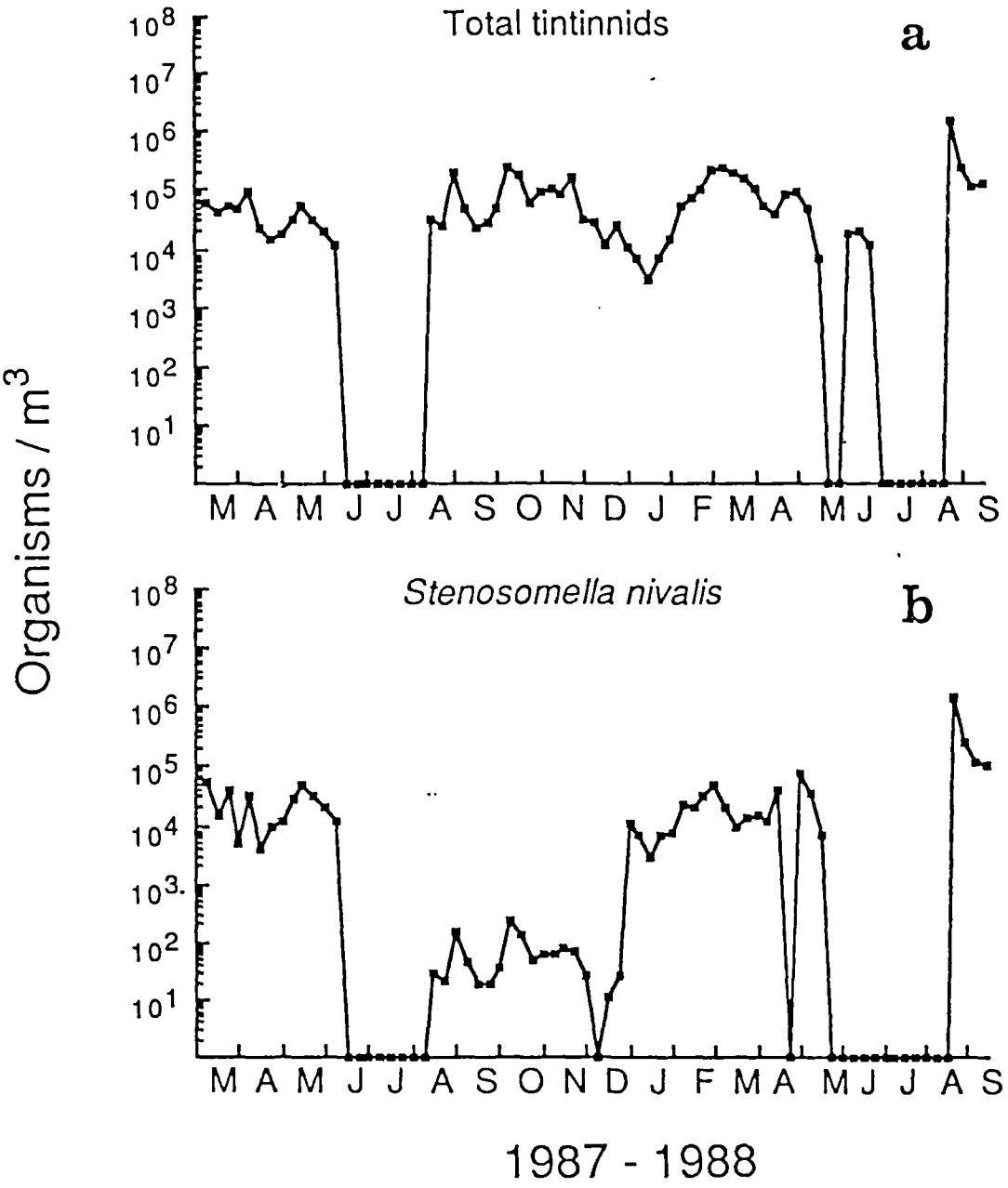
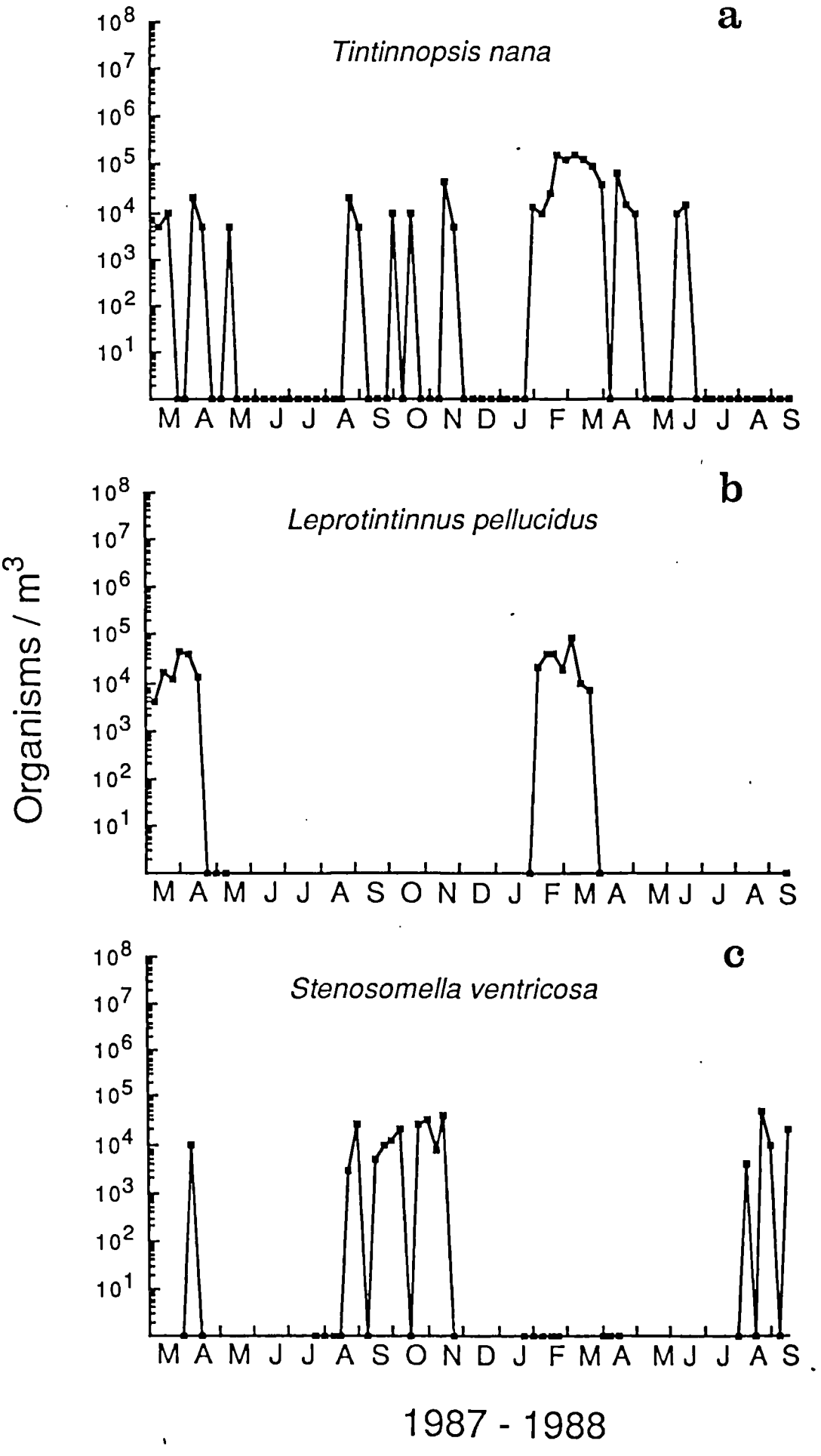


Fig. 21. Seasonal cycle of (a) total tintinnids and (b) *Stenosomella nivalis* in Port Erin Bay.

Fig. 22. Seasonal cycle of some tintinnid taxa in Port Erin Bay;
(a) *Tintinnopsis nana*
(b) *Leprotintinnus pellucidus*
(c) *Stenosomella ventricosa*


a
Tintinnopsis nana
b
Leprotintinnus pellucidus
c
Stenosomella ventricosa
Organisms / m3
10^8
10^7
10^6
10^5
10^4
10^3
10^2
10^1
M A M J J A S O N D J F M A M J J A S
1987 - 1988

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Codonellopsis lusitanica	.	.	+	.	.	.	.	.	++	+	.	.
Codonellopsis pusilla	.	+	+	+	.	.	+	.	.	.	.	.
Ptychocylis sp.	+	.	.	++	.	+	+	+	.	.	.	
Tintinnopsis beroidea	+	++	++	+	.	.	++	+	.	.	.	
Tintinnopsis campanula	.	.	.	.	.	.	.	+	+	+	.	.
Tintinnidium mucicola	.	.	.	+	++	+	.	.	.	.	+	.
Tintinnus inquilinum	+	+	+	.	+	+	+	+	.	.	+	+

Fig. 23. Maximum abundance for each month for the less common tintinnid species in Port Erin Bay. + = < 10^3; ++ = > 10 - < 5 x 10^3 organisms / l.

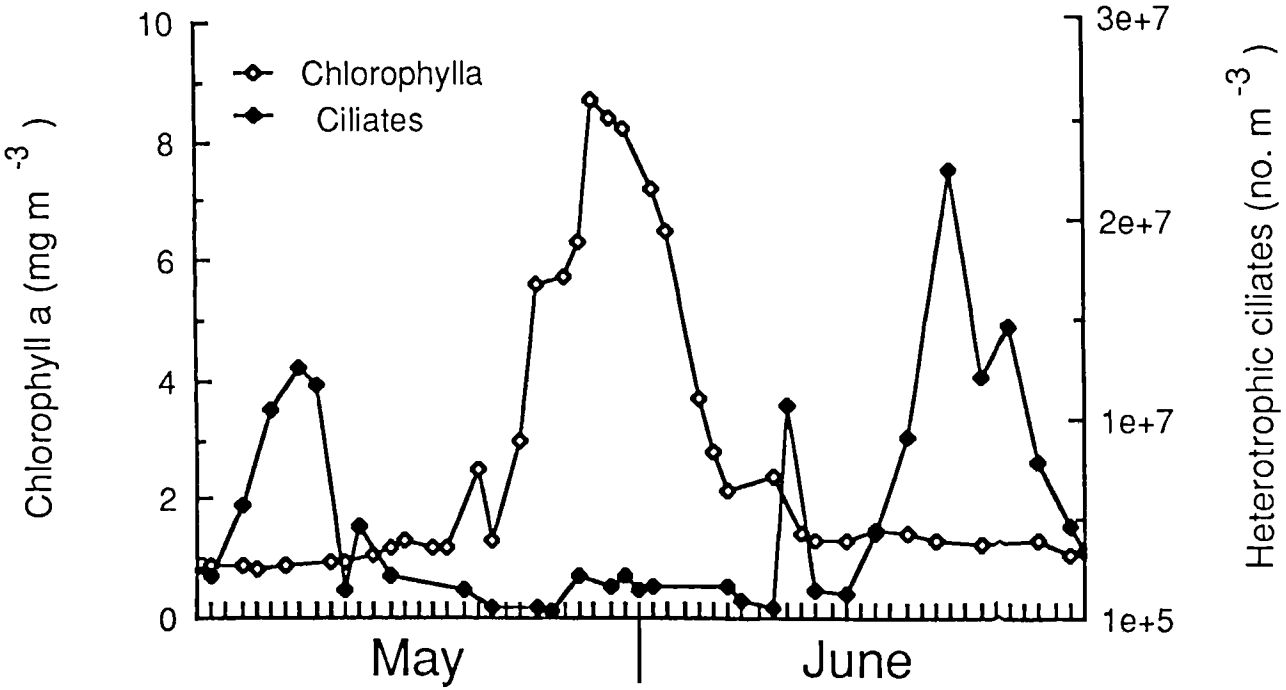


Fig. 24. Ciliate dynamics during the 1988 phytoplankton bloom in Port Erin.

SECTION FOUR

OBSERVATIONS ON THE MESOZOOPLANKTON CYCLE

4.1. INTRODUCTION

Details of the general distribution of zooplankton in the Irish Sea are relatively well known. Herdman and his various co-workers (1908-1921) studied the long term cycle of the plankton in Port Erin Bay; Williamson (1952, 1956 a, b, 1963,1975) and Khan & Williamson (1970) studied the coarse-scale horizontal distribution of the plankton of the Irish Sea in relation to water movements; Lee (1971) and Lee & Williamson (1975) studied the vertical distribution of plankton at a number of stations around the Isle of Man; Leigh (1977) and Scrope-Howe & Jones (1985a, 1985b) studied zooplankton distributions associated with the western Irish Sea frontal system; Kendaris (1979) and Floodgate *et al.* (1981) carried out similar work on the Liverpool Bay discontinuity in the eastern Irish Sea; the ecology of *Sagitta* was studied by Pierce & Orton (1939) and Pierce (1941) in the eastern Irish Sea and Khan & Williamson (1975) and Alvares (1988) in the eastern and western north Irish Sea; the distribution of zooplankton along the I.M.E.R. Continuous Plankton Recorder route for the Irish Sea (from Liverpool to Dublin), for the period 1948-1976, has been reported by Colebrook (1979).

A number of such authors have shown that in the Irish Sea there exist great differences in biological activity between mixed and stratified waters (Williamson 1952, 1956 a, b, 1963; Fogg *et al.* 1985 a, b and ref. therein). The fine scale relationship between zooplankton abundance and the relative stability of the water types in the Irish Sea has been clearly demonstrated by Scrope-Howe & Jones (1985). Working along a transect from well stratified to well mixed conditions in the western Irish Sea they observed that the shallower, mixed isothermal region supported a significantly lower density of total zooplankton (less than 63 % than in stratified waters) and the maxima occurred at least one month later than in the stratified waters. Given the well mixed nature of the Irish Sea at large, the potential impact of such an hydrographic environment on overall zooplankton productivity is shown by the Continous Plankton Recorder data for the approximately mixed waters of the

Liverpool to Dublin route which show that copepod numbers in these waters are less than one third of those of neighbouring areas of stratified waters (Colebrook 1979).

In recent years considerable attention has been given to the effects of turbulence on the development of copepod populations. Hanson *et al.* (1986) observed zooplankton grazing to increase in response to an upwelling event in the Ria de Arosa, Spain, and Mullin *et al.* (1985) found that the abundance of copepod nauplii increased in response to a storm event off southern California. A similar result was predicted by the computer model of Wroblewsky & Richman (1987). Kiorboe *et al.* (1988) found that *Acartia tonsa* responded to a storm by increasing its rate of egg production even though the phytoplankton biomass (in terms of chlorophyll) declined. Alcaraz *et al.* (1988) have suggested that turbulence might reduce zooplankton biomass through changes in the demographic composition (lower proportion of males and higher developmental rates) and probably by increasing the metabolic activity of copepods (feeding pressure and excretion rates). Although these findings might be explained if the storm-generated turbulent mixing per se stimulated zooplankton fecundity or grazing, in view of the lack of data relating zooplankton activity directly to water column stability, an explanation such as that the input of nutrients to the surface might have made the algae more edible to the copepods in terms of size distribution (cf. Peterson & Bellantoni 1987) or chemical composition (e.g.Goldman 1980) at present appears more likely. At present then most evidence suggests that the difference in production timing and phytoplankton assemblage that characterizes mixed and stratified waters are the most important factors in control of zooplankton abundance. Although the zooplankton studies in the Irish Sea provide a considerable background of data on the plankton fauna of the Irish Sea, few workers have studied zooplankton dynamics closely in relation to the phytoplankton cycle. Of the latter, Herdman *et al.* (1908-1921) studied only the netphytoplankton (> 60 μm); Williamson (1952) used phytoplankton colour as an approximate measure of the standing stock of phytoplankton following the practice adopted with the Continous Plankton Recorder (Colebrook & Robinson 1965); Scrope-Howe & Jones (1985) studied the zooplankton

as part of a wider study on the biology of tidal fronts but, although a considerable background of information was available on bacteria and phytoplankton biomass (in terms of chlorophyll *a*) the specific composition of the latter was not studied. Although it is well recognized that the different duration of the phytoplankton growth season, and hence the availability of food, is a factor of primary importance regulating the abundance of zooplankton (Colebrook & Robinson 1965; Colebrook 1979) the precise nature of the link between phytoplankton and zooplankton production is still unclear and the factors determining different zooplankton abundance in mixed and stratified waters are still not known.

Seasonal and higher frequency changes in the thermal structure of the water column lead to time varying changes in stability, which in turn lead to changes in the vertical distribution and abundance of phytoplankton and to changes in phytoplankton species composition and mean cell size. For example, chain forming diatoms dominate the phytoplankton assemblages of mixed water columns, but small dinoflagellates and cryptomonads (those < 20 μm) dominate in stratified water columns (Conover 1956; Holligan & Harbour 1977; Grice *et al.* 1980). The recent findings that phytoplankton species differ significantly in their nutritional value and that this can vary according to their physiological state (which in turn is related to the hydrographic environment) suggest that food supply is of overwhelming importance for zooplankton dynamics. Thus, from the viewpoint of a herbivorous copepod, the food environment changes radically depending upon the degree to which the water column is mixed or stratified.

The aim of this work is therefore to decribe how changes in zooplankton composition and abundance in well mixed and stratified waters in the north Irish Sea could be related to the timing of the phytoplankton cycle and seasonal changes in cell size and species composition. For this purpose from April 1986 to October 1987 zooplankton net tows were included in the sampling programme of each cruise on the R. V. Cuma and additional samples were collected from the R. V. Sula off Port Erin Bay. Because of time constraints, in this account data are presented only as the mean

for the east and west transect.

4.2. MATERIAL & METHODS

4.2.1. Sampling and field methods

At each station two samples were collected by towing obliquely two nets with mesh apertures of respectively 140 and 350 μm and 0.45 m diameter. The volume of water filtered was measured with General Oceanics Digital Flowmeters, Model 2030, tied into the mouth of each net. Whereas throughout most of the year standard tows were of 10 minutes duration each, during summer, the towing times were limited to 5 minutes to minimize clogging of the 140 μm nets. Whereas average tows during winter filtered 100 m^{-3} and only slight differences were observed between the 140 and the 350 μm nets, from May to August filtering efficiency by the 140 μm nets was approximately < 10 % that of the 335 μm nets with average tows of approximately 1C m^{-3}. After each haul the nets were carefully washed and the collected samples immediately preserved in a 5 % neutral formalin seawater solution.

At all stations samples for microzooplankton were obtained by pooling together whole-water subsamples collected with a Nansen-Peterson water bottle from 4 to 5 depths (1, 5, 15, 20 and 30 m) to give a final 10 l composite water sample. These samples were immediately fixed with a 1% final solution of Lugols Iodine.

4.2.2. Laboratory methods

Samples were usually processed within one month of collection. In order to obtain a more representative sample of the plankton the counts of the two samples collected at each station were pooled. To avoid as far as possible any overlap the 140 μm net samples prior to counting were resuspended in sea water and gently screened through a 350 μm mesh and repeatedly rinsed to separate the 140-350 μm size fraction.

Large specimens, (mainly medusae, euphasids and ctenophores) collected by the 350 μm net were counted directly. Subsampling was necessary for all other specimens. Aliquots size was chosen to provide aat least 100 organisms for counting

(Winsor & Walford, 1936); therefore, 95 % confidence limits for single counts were± 20 % or less. Aliquots were taken with a wide mouthed pipette after the contents of a sample had been randomly distributed by a series of stirrings and backstirrings. For the 350 µm net samples, a 2-10 ml subsample was drawn from 100 ml of the sample and counted in a counting tray (Bogorov 1927). The 140-350 µm samples often contained very high numbers of specimens and large quantities of phytoplankton and detritus so that 2-10 ml subsamples from 1 l were taken. All zooplankton in the aliquots were identified to as low a taxonomical level as practicable. Whereas most copepods, cladocerans and adult organisms were identified to species level all larvae were merely separated into major taxonomic groups. Once the numerical abundance of each species in each sample had been calculated the total abundance of each species was obtained by adding the values from the 140-350 µm sample and the > 350 µm sample. Abundance is expressed as log numbers per cubic meter.

The whole-water samples were concentrated to 10 ml by a three step settling process as described in chapter 2. After the smaller forms (e.g. copepod nauplii, rotifers, *Fritillaria borealis*) had been enumerated in replicate Sedgwick-Rafter cells at a 100 X magnification the whole concentrated sample was searched in a Bogorov tray for larger organisms. Data are presented as the mean for the transect to the west (stations 1-2-3) and for the east (stations 4-5-6) for each month. Abundance is expressed as organisms m^{-3}.

A total of 240 zooplankton net-samples and 106 whole water samples were collected throughout the study period at the open water stations. No samples were obtained from the R. V. Cuma in December 1987. Zooplankton data for this month are derived from a single set of samples collected from the R. V. Sula at station 3 only. Samples for the east side were obtained from the end of the pier in Port St. Mary harbour. Some samples were not collected on several other occasions and others were lost due to bad fixation or to malfunctioning of the flowmeters.

The Wilcoxon rank test (Zar, 1984) was used to compare the abundance of zooplankton species or groups of species on the west and east side.

4.3. RESULTS

4.3.1. Total zooplankton

The seasonal cycle of total zooplankton was characterized by a summer maximum with highest abundances between May and August with lowest concentrations in winter (Fig. 25). The composition of the zooplankton fauna was typically neritic. Significantly higher ($p < 0.001$) abundances of total zooplankton numbers were found at the western rather than the east transect. The individual seasonal cycle of the dominant taxonomic categories is as follows:

4.3.2. Hydrozoa (Fig. 26a)

Hydrozoa were found throughout the year with maximum abundances between May and July. Very low numbers were observed during winter when they were only recorded for presence. These counts include also small numbers of ephyrae of the Scyphozoan *Aurelia aurita*. Many mature specimens of the latter were observed stranded on the beach of Port Erin Bay between June and July.

4.3.3. Ctenophora

Because detailed analysis of this group was beyond the scope of the sampling procedures no detailed account can be given for this group. Always present in the samples in June and July its abundance was however always very low. The largest number ever to be collected was 12 specimens of *Pleurobrachia pileus* at station 6 in June 1987. It seems to be generally agreed that ctenophores occur at or near the surface of the sea during summer, (Savage 1926; Bigelow 1915; Fraser 1970). Since in this study oblique tows rather than collections at discrete depths were collected this also might account for the low numbers sampled.

4.3.4. Rotifera (Fig.26b)

Rotifers of the genus *Synchaeta* were present in the study area throughout the period of investigation. Their abundance, however, was usually extremely low. Highest densities (> 10^4 organisms m^{-3}) were found only between April and September with the highest peak (1.2 x 10^5 organisms m^{-3}) observed at the deep water station 1. Because they were always reported in such low concentrations no effort was made to identify the rotifers down to species level. On the occasion of the maxima however, it was possible to identify *Synchaeta triophtalma* as comprising ≈ 70 % of total rotifers. Because of the difficulty involved in identifying preserved material it was not possible to go beyond *Synchaeta* spp. for the other specimens. Previous studies have found that rotifer blooms are very limited timewise (3-4 weeks) and thus not detectable with a low frequency sampling programme (Halbach 1970; Hernroth 1983). This might be partly responsible for the low number of occasions when such organisms were reported in fairly high concentrations. According to Hollowday (1949) and Hernroth (1978) rotifers appear more abundantly in coastal areas than in the open sea. In this study however, rotifers in concentrations > 10^4 organisms m^{-3} were never found in Port Erin Bay, despite the fact that a total of 101 whole water samples were taken at weekly or biweekly intervals from January 1987 to September 1988 from the pier at the mouth of Port Erin Bay (in Section Three).

4.3.5. Annelida

Tomopteris helgolandica - Although recorded only at some stations and always in very low numbers, *Tomopteris helgolandica* was found throughout the year. During July, although still in abundances between 1 and 10 organisms m^{-3} it was found at all the stations along the transect. Highest numbers ever recorded in a discrete sample were ≈ 30 organismsm^{-3} in July 1987.

4.3.6. Arthropoda

4.3.6.1. Cladocerans

a. Evadne nordmanii (Fig. 27a).

Just recorded in April, in both years its abundance increased abruptly to reach a peak of in May. This was followed by relatively high numbers until July-August and then by a drastic decline in September. By October it was only scarcely recorded. No significant difference was observed in the abundances of this species on the east and west side.

b. Podon intermedius (Fig.27b)

Three species of *Podon* (*P. intermedius, P. polyphemoides* and *P. leuckarti*) have been recorded in the Irish Sea. Because two of these occur only in very low abundance (Williamson, 1956 a), in this study all species of this genus were integrated under the name of *Podon intermedius*. As for *Evadne nordmani* the seasonal cycle of this species was characterized by its presence in the plankton only from May to October. Highest abundances of *Podon* were found also in May on the western transect during both years. Highest values on the eastern transect were in July and May in 1986 and 1987 respectively. As for *Evadne nordmanii* no significant differences in abundance were observed between the east and west side.

4.3.6.2. Copepoda

Copepods were always the overwhelmingly dominant group and accounted for most of total zooplankton numbers (Fig. 28). Only few species made a significant contribution to total copepod numbers and no differences were observed in species composition between the east and the west side (Fig.29a,b). Abundances on the west side, however, were significantly ($p < 0.005$) higher than on the east side. The detailed seasonal cycle of these species is as follows;

a. Calanus spp. (Fig. 30a)

Because it was difficult to separate them, specimens of *Calanus helgolandicus* and *Calanus finmarchicus* were treated as a single group. Collected in every month of the year highest abundances were reached between May and June in 1986, and in June in 1987. Abundances were significantly higher ($p < 0.005$) at the western rather than the eastern stations. Whereas on the west side concentrations were as high as 10^4 organisms m^{-3} values at the eastern stations values never exceeded 10^3 organisms m^{-3}. These findings compare with the results of Williamson (1952) and Scrope-Howe & Jones (1985), who also found *Calanus finmarchicus* to be consistently more abundant in the stratified region of the western Irish Sea and comparatively rare in the mixed isothermal water to the west of Anglesey. Williamson (1952) considered it unlikely that the *Calanus finmarchicus* population was endemic and proposed the seasonal replenishement of a non-breeding stock into this area by the southward-flowing current originating to the north of Ireland, where the copepod is abundant at all times of year.

b. Pseudocalanus elongatus (Fig. 30b)

Following the practice adopted by Williamson (1952) and Scrope-Howe & Jones (1985) specimens of *Paracalanus parvus* were grouped with *Pseudocalanus elongatus* as a single species. Herdman *et al.* (1907-1921) with their 14 years records from 1907 to 1920 showed that the maximum number of *Paracalanus parvus* always occurred in September, while negligible numbers, or no specimens at all were caught from April to June. Williamson (1952) also reported that *Paracalanus parvus* constituted an appreciable part of the total (*Paracalanus parvus* + *Pseudocalanus elongatus*) only in autumn. Lee (1971) found that *Paracalanus* occurred throughout the year but its numbers were always fairly low, the greatest density of ≈ 450 organisms m^{-3} being found in late July. In this study *Pseudocalanus* was one of the most prevalent and abundant of the calanoid copepods during the summer maximum. Very common and occurring in every month of the year its abundance ranged from a

winter minimum of less than 50 organisms m^{-3}, to values generally > 1 x 10^3 organisms m^{-3} from May to September. Significantly higher ($p < 0.05$) abundances were observed at the western rather than the eastern stations. Highest abundance in 1987 was reached in June on the west side (approx. 13 x 10^3 organisms m^{-3}) and in late July on the east side (approx. 14 x 10^3 organisms m^{-3}). In 1986 maximum abundance was reached in June on both sides (21 x 10^3 and 4.5 x 10^3 organisms m^{-3} at the eastern and western side respectively). Whereas in discrete samples its local abundance was occasionally exceeded by either *Temora longicornis* or *Acartia clausii* during the summer, mean values along the transect always exceeded these two species in numbers.

c. Centropages spp. (Fig. 31a)

This group includes *Centropages hamatus* and *Centropages typicus*. Whereas the former is a resident species in the Irish Sea reaching abundances as high as 200 organisms m^{-3} during summer (Lee 1971), *Centropages typicus* is considered an immigrant species (Williamson, 1952, 1956 a, b; Khan & Williamson 1970), present only in very small numbers. According to the findings of Khan & Williamson (1970) the specimens reported in late spring-early summer could be *Centropages hamatus* whereas those found from August onwards could be *Centropages typicus*. In this study no distinction was made between different species. *Centropages* spp., occurred mainly in summer and although found in every month it was practically absent for the rest of the year. Highest values of $\approx 10^3$ organisms m^{-3} were reached only between May and June and then declined to $\approx$ 100 organisms m^{-3} during September-October. No consistent differences were observed between the two transects.

d. Temora longicornis (Fig.31b)

Although abundant during much of the year, during winter *Temora longicornis* , was found only in extremely low numbers. Its abundance increased from March but it was only during summer, from May to September, that it become abundant. No

apparent differences were observed between the two sides. Whereas in 1986 maximum abundance on the east side was reached as early as May (approx. 3.5 x 10^3 organisms m^{-3}), highest abundances on the western side (approx. 6 x 10^3 organisms m^{-3}) and in 1987 were reached in June (approx. 5 x 10^3 and 7 x 10^3 organisms m^{-3} for the eastern and western side respectively). Its abundance along both transects was consistently lower in 1986 than in the following year. In 1987 *Temora* was in fact the second most important copepod species after *Pseudocalanus elongatus*. Occasionally in discrete samples its abundance exceeded also that of this latter species.

e. Acartia clausii (Fig. 32a)

This organism was very scarce from October to the following April (< 10 organisms m^{-3}) but it rapidly increased in May and concentrations > 10^3 organisms m^{-3} were maintained throughout the summer until the end of September. During 1986 maximum abundance was reached in June on the west side (approx. 10^4 organisms m^{-3}) and in August on the east side (approx. 6 x 10^3 organisms m^{-3}). Highest abundance in 1987 was in June for both sides (approx. 10^4 and 2.5 x 10^3 organisms m^{-3} at the eastern and western station respectively). No significant differences in abundance were observed between the mean values at the eastern and western transect. In terms of total copepods *Acartia* was one of the most important species during the summer maximum. Although in discrete samples it was occasionally the overwhelmingly dominant species, in mean values for the whole transect it was the most important species only in May of 1986 on the east transect. During 1986 it was generally the second most important species in terms of numerical abundance in 1987; both *Pseudocalanus elongatus* and *Temora longicornis* were always more abundant.

f. Oithona similis (Fig. 32b)

Although two distinct species of *Oithona* (*Oithona similis* and *Oithona nana*) are recorded in the the Irish Sea, in this study species of this genus were all attributed to *Oithona similis*. Williamson (1956 a) and Lee (1971) showed that *Oithona nana*

occurred in such small numbers that the seasonal abundance of the dominant species, *Oithona similis* would not be seriously affected by these small values of abundance. Therefore in this study no attempt was made to distinguish between these two species in routine counts. *Oithona* was the dominant species from August to the following May accounting for as much as 50 and 90 % of total copepod numbers from November to February inclusive (Fig. 29a,b). Its abundance was significantly higher ($p < 0.001$) on the west side than on the east side. Its contribution to total copepod numbers was also significantly (z= ; p , 0.001) higher on the west rather the east side. Wheras along the western transect, on an annual basis, it accounted for 44.2 of total copepod abundance, on the east side its contribution to total copepod numbers was only 26.8 %. In 1986 highest numbers occurred in August on both the east ($\approx 7 \times 10^3$ organisms m^{-3}) and the west side (1.5×10^4 organisms m^{-3}). Maximum abundance in 1987 were observed in May along the eastern transect ($\approx 3.2 \times 10^3$ organisms m^{-3}) and in June along the western transect ($\approx 4.5 \times 10^3$ organisms m^{-3}). Lowest numbers (≈ 30 organisms m^{-3}) all along the transect were reached were reached between December and March. Despite being the overwhelmingly dominant species during the winter months its abundance was generally exceeded by that of the calanoid copepod species *Pseudocalanus elongatus, Acartia clausii* and *Temora longicornis* during the summer.

g. Other copepods

Several other copepod species were found in this study but their abundance was always irregular and extremely low (always < 1 % of total copepods). These included *Isias clavipes, Microcalanus pusillus, Anomalocera patersoni, Candacia armata* and *Metridia lucens*. None of these species, however, was numerically ever important and in general only few specimens were found in discrete samples.

h. Harpacticoid copepods

Harpacticoid copepods were collected throughout the study period, possibly as a result

of the oblique tows being carried out close to the bottom. Highest abundances were found in winter, possibly as a result of strong mixing. Previous studies (Lee 1971) suggest that the most abundant species were *Euterpina acutifrontis, Harpacticus* sp., *Altheutha* sp., *Tisbe* sp., *Rynchothalestris* sp., *Danielssenia* sp. and *Clytemnestra* sp.

i. Copepod nauplii (Fig. 33)

Nauplii of copepoda were treated as a single group. Considering the relatively low numbers of other species seasonal fluctuations in nauplii numbers can clearly be attributed to breeding of *Oithona similis, Acartia clausi, Pseudocalanus elongatus* and *Temora longicornis*. Nauplii were present in the water column throughout the winter suggesting that breeding of some species, although at low magnitude, occurs throughout the year (Dr. Williamson, pers. comm.). Significantly higher ($p < 0.001$) abundances were found at the western rather than the eastern stations. In 1986 the production of nauplii was characterized by a series of peaks from May to August. In 1987 the production cycle showed a single peak centered on early summer. Highest values were observed in May and June which agrees fairly well with the highest values of adult copepod abundance in June. In net samples (Fig. 33a) maximum abundances during May ranged around 10^4 organisms m^{-3}. Values decreased considerably by August and this was particularly pronounced at the stations to the east. Low numbers later in the year suggest that breeding is largely confined to late spring and summer. Highest numbers at the stations to the west reached a peak in May.

The seasonal cycle of copepod nauplii as deduced from whole water samples (Fig. 33b) showed a pattern similar to that inferred from the net samples. Concentrations in these samples were however, considerably higher and showed that net samples underestimated by about 10-fold the abundance of these organisms in the water column. A first peak in 1986 in May was followed by second peak of higher magnitude on both sides with high number of nauplii until October. In 1987 concentrations on the west side first peaked in May but highest values were observed

in July. This is in disagreement with the results from the net samples but could be explained by the dominance of organisms too small to be not sampled by the net.

4.3.6.3. Euphausiacea

Meganyctiphanes norvegica and *Nyctiphanes couchii* are known as the only species recorded in the Irish Sea (Williamson 1956a). Larvae of either species occurred in the samples but owing to their similarity they were not identified further. Recorded throughout most of the year their numbers were always very low and only at station 1 did they ever exceed 20 organisms/catch. As already mentioned for the ctenophores the sampling strategy was not suited to catch such organisms and no detailed acount was possible for such organisms. Highest numbers, however always occurred between May and July.

4.3.6.4. Chaetognatha (Fig. 34)

Four species of *Sagitta* have been recorded for the Irish Sea; *Sagitta serratodentata, Sagitta cephalotera, Sagitta elegans* and *Sagitta setosa.* Of these only *Sagitta elegans* and *Sagitta setosa* are common in the north Irish Sea (Lee 1971), the former occurring throughout the year, the latter being common in the plankton only off the east coast from August to December (Williamson 1952, 1956a). In this study *Sagitta elegans* was found throughout the year (Fig. 34a). In both years highest abundance was reached during summer when it was approx. 100 organisms m^{-3}. No significant differences were observed in the distribution of this species on the east and west side. Alvares (pers. comm.) found that specimens of *Sagitta elegans* reached a larger terminal size but no differences were found in terms of production timing and overall levels of abundance. *Sagitta setosa* was found only from September to February (Fig. 34b). In September its distribution along the transect was limited just to the stations to the east, where its densities were $\approx$ 40 organisms m^{-3}. By November few specimens were found also at all the stations to the west

4.3.6.5. Tunicata (Fig.35a).

In routine counts the two appendicularian species*Oikopleura dioica* and*Fritillaria borealis* were grouped together. Both species were found during every season but their abundance was high only from March to October. No distinctive peak was observed during this period in any particular month. Significantly higher ($p < 0.05$) abundances were found at the western rather the eastern stations.

4.3.6.6. Meroplanktonic larvae

a. Polychaete larvae (Fig. 35b)

The animals taken during the two years were mostly spionid, polynoid and nereid larvae in their varying developmental stages from metatrocophore to late larval forms. All larvae were therefore enumerated under the general term "Polychaete larvae". Because maximum numbers occurred at different times at different stations the seasonal cycle of this group appears very irregular. Isolated peaks were found practically in every month and concentrations at close stations ranged from 0 to more than 500 organisms m^{-3}. Concentrations were significantly higher ($p < 0.01$) at the western rather than the eastern stations. Herdman *et al.* (1907-1920) with their intensive study of the plankton of Port Erin Bay observed that in most cases the maximum occurrence of polychaete larvae was in March. They observed however that drastic variations occurred from year to year. Working at different stations Lee (1971) observed that the maximum varied between March and July.

b. Cirripede larvae (Fig. 36a)

Cirripedia larvae were first observed in March and disappeared or were reduced to very low abundance during summer. During 1986 nauplii first appeared in March and

disappeared at all stations by July. In 1987 nauplii appeared again in March but they were present in the plankton until August with a further peak in September. Highest numbers were found in April in 1986 (> 10^3 organisms m^{-3}) and in May in 1987 (10^3 organisms m^{-3}). The highest peak (> 2 x 10^3 organisms m^{-3}) was found at station 6 in May 1987.

c. Decapod larvae (Fig. 36b)

A fairly distinctive seasonal cycle was observed both years with abundances increasing in spring, building to a maximum in summer (July to September). In both years highest abundance did not exceed 100 organisms m^{-3}. Peaks of up to 400 organisms m^{-3} were occasionally observed in discrete samples. Larvae were totally absent from October to February inclusive. Abundances in 1986 appeared to be higher on the east rather than the west side. In 1987 decapod larvae appeared three months before than on the west side.

d. Gastropod larvae (Fig. 37a)

Gastropods concentrations never exceeded 10^3 organisms m^{-3}. Their seasonal cycle was characterized by a very irregular distribution with isolated peaks occurring throughout the year. Although a clear seasonal pattern could not be observed concentrations appeared to be higher during late summer in 1987. Significantly higher ($p < 0.001$) numbers were observed at the stations to the west than to the east where they were occasionally completely absent.

e. Lamellibranch larvae (Fig. 37a)

As for the gastropods lamellibranch veligers were significantly ($p < 0.001$) higher on the west than on the east side. Concentrations were highest from May to August and then declined in winter. Peaks of > 10^3 organisms m^{-3} were often observed.

f. *Membranipora membranacea* (Fig.38a)

Cyphonaute larvae were found practically throughout the year. Highest numbers ($<10^3$ organisms m^{-3}) during 1987 were found during early spring and the high value for the west transect in 1986 appears to suggest the same pattern. Isolated peaks of low magnitude were observed throughout the year. Larvae were significantly ($p < 0.01$) more abundant on the west rather than the east side.

g. Echinoderms (Fig.38b)

During both years highest numbers were taken in spring but isolated peaks occurred at all stations at different times. There were virtually no larvae in any samples collected in June, September and December in 1986 and January and June in 1987. Highest peaks were reached in August at both stations in 1986 and in April and May on the west and east side respectively. Abundances on both sides generally never exceeded 10^3 organisms m^{-3}. Abundances, however, were significantly higher on the west rahter than on the east side.

h. Fish larvae and eggs.

Many larval and post-larval herring were taken at stations 5 and 6 from September until November. These waters are known as a breeding ground for herring, and their spawning period extends from the beginning of September to the mid of November (Bowers 1969). Fish eggs were never very numerous but highest numbers were observed between March and June.

4.4. DISCUSSION

In temperate waters the life history of most copepod species appears to be well adapted for effective utilization of the seasonal phytoplankton production; late preadult stages spend the winter in diapause, thus enduring the scarcity of food resources, and molt into adults in late winter or early spring, ready to take advantage of the vernal increase in algae. The potential for the hydrographic environment to influence recruitment rates of copepods at this time, by modulating the availability and the quality of food has been clearly shown by a number of authors.

A good example of the impact of the hydrographic environment on zooplankton production mediated by phytoplankton availability is given by the work of Runge (1985) in two basins with different environmental conditions. Studying the egg production by the copepod *Calanus pacificus* in Puget Sound and Dabob Bay, Washington, U. S. A., he observed that in Puget Sound, where the time of the onset of the spring bloom occurred reliably from year to year and food was frequently available throughout the summer, egg production was high. In Dabob Bay, on the other hand, where the timing and duration of food resources appeared to depend on wind events and was much less predictable and the phytoplankton was characterized by a late and short production cycle, the input of new individuals (i.e. egg production) occurred less frequently and usually at lower magnitude.

A good correlation between in situ changes in the fecundity of herbivorous copepods and phytoplankton availability should not be unexpected. Marshall & Orr (1961) showed that P_{32} in radio-labelled phytoplankton appeared in *Calanus finmarchicus* eggs within 8 hrs of being ingested. In Dagg's (1977) experiments on the effects of temporal variations in food concentration on copepod fecundity, egg production in the copepods *Centropages typicus* and *Acartia tonsa* immediately declined when the animals were exposed to very brief periods (a few hours) of starvation. Checkley (1980) showed, for *Paracalanus parvus*, that the lag between renewed ingestion following several days of starvation and the start of egg production

was about 12-24 hrs. Peterson (1980) found that *Calanus marshallae* produced eggs only from recently ingested food rather than from any body reserves. The short-term effects of food on copepod fecundity are further shown by Durbin *et al.* (1983); enrichment experiments demonstrated that the copepod responses were strongly linked to the availability of food during the preceding 48 hrs. Further, copepod responses were significantly correlated with field chlorophyll *a* on the day of collection but were not correlated with chlorophyll *a* measured 3-4 days previously. In their study of egg production rates by *Acartia tonsa* in Long Island Sound, Beckman & Peterson (1986) found that fecundity values changed by as much as 60 % within a 2-day period. Parrish & Wilson (1978) and Kiorboe *et al.* (1985) also, have shown that changes in food are made apparent by changes in egg production within this time scale.

Given such strong correlations between changes in the food supply and the limited life span of most mature copepods (between 3 and 5 days according to Landry 1978; Peterson 1980, 1985; Johnson 1981; Uye 1982) these findings clearly suggest that the total reproductive output for a certain copepod could be very dependent on the match-mismatch between a mature female and a food environment favorable for egg production.

Since good feeding conditions for copepods are dependent upon an early start of the phytoplankton bloom and the duration of the growth season, in mixed waters the frequency of stabilization-destabilization of the water column by preventing phytoplankton development or by diluting patches of phytoplankton to a greater depth the water column, can exert a strong impact on phytoplankton availability. Lasker (1975) for instance, has demonstrated that a storm can, by mixing the water column, result in a a food concentration too low for successful feeding by anchovies.

By comparing the abundance of zooplankton in different areas worked by the Continous Plankton Recorder routes (Colebrook 1979) it is clear that the abundance of copepods in the approximately well mixed waters of the Irish Sea route from Liverpool to Dublin is less than one third of that in stratified waters of neighbouring areas of shelf. In their long term studies with the Continous Plankton Recorder, Colebrook &

Robinson (1965) and Colebrook (1979) have shown a strong correlation between the length of the phytoplankton growth season and zooplankton abundance. In shallow inshore areas of the shelf of northern Europe for example, late winter-early spring phytoplankton blooms can occur beginning in early February and high levels of phytoplankton are found well into the autumn. In the Irish Sea the phytoplankton is characterized by a late, short growth season where phytoplankton biomass (in terms of chlorophyll *a*) exceeds 1.0 mg m^{-3} only from late May to August. The gap between successive vernal increases in algae mean that food availability for many months is very low. Such concentrations, while they might allow the survival of certain zooplankters, may not be high enough to enable these species to reproduce successfully. Colebrook (1979) and Colebrook & Robinson (1965) suggested that higher abundances of copepods in certain areas might be due to their higher levels of overwintering stocks. The longer gaps between successive blooms in the Irish Sea and delays in the timing of the phytoplankton bloom due to the instability of the water column in mixed waters, might affect the size of these stocks more than in stratified waters. The importance of stored reserves or low metabolic rates might thus be an important factor in control of the species success during this period. For instance, *Acartia* species store little energy, and thus function mainly on their present supply of food (e.g. Durbin *et al.* 1983). Their absence for most of the year might thus be linked to the unavailability of food.

In this study phytoplankton chlorophyll *a* data for 1986 show clearly that even during this limited growth season period drastic fluctuations occur in the levels of phytoplankton standing stock (Fig.1 in chapter 1). Phytoplankton chlorophyll *a* concentrations > 2.0 mg m^{-3} in May at stations 4 and 5 were followed by a period in June when the phytoplankton was practically absent and comparable to winter levels. High concentrations in the first half of July were then followed by chlorophyll *a* values again lower than 0.5 mg m^{-3}. The second half of the month and August were instead characterized by high concentrations. The influence of a discontinous and patchy food supply on zooplankton production is clearly reflected by the second peak

in abundance of total zooplankton and of copepod nauplii. In contrast the single maximum in zooplankton abundance clearly reflects the availability of high levels of phytoplankton only during a limited period.

As well as influencing copepod abundance, patchiness in the food supply might also control the seasonal succession of species. Recent studies have shown that whereas rates of egg production in species which closely track their food environment are fairly sensitive to brief periods without food, species that are capable of damping much of the short term variability in their food environment produce eggs at more or less the same continous rates whether they are in a "patchy" or a homogeneous food environment. The success of different species at different times of the year could thus be explained by how they adapt to respond to different scales of food availability in their food environment. For example, while some species require a constantly available food supply, without which starvation can occur only after a few days, others can tolerate long periods virtually without any food, without their reproductive potential being affected (Dagg 1977). Laboratory determinations of the time taken for copepods to starve to death and of the effects of discontinuous food availability on egg production were used by Dagg (1977) to determine the different adaptation of different copepod species to different scales of patchiness in the food environment. Whereas in their experiments *Acartia tonsa* and *Centropages typicus* depended upon constant food availability and were therefore very sensitive to small scales of patchiness, *Pseudocalanus minutus* and *Calanus finmarchicus* were able to remove themselves from such small-scale variability. Starved *Centropages typicus* lived only a few days (3-6); *Acartia* withstood starvation only slightly better (6-10 days); copepodid stage V of *Calanus finmarchicus* showed no difference in survival after a period of 3 weeks at which time the experiments were terminated. *Pseudocalanus minutus* was also capable of withstanding extended periods of starvation.

In similar experiments Corkett & MacLaren (1969) found that the number of eggs produced by temporarily starved females of *Pseudocalanus elongatus* after a two-week starvation period did not differ significantly from the numbers produced by

continuously fed females. The effect of a brief starvation period was to destroy the output of eggs during that period but not significantly to affect the later rate of egg production or to shorten life. The effect of food shortage thus appears to act mainly by lengthening the period between production of eggs; below certain food levels eggs may not be produced at all while above certain levels they are produced at temperature and other factor controlled rates. The ability of *Pseudocalanus* to withstand long periods of time without an adequate food supply, at a time when other species cannot, might be a key factor determining the dominance of this species in the Irish Sea (Herdman *et al.* 1908-1921; Williamson 1952, 1956a; Lee 1971; Scrope-Howe & Jones 1985). It might not be just a coincidence that *Centropages*, which in Daggs (1977) experiments survived only for a few days in the absence of food, is in fact the least abundant of the copepods found in the north Irish Sea and *Centropages typicus* in particular is regarded as an immigrant non-breeding species (Williamson 1952, 1956 a, b; Khan & Williamson 1970).

The absence of *Acartia clausii* or *Temora longicornis* for most of the year might be due to the fact that high levels of phytoplankton are found only during the short summer maxima. Several studies have shown that *Acartia clausi* is very sensitive to starvation and seems to have adapted to a constantly available food supply (e.g. Uye 1981; Reeve & Walter 1977; Paffenhofer & Stearns 1988). Many species of this genus inhabit neritic waters where primary production is generally high, and consequently food is often abundantly present. In such environments, its ability to develop rapidly and produce eggs continously, allows them to be one of the dominant species. Herdman and his various co-workers (1908-1921) in their intensive study of the plankton of Port Erin Bay reported swarms of *Acartia clausi* and*Temora longicornis*. Results from Williamson (1952,1956 a), other workers and this study also show that during the growth season, the local abundance of the dominant species *Pseudocalanus elongatus* is often exceeded in samples by either *Temora* or *Acartia*. The dominance of these species at certain times of year might be explained by the higher reproductive value, fast developmental rate, and short adult life span that enable

them to reach very high abundance when conditions are particularly favourable (Uye 1982).

The relatively low abundance of *Oithona* during the growth season all along the transect, despite it being the overwhelmingly dominant species throughout the winter is more difficult to explain. Several studies on this genus (e. g. Marshall 1949; Frolander 1962; Heinrich 1962; El-Maghraby 1965) report on reproduction throughout the year and on the maintenance of high population densities throughout the winter. Lampitt & Gamble (1982) reported low respiration rates for *Oithona nana* and suggested that this may be a means of exploiting environments with low food concentrations. The cost of such a strategy could be that when food does become abundant *Oithona nana* is unable to increase its reproductive rate in proportion to the increase of food. If this was the case for other species of *Oithona,* e.g. *Oithona similis* in the Irish Sea, this might provide an explanation for its relatively low abundance during spring and summer as compared to the winter period, when it is numerically the most abundant species.

In this study whereas *Calanus* was fairly abundant at the deep water station 1 where the more stratified conditions for the whole transect occur this species was fairly abundant and high concentrations were found during the summer maxima (approx. 10^4 organisms m^{-3}). On the other hand this species was present in very low abundance at the well mixed stations to the east. Such results were reported by Williamson (1952) and Scrope-Howe (1985) who also found *Calanus* to be more abundant in stratified waters and comparatively rare in mixed isothermal waters. The dominance of this species in these waters might thus be related to the different phytoplankton cycle of these waters. On the basis of field observations several workers (e.g. Ruud 1929; Ussing 1938; Marshall & Orr 1961) believed that successive broods of *Calanus* depend on outbursts of phytoplankton growth. Experimental studies on the relationship between algal food concentration and growth rates (Vidal 1980) and egg production rates (Runge 1984) of *Calanus pacificus* suggests that this species is physiologically adapted to exploit high phytoplankton concentrations. Comparing the

functional relationship between egg production rate and phytoplankton concentration for *Calanus pacificus* and *Acartia clausii* and *Paracalanus parvus* Runge (1984) observed that reproductive success for the smaller species was much less dependent on high phytoplankton concentrations than for *Calanus*.

Besides influencing the availability of the food supply the hydrographic regime can be an important factor in control of zooplankton abundance by determining the structure of the phytoplankton assemblage. Phytoplankton cell size has been suggested to be important in determining trophic level structure and the efficiency of food chain energy transfer (Parsons *et al.* 1967; Ryther 1969; Parsons & LeBrasseur 1970). Seasonal and higher frequency changes in the thermal structure of the water column lead to time varying changes in stability, which in turn lead to changes in the vertical distribution and abundance of phytoplankton and to changes in phytoplankton species composition and mean cell size. For example, chain forming diatoms dominate the phytoplankton assemblages of mixed water columns, but small dinoflagellates and cryptomonads (those < 20 μm) dominate in stratified water columns (Conover 1956; Holligan & Harbour 1977; Grice *et al.* 1980).

Peterson (1985) showed that in Long Island Sound egg laying rates of *Temora longicornis* reached a maximum only at very high chlorophyll *a* concentrations, and were nil at concentrations ranging from 2-5 mg m^{-3}. For *Acartia clausii,* Landry (1978) found that in situ egg production rates approached a maximum of 15 eggs/day only at chlorophyll concentrations in excess of 22 mg m^{-3}. Durbin *et al.* (1983) reported that maximum egg laying rates of 40 eggs/female/day for *Acartia tonsa* were only achieved at chlorophyll concentrations of 20 mg m^{-3} (Herdman *et al.* 1908-1921; Williamson 1952, 1956a; Lee 1971; Scrope-Howe & Jones 1985) and higher. In contrast studies by Uye (1981) on *Acartia clausii* and *Acartia steurii* and Valentin (1972) on *Acartia clausii* showed that maximum egg production rates in the field occurred at chlorophyll concentrations comparable to laboratory-measured rates (i.e., at ≈ 2 mg chlorophyll *a* m^{-3}).

Such results show clearly that the different nutritional quality of phytoplankton

assemblages is of great importance. Size has been shown by several authors to be an important limiting factor for many zooplankton species (e.g. Frost, 1972). By partitioning phytoplankton biomass (as chlorophyll) by size Runge (1985) and Ambler (1986) showed that the > 5 μm was a better predictor of copepod fecundity than total chlorophyll *a*. Similarly for copepods in Long Island Sound Peterson & Bellantoni (1987), found that fecundity was not correlated with the < 10 μm or 5-10 μm size fractions, but statistically significant correlations were found for the > 10 μm and >20 μm size fractions as relatively low concentrations of larger - sized particles were sufficient to ensure maximum rates of egg production for *Acartia tonsa* and *Temora longicornis*. Whereas these findings illustrate the importance of larger particles in copepod diets and might suggest that the dominance of large diatoms in the present study area might be favourable for adult copepods and larger copepodites it might instead be a limiting factor for copepod nauplii that require smaller cells, such as heterotrophic flagellates, and might instead face a reduced supply of potential food (Townsend & Cammen 1988). Thus the significantly higher abundance of nauplii on the west side might be related to the higher abundance of microflagellates.

The different nutritional value of the phytoplankton assemblage that characterizes mixed and stratified waters might also be very important. Studying plankton dynamics in experimental mesocosms Oviatt (1981) reported that zooplankton biomass was far greater in stratified than in mixed mesocosms and Peterson (1985) suggested that this could have been as a result of differential fecundity and growth rates arising from observed differences in phytoplankton taxonomic composition (flagellates vs. diatoms) in the two experimental systems. Comparing the size-dependent organic composition of marine diatoms and dinoflagellates, Hitchcock (1982) has clearly shown that as a general rule diatoms contain half the caloric value of a dinoflagellate on a per cell base and have less carbohydrates, proteins and lipids on a volume base. Although it is well recognized that many factors are all equally important in determining nutritional values of individual phytoplankton species (Poulet & Marsot 1978; Frost 1972) a limited number of feeding studies have shown that in

some cases herbivores can exhibit a preference for, or have enhanced growth rate, when fed on dinoflagellates in contrast to diatoms. The copepods *Acartia tonsa* and *Paracalanus parvus* have a 10-fold greater rate of egg production when fed a diet of *Gonyaulax polyedra* in contrast to a diet of the diatoms *Leptocylindrus danicus* or *Chaetoceros curvisetum* (Morey-Gaines 1979). *Calanus helgolandicus* attains adulthood in a shorter period of time when fed the dinoflagellate *Gymnodinium splendens* rather than the diatoms *Lauderia borealis* and *Skeletonema costatum* (Paffenhofer 1970).

Since according to the findings of Hitchcock (1982) a grazer selecting food particles solely on the basis of size would ingest 3 - 5 times more calories, proteins and lipids from a dinoflagellate than from a diatom cell of an equivalent volume, the dominance of diatoms (or the absence of a dinoflagellate-dominated phytoplankton assemblage during summer), as is the case in mixed waters in the north Irish Sea, might limit zooplankton production relative to other areas where a summer peak of dinoflagellates might provide them with a more nutritious diet. Such an hypothesis is supported by the work by Price *et al.* (1983) and others, who have shown that some copepods have very sophisticated feeding behaviours and are capable of manipulating particles which may be ingested or rejected on an individual basis. Such selective feeding behavior may very well be linked to day-to-day nutritional needs. For example, a ripe female which is producing eggs may require a higher daily intake of lipids (or lipids precursors) than immature individuals, because eggs have a different ratio of lipid to biomass than a whole animal. Higher abundance of dinoflagellates in the plankton at such a time might then provide them with a more plentiful supply of such metabolites. Also, phytoplankton during summer is often nitrogen limited and hence nitrogen deficient. Protein then, may limit the specific production of particle grazing copepods in the field (Checkley 1980). Given their higher concentration of such compounds, the presence of dinoflagellates might therefore provide a food supply of higher nutritional value.

The experiments by Oviatt (1981) also show that zooplankton diversity was

consistently higher in stratified rather than mixed treatments. As already mentioned by Williamson (1956) one of the most remarkable features of the Irish Sea plankton is the number of species which fail to occur. Currents enter the area from the Atlantic through both the St. George's Channel and the North Channel, and yet the vast majority of those tintinnids, thaliaceans, euphausids, copepods, pteropods, chaetognaths and siphonophores which have been associated with Atlantic penetration in other European waters have seldom, if ever, been recorded for the Irish Sea (c.f. Russell 1935, Rae & Rees 1947; Marshall 1948; Fraser 1952; Glover 1952; Lindley 1975). It might be suggested that the hydrographic environment and its primary production cycles are primary factors regulating the success of different species in the Irish Sea. Without understanding of the physical processes involved, however, ecological comprehension becomes very difficult.

Very few studies have been carried out on this topic. The Irish Sea with its tidal mixing gradient would provide the zooplanktologist with a unique situation in which to test specific hypothesis on the effects of variations in phytoplankton abundance and species composition on the dynamics (i.e. fecundity, grazing and growth rates) of copepod populations in the field.

Fecundity can be investigated using bottle incubation techniques, over 6 to 24 hour intervals. In this method, a small number of females are added to one liter bottles filled with 64 μm filtered natural seawater and incubated for one day or less. At the end of the experimental period, the contents are filtered onto a fine-mesh Nitex screen, and the numbers of eggs and females counted. This simple technique has been successfully used to describe *in situ* rates of egg production of a number of coastal copepods including *Centropages typicus* (Dagg 1978), *Acartia clausii* (Uye 1982), *Acrocalanus inermis* (Kimmerer 1984), *Calanus pacificus* (Runge 1985), *Pseudocalanus* sp. (Dagg *et al.* 1984), and *Acartia tonsa* (Beckman 1985).

Feeding activity can be rapidly assayed by using the gut fluorescence technique, and feeding rates can be calculated from empirically derived data on gut evacuation rate as a function of temperature (Dagg & Wyman 1983).

Growth rate of copepods may in some cases be estimated from measurements of moulting rates of field collected animals, held in containers for one or two days. This notion was first tested by Burkhill & Kendall (1982). However, Miller *et al.* (1984) have shown that this technique may not always give unbiased results because there may be a diel cycle in copepod moulting. In conclusion, a number of simple techniques exist that allow the researcher easily to study the indirect effects of temporal variations in hydrodynamic processes on second trophic level organisms. Field measurements of fecundity, feeding and growth could be supplemented with controlled laboratory experiments which look at the effects of various dinoflagellate and diatom clones on copepod fecundity (cf. Checkley 1980) feeding and growth. Until such field measurements and laboratory experiments are done, we really cannot proceed very efficiently towards an understanding of the importance of hydrodynamic processes and changes in phytoplankton species composition and food quality on zooplankton population dynamics in the Irish Sea.

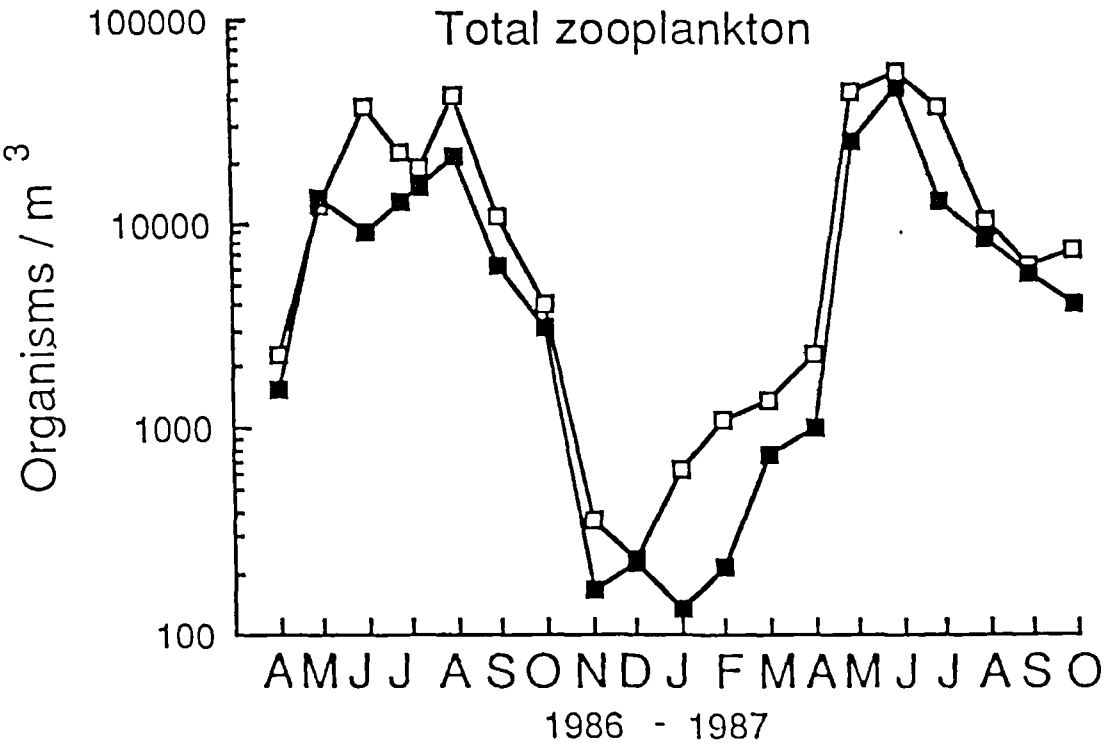


Fig. 25. Seasonal cycle of total zooplankton.
Empty squares indicate the west transect,
filled in squares the east transect.

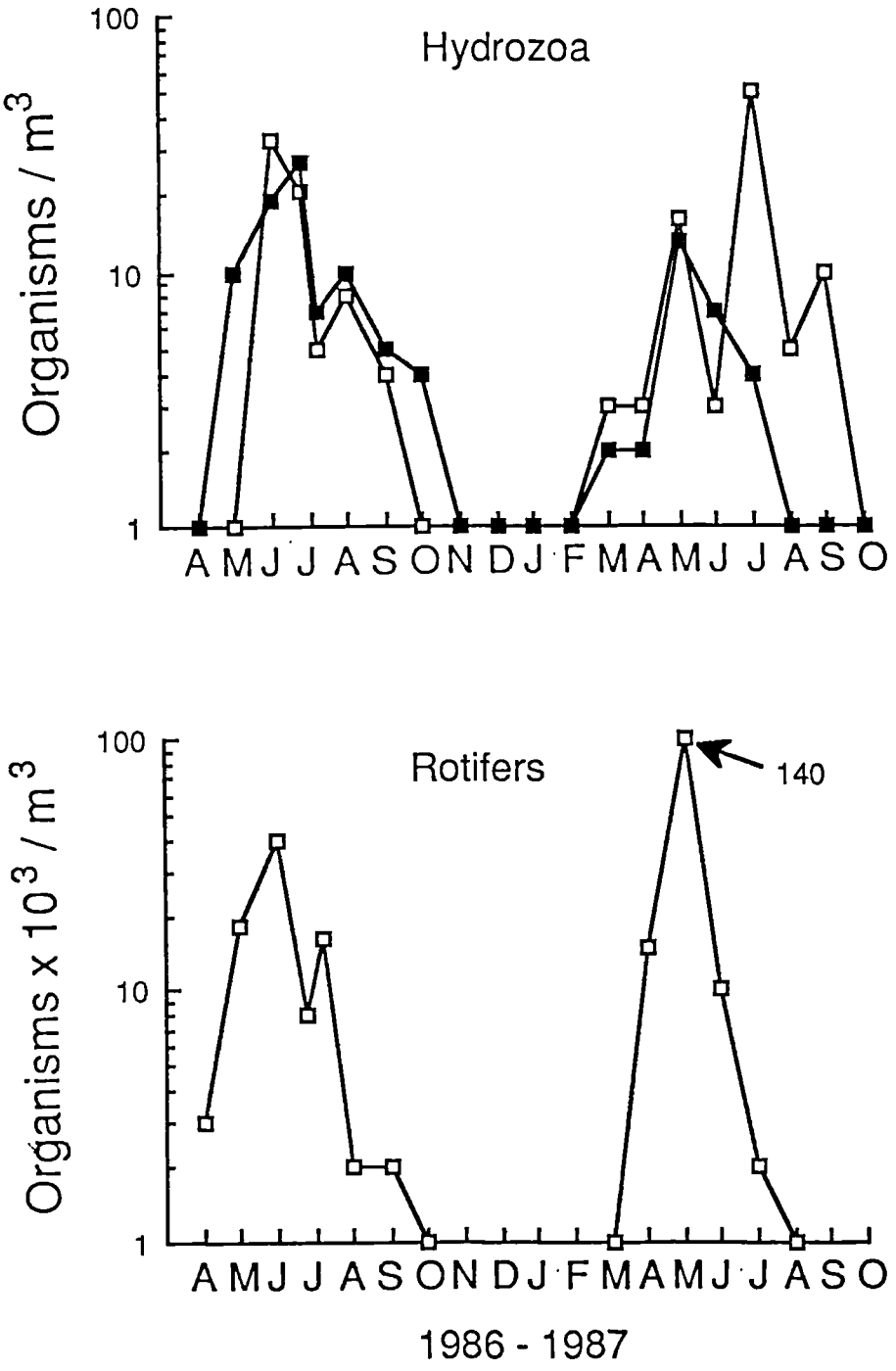


Fig. 26. (a) Seasonal cycle of hydrozoa.
(b) Seasonal cycle of rotifers at station 1.
Symbols as in Fig. 1.

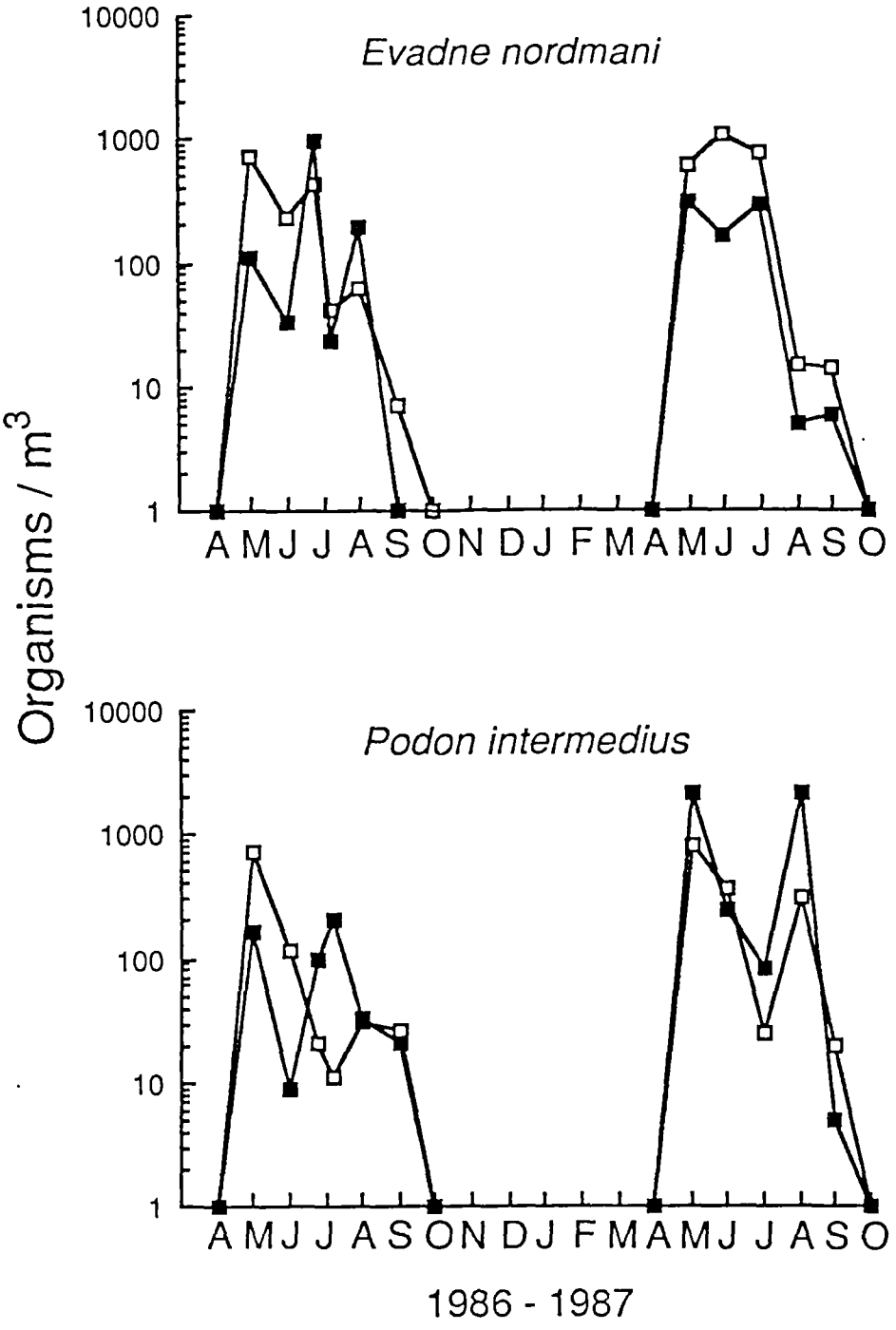


Fig.**27** . Seasonal cycle of cladocerans.
Symbols as in Fig. 1.

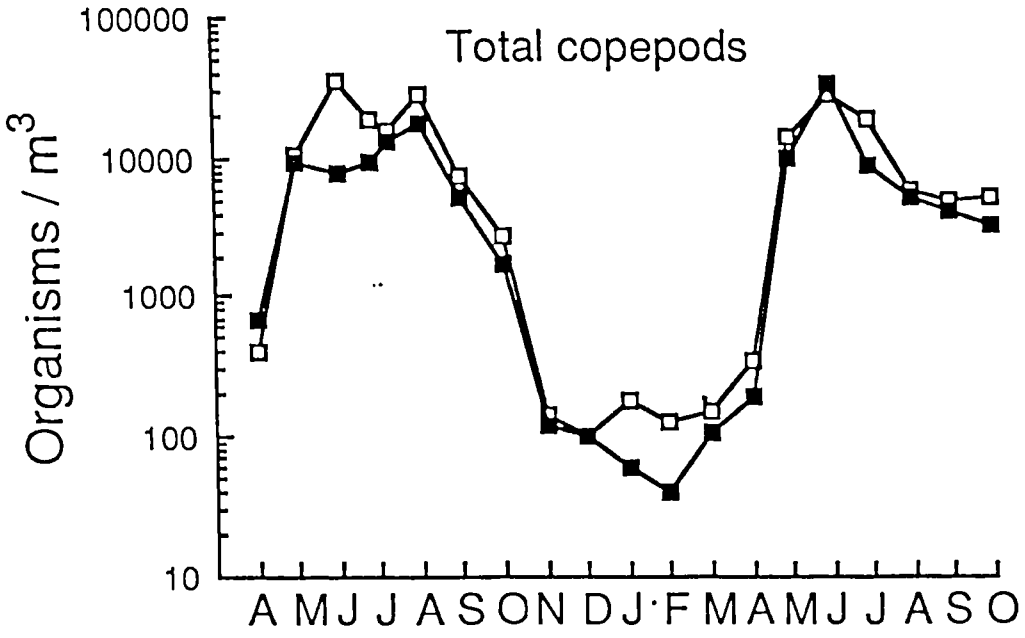


Fig. 28. Seasonal cycle of total copepods.
Symbols as in Fig. 1.

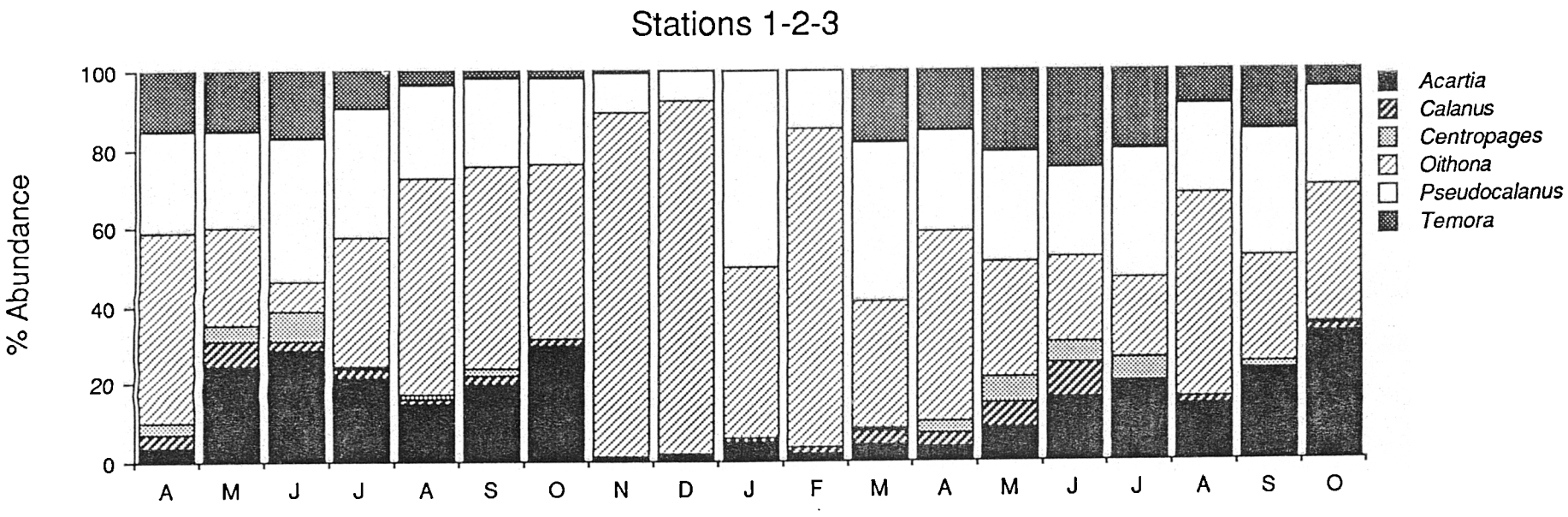


Fig. 5a. Percentage contribution of dominant species to total copepod abundance.

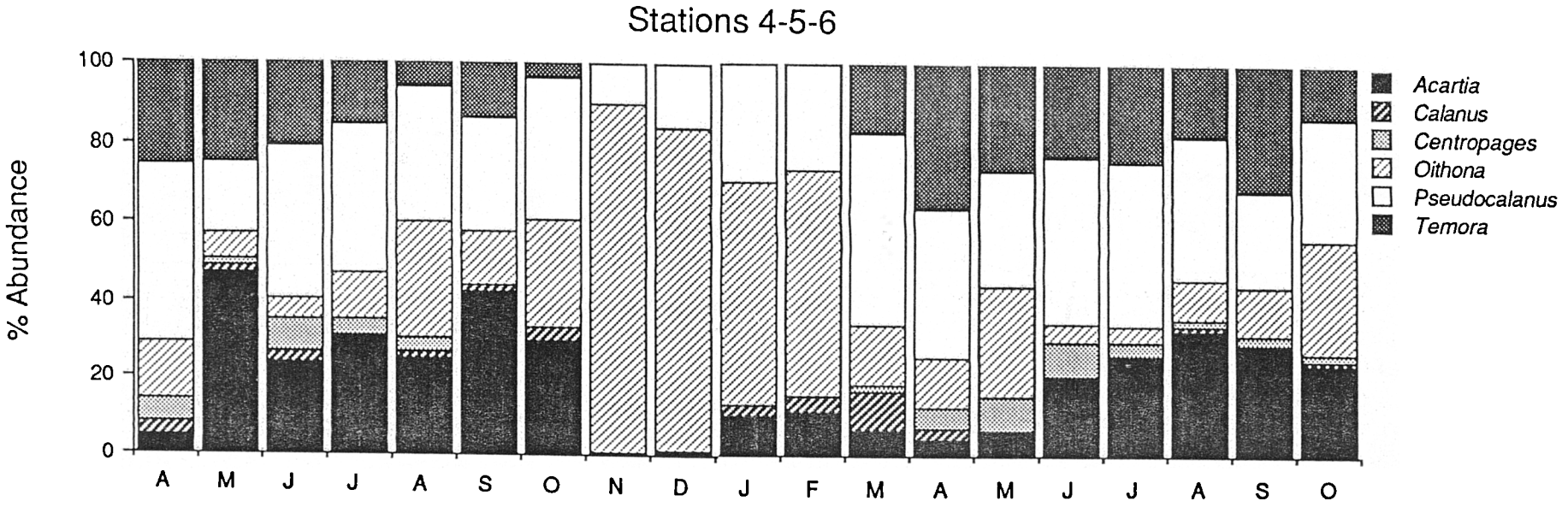


Fig. 29b. Percentage contribution of dominant species to total copepod abundance.

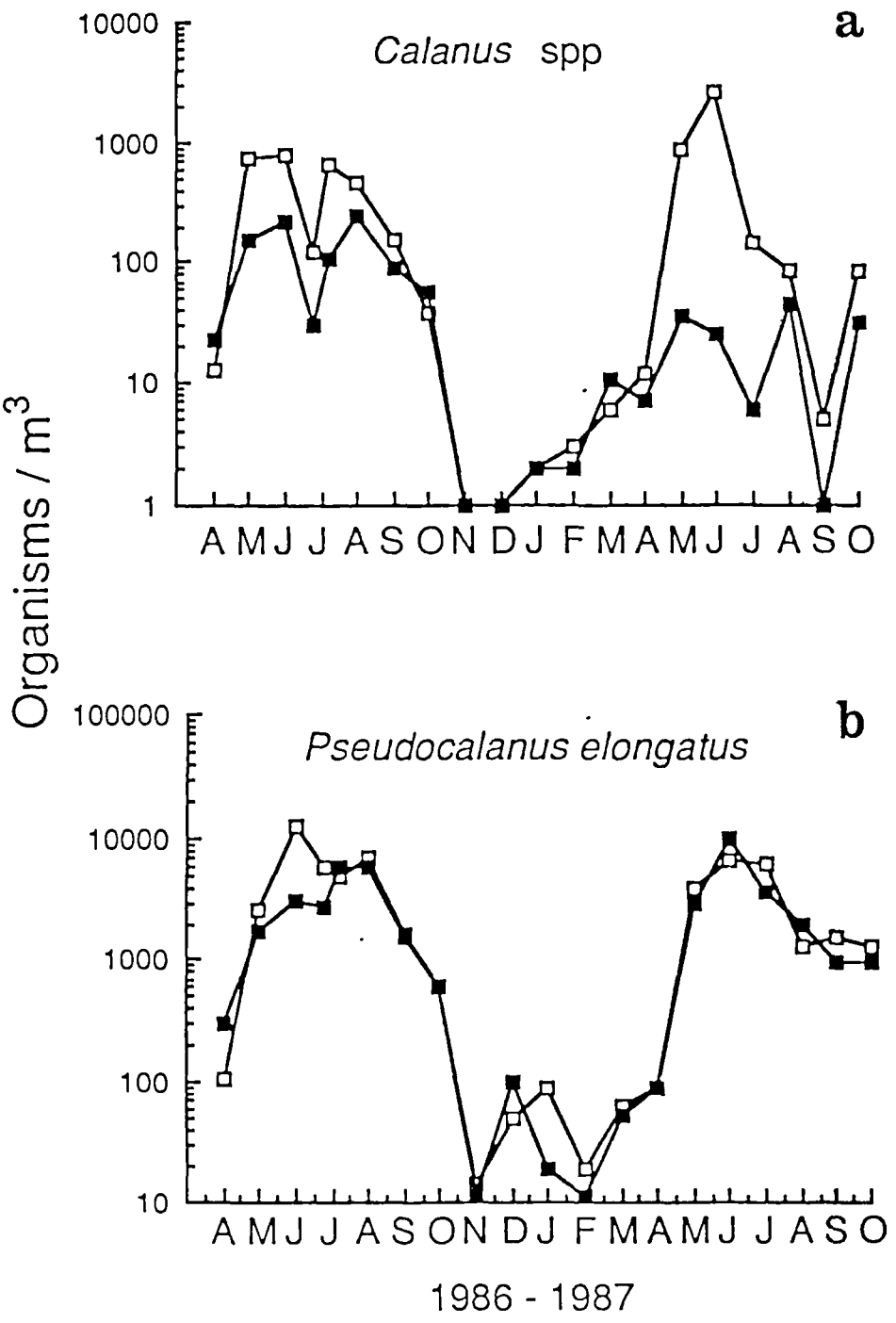


Fig. 30. Seasonal cycle of dominant copepod species. Symbols as in Fig. 1.

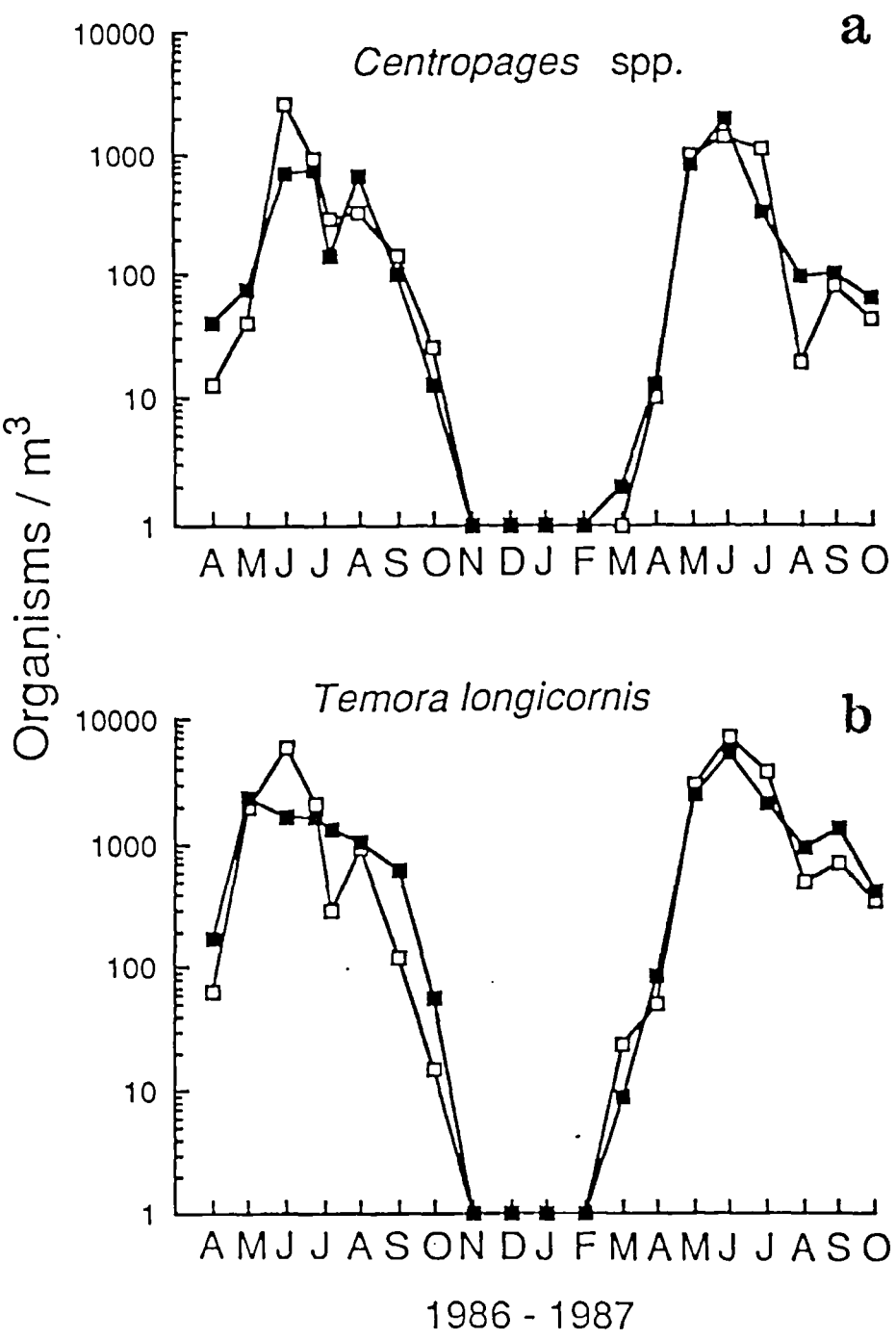


Fig. 31. Seasonal cycle of dominant copepod species. Symbols as in Fig. 1.

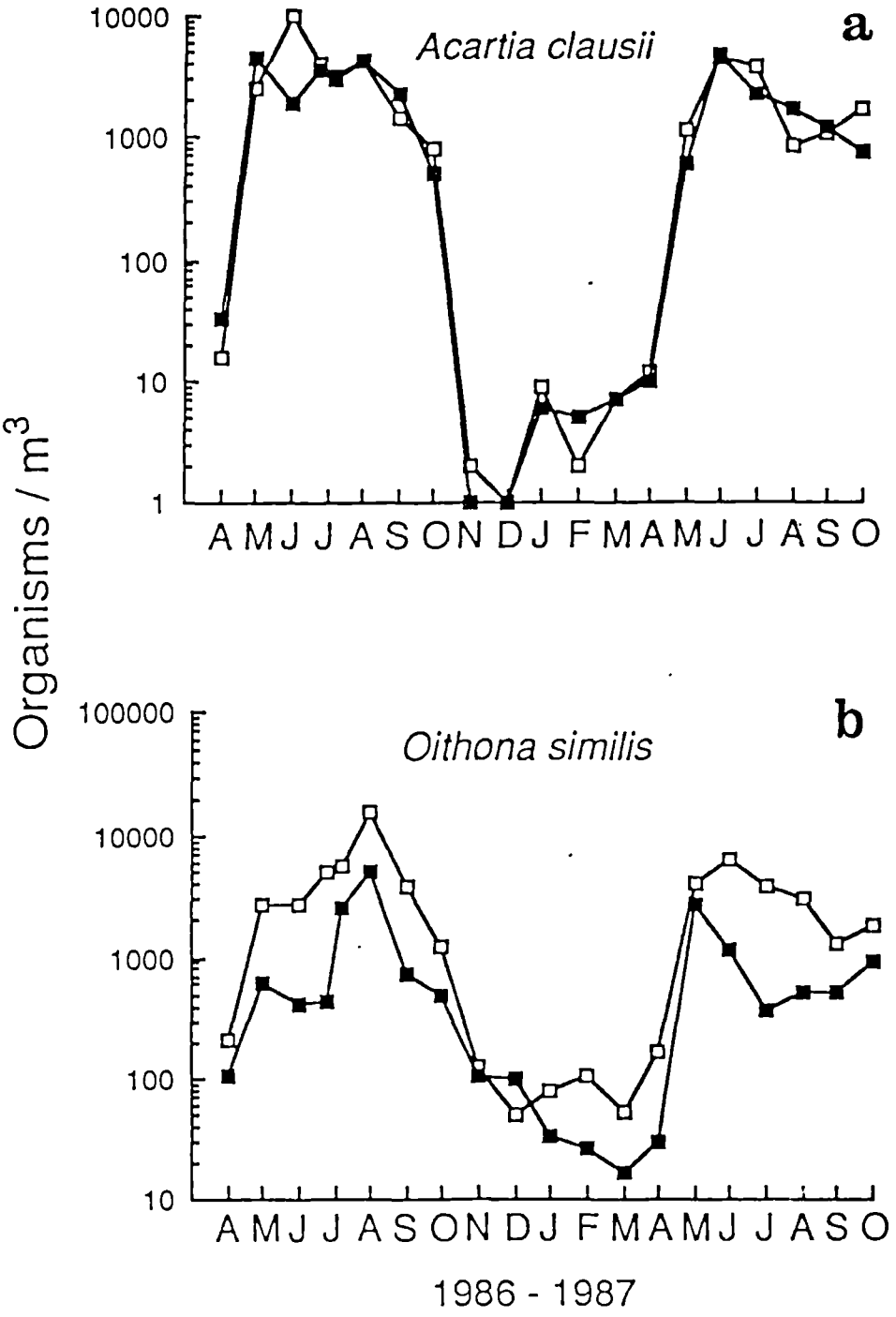


Fig. 32. Seasonal cycle of dominant copepod species. Symbols as in Fig. 1.

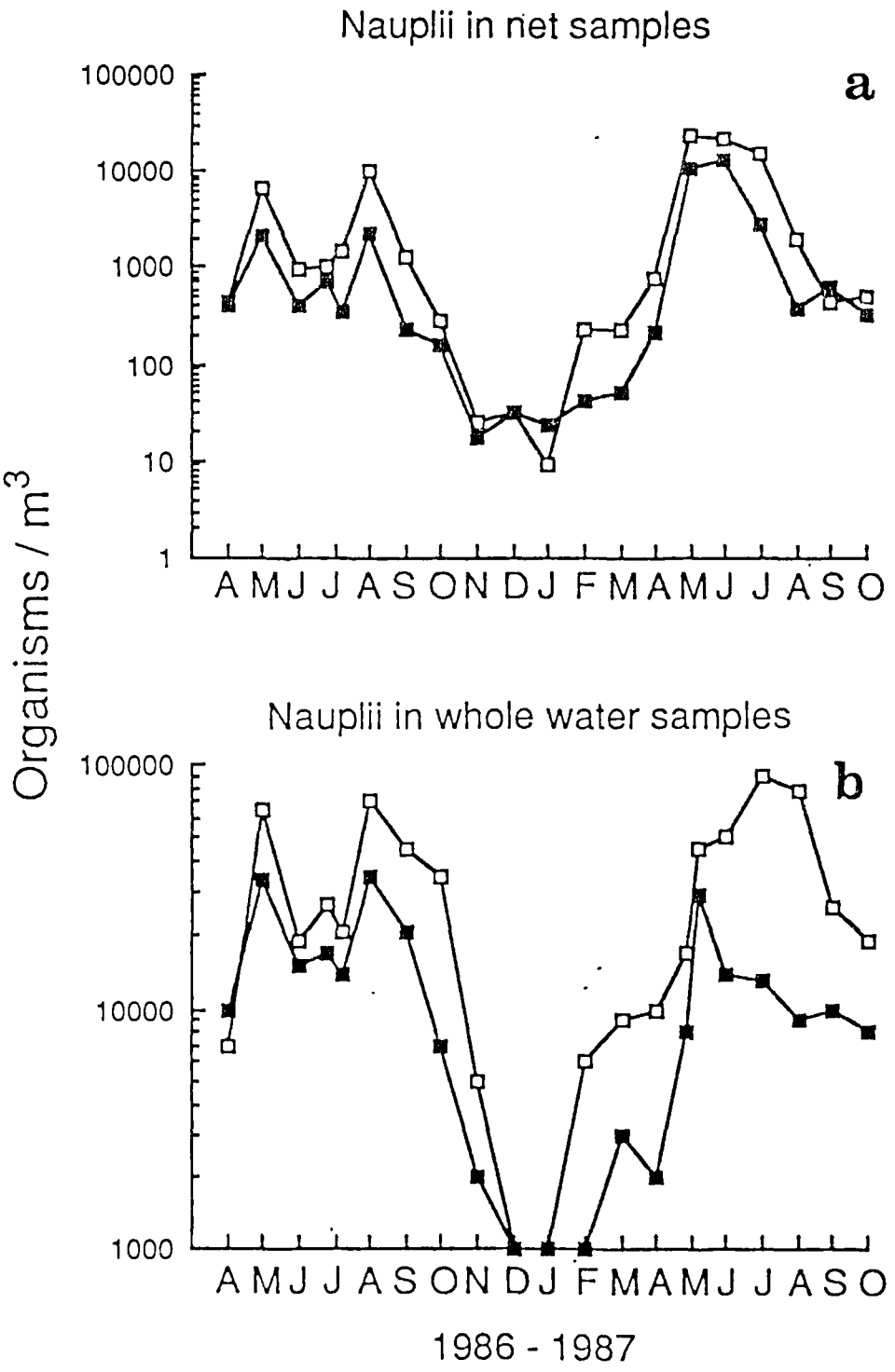


Fig. 33. Seasonal cycle of copepod nauplii.
Symbols as in Fig. 1.

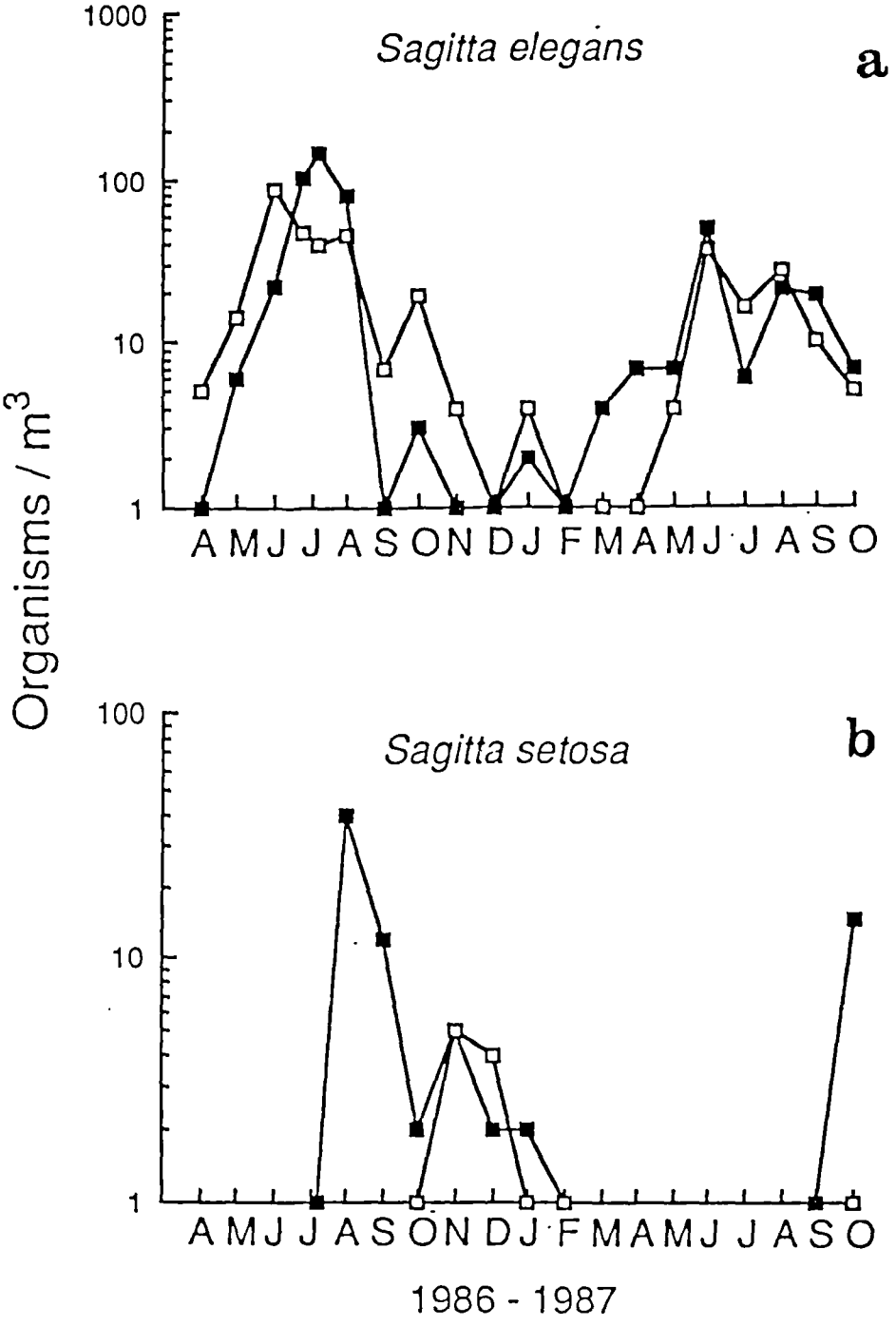


Fig. 34. Seasonal cycle of chaetognaths. Symbols as in Fig. 1.

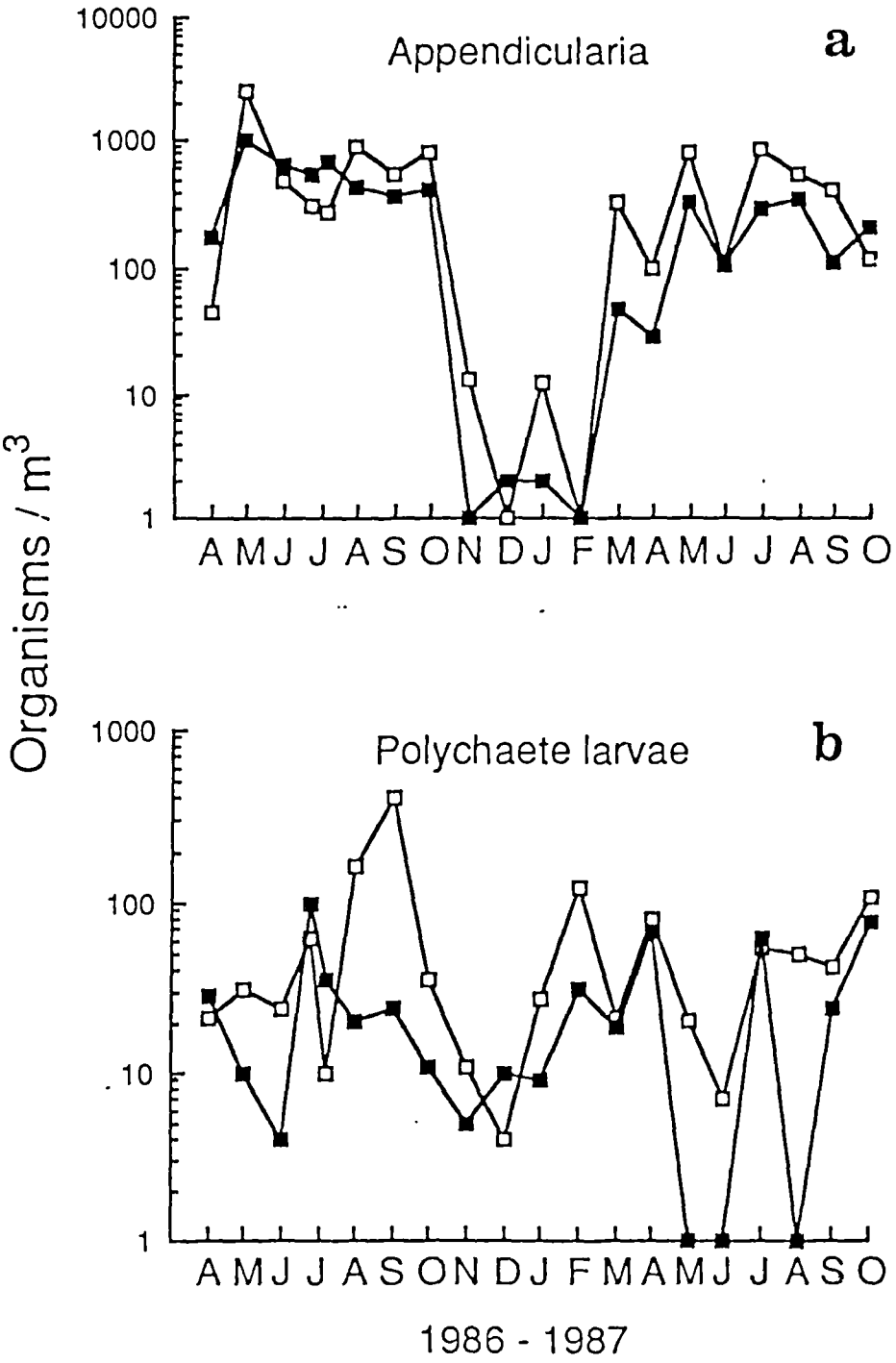


Fig. 35. Seasonal cycle of (a) tunicates and (b) polychate larvae. Symbols as in Fig. 1.

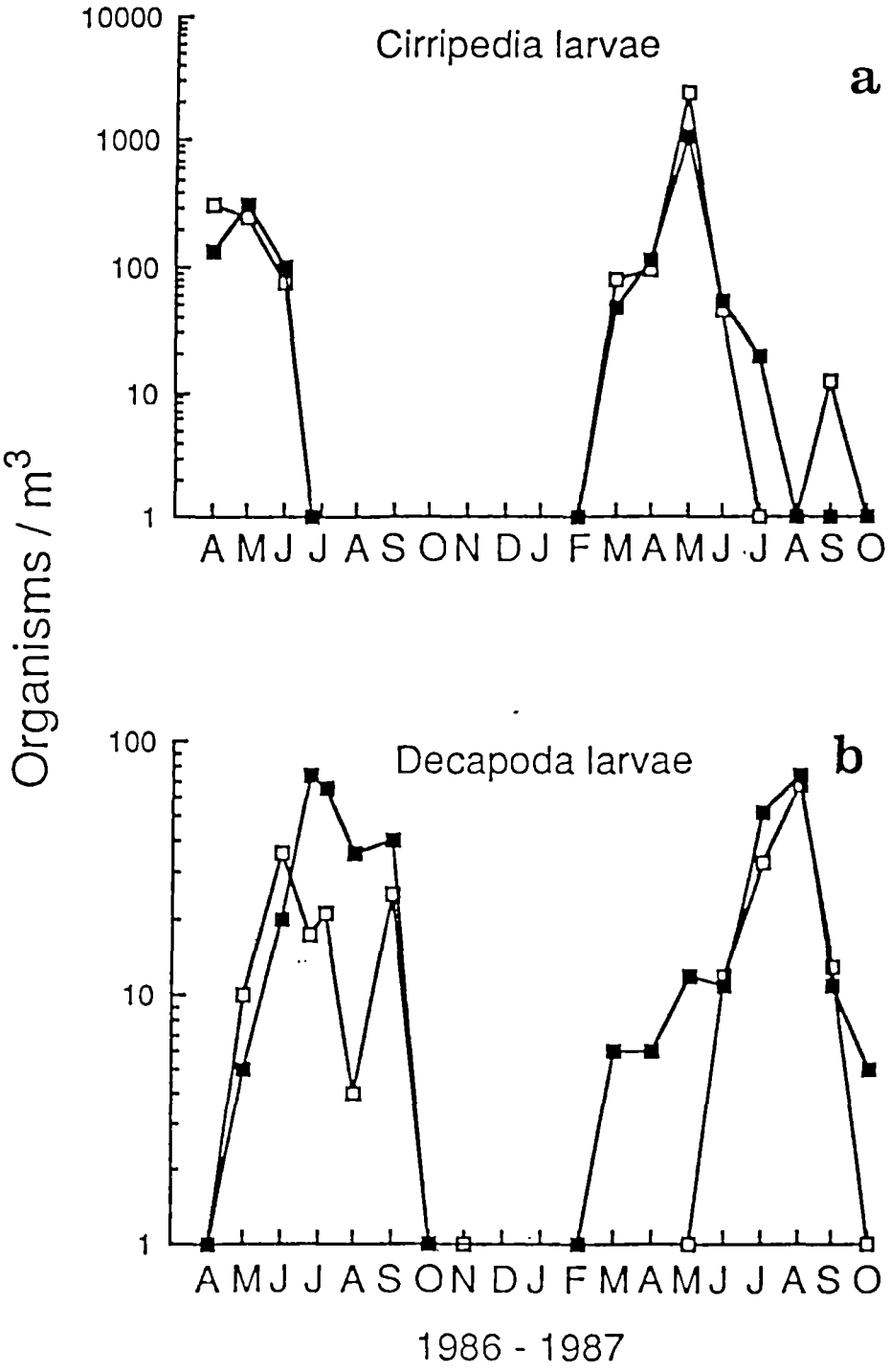


Fig. 36. Seasonal cycle of meroplanktonic larvae. Symbols as in Fig. 1.

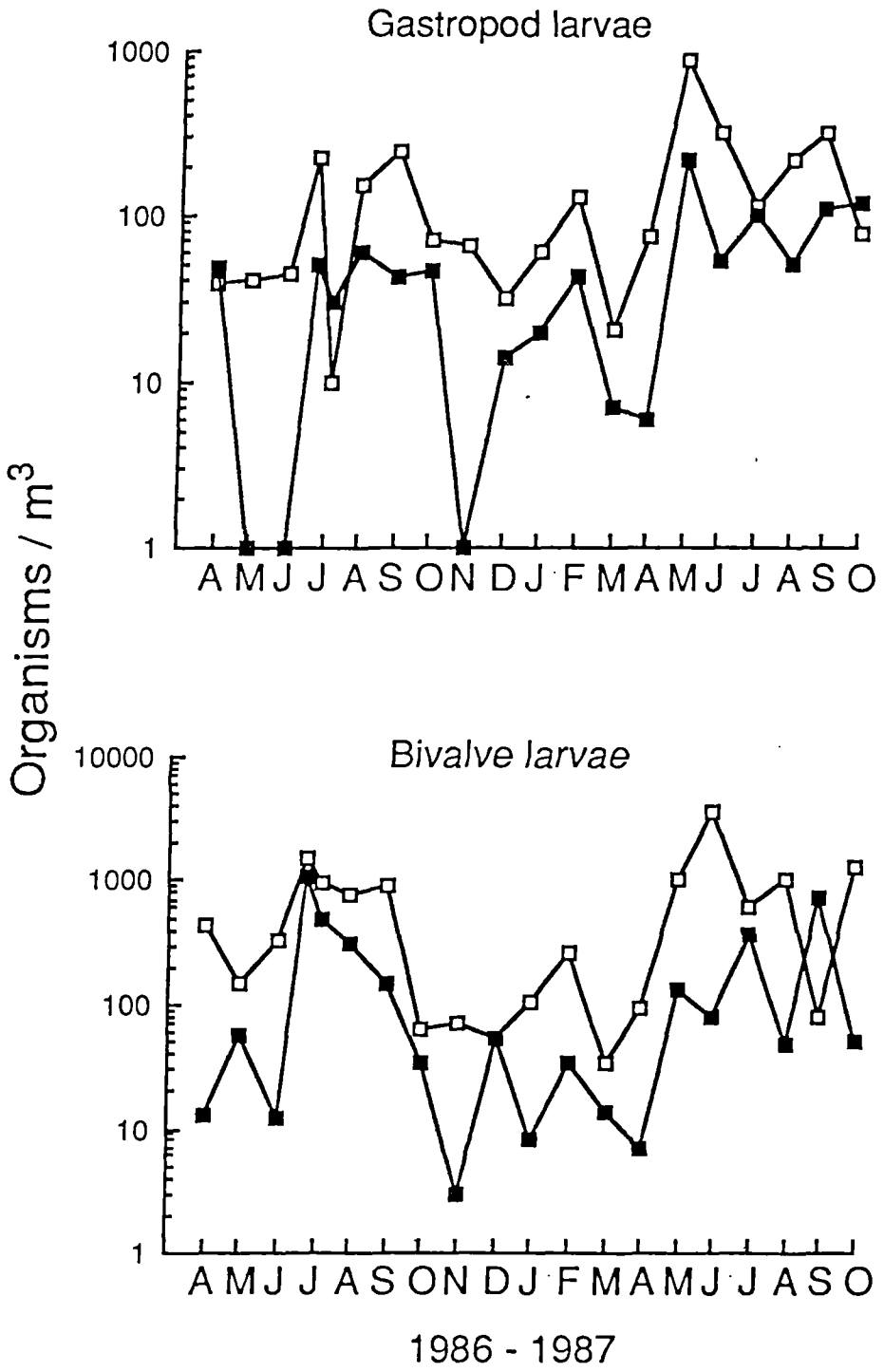


Fig. 37. Seasonal cycle of meroplanktonic larvae. Symbols as in Fig. 1.

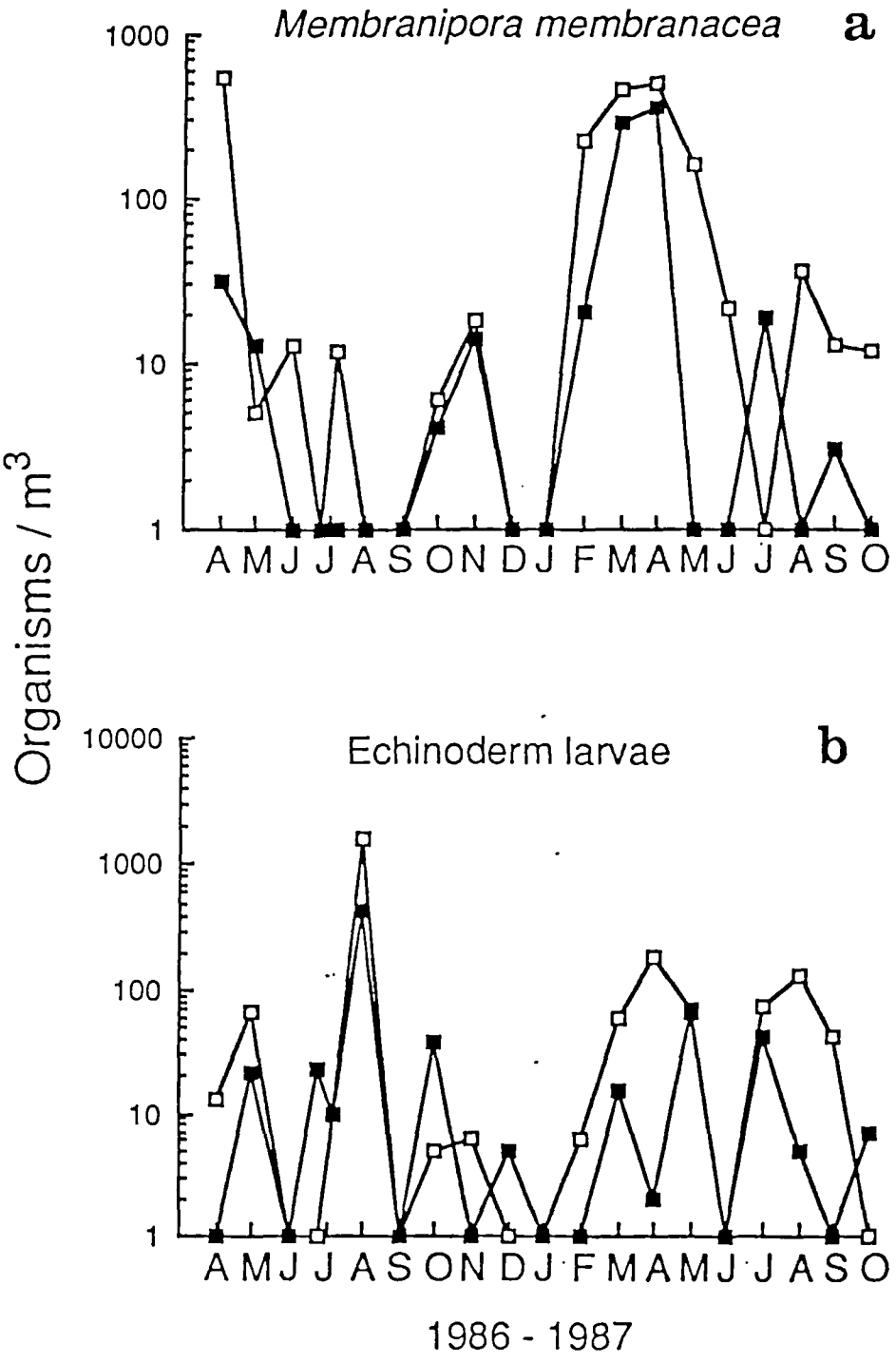


Fig. 38. Seasonal cycle of meroplanktonic larvae. Symbols as in Fig. 1.

SECTION FIVE

GENERAL DISCUSSION

In their study of the western Irish Sea Fogg *et al.* (1985a,b) observed that three, possibly four distinct ecosystems, associated with the tidal mixing, developed each year in the vicinity of the front. Their conclusions were based on observations made from frequent stations at several depths along an extensive transect, on a multidisciplinary approach combining the expertise of a number of workers and on a very refined statistical analysis of the results (Kassab *et al.* 1985).

Because of the simple descriptive nature of this study it is not possible to reach any definite conclusions regarding the precise nature of the hydrographic environment like those found by Fogg *et al.* (1985a,b). The front dividing mixed from stratified waters in the western Irish Sea extends approximately from the southern tip of the Isle of Man to the Irish coast near Dublin. It is possible therefore that on some occasions some of the stations worked in the present study might have been in frontal waters. Also, since samples for phytoplankton analysis were collected only from 5 and 15 m a deep chlorophyll maxima at the deepest stations 1 and 2 may have been overlooked. Slinn (1974) reported that deep subsurface chlorophyll *a* maxima developed each year at the deeper stations on a section along the 54° parallel cutting across the northern boundary of the highly stratified region to the southwest of the Isle of Man. North of the 54°00'N parallel temperature layering is also apparent in the summer, but temperatures, in general, are not as great as further south and Δt rarely exceed 4° C). Despite these limitations, however, this study has shown a number of highly significant differences in biological parameters between the well mixed waters to the east of the Isle of Man and the more stratified waters to the west. In general most groups examined showed significantly higher abundances along the west rather than the east transect. The significantly higher abundances of microflagellates in the more

stratified waters to the west, as compared to the east, fall in well with the observations of Beardall *et al.* (1982) that microflagellates made a higher contribution to total phytoplankton numbers moving from mixed to progressively more stratified waters in the western Irish Sea. Similarly, the higher abundances of dinoflagellates on the west side are in accordance with the findings of Holligan et *al.* (1980) that increased stability of the water column is characterized by higher dinoflagellate numbers. The significantly higher abundances of ciliates on the west support the findings of Holligan *et al.* (1984) and Fogg *et al.* (1985) of the greatest importance of microheterotrophic processes in stratified rather than mixed waters. The greatest abundance of several copepods species and most meroplanktonic larvae are in accordance with the findings of Williamson (1952, 1956a, b) and Scrope-Howe & Jones (1985) that zooplankton biomass is significantly higher in more stratified rather than mixed waters. The higher numbers of nauplii at the westernmost stations also suggests a higher zooplankton production in more stable waters. The different percentage contribution to total zooplankton abundance by different species (e. g. *Oithona similis* or *Pseudocalanus elongatus*) also falls in well with the observations of Scrope-Howe & Jones (1985) of the different composition of zooplankton in mixed and stratified waters in the western Irish Sea.

All these findings support the hypothesis that the well mixed nature of the hydrographic environment is responsible for the low production of the Irish Sea (Brander & Dickson 1984). The findings that even at the westernmost stations, which can be considered as representative of stratified waters in the Irish Sea (Pingree & Griffiths, 1978; Fogg *et al.*1985a), plankton production is characterized by a late, short cycle, suggests that even in these waters tidal mixing exerts a major impact.

The implications of the effects of tidal mixing on phytoplankton production and on the success of higher trophic levels have been discussed by a number of authors. If production is reduced during the year due to a late start, an early finish, or to lessened photosynthesis during the growth season, then the copepods and fish will either grow less or store less fat, or both. Extension of the season later than normal

may not make good this misfortune, as they might already at that time have responded to the stimuli that send them on their autumn migration or induce them to encyst. The result of an inadequate store of food reserves may not become apparent until near the end of the winter period, that is shortly before the following spring, when the populations could be approaching starvation. This may arise in the way stated, or after normal fattening in one year followed by a delayed spring bloom the next. In any case the population would be inadequately insured against stress. One further possible consequence of poor feeding conditions in the preceding year is the effect on reproductive potential. Many fish spawn at the end of winter before the spring bloom begins, so that the resources which can be devoted to fecundity are acquired the year before. Starvation or lower than average food reserves may then lead to fewer eggs than usual being produced. In the absence of information on egg and larval mortality, this effect may produce an unexpected mismatch, even though mismatch has not occurred. The opposite situation, where a good season is followed by above-average fecundity, will similarly simulate a very good match. The laying down of fat in herring is known to be related to the abundance of zooplankton, and the autumn spawning herring from the Isle of Man lay down fat 2-4 weeks later than autumn spawned herring from the North Sea. Consequently their breeding season is also 2-4 weeks later. Whereas at the same time larval herring in the North Sea would be benefiting of the autumnal bloom, in the north Irish Sea fish larvae hatch at a time when phytoplankton biomass is at its lowest and zooplankton abundance is also rapidly decreasing. In such conditions fluctuations in plankton production could have an enormous impact on the survival and recruitment of this species.

By comparing fish production between different areas of shelf around the British Isles Brander & Dickson (1984) observed that in the Irish Sea yields per unit area were consistently lower than elsewhere. In contrast they observed that shellfish yields in proportion to the total were considerably higher. They suggested that this might be an indication of greater flow through the benthic food chain.

A number of studies have shown that in temperate and high-latitude regions the

settling spring bloom is one of the main inputs of particulate organic matter from the pelagic to the benthic system and can deliver as much as one-third of the annual phytoplankton production and represent over one-half of the total annual input of organic carbon to the benthos (e.g. Parsons *et al.* 1977; Smetacek *et al.* 1978; Smetacek 1980). This pulse of organic matter can also be seen in some deep-sea sediments at 4000 m (Billet *et al.* 1983). Given the shallowness of most of the Irish Sea, and the intensity of mixing phytoplankton material may arrive at the sediment surface very rapidly and in a little decomposed state. The availability to the benthos of phytoplankton in a living or relatively intact form would mean that this material would presumably be much more readily available to meiofauna and macrofauna, thus increasing the efficiency of the transfer of energy to higher trophic levels. In stratified waters, in contrast where smaller losses occur to the benthos, most of the material flux to the surface sediments is mostly in the form of fecal pellets and non-living detritus, forms largely unavailable to benthic fauna without first being transformed by microbes; a transformation which would result in a net loss of perhaps half the available energy.

At present, because relatively little is known about production processes in mixed waters in the Irish Sea speculation could be endless. Brander & Dickson (1984) have emphasized on the need for further studies. It is hoped that this investigation might provide some useful information on some features of this environment.

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