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Temporal variability of viruses, bacteria, phytoplankton and zooplankton in the western English Channel off Plymouth

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The temporal distribution of autotrophic and heterotrophic components of the planktonic community was studied from samples collected weekly at station L4, located to the south of Plymouth, UK, from October 1992 to January 1994. Phytoplankton succession followed the typical pattern of temperate waters, the development of a summer *Gyrodinium aureolum* bloom being the most prominent feature. Bacterial numbers were significantly correlated with temperature during autumn and winter, whereas resource availability and predation, including viruses, appear to be the most important controlling factors in spring and summer. High mesozooplankton densities, mainly copepods, were observed throughout most of the study associated with a series of diatom blooms, and also during autumn when low phytoplankton biomass was measured. This data set was analysed in order to build up conceptual trophodynamic models whereby the role of biological communities on the cycling of organic matter could be inferred. The results obtained in this study provide empirical evidence supporting the existence of a sucession of trophic organization patterns in a coastal temperate environment. Classical models (herbivorous or microbial webs) appeared episodically whereas transition models (multivorous web) dominated throughout most of the seasonal cycle.

INTRODUCTION

Two models of trophic organization are generally recognized in planktonic ecosystems: the herbivorous web and the microbial food loop (Fenchel, 1988; Cushing, 1989; Legendre & Le Fèvre, 1989). The herbivorous web is characteristic of recently stabilized, nutrient-rich waters, being typical of the spring bloom in temperate regions (e.g. Brunet et al., 1996). The microbial loop predominates in oligotrophic waters where a large portion of primary production is due to small-sized organisms (e.g. Li et al., 1983; Caron et al., 1995). Legendre & Rassoulzadegan (1995) described two intermediate conceptual models: the multivorous web, where herbivorous and microbial processes are of similar importance, and the microbial web, where autotrophic pico- and nanoplankton, heterotrophic bacteria and zooflagellate grazers are the basis of planktonic functioning.

An approach to study the succession of trophic organizations and their role in the cycling of organic matter is to analyse the temporal variability of planktonic components (Michaels & Silver, 1988; Legendre & Le Fèvre, 1989; Banse, 1992). In this context, several papers have described the successional patterns of phytoplankton in North Atlantic waters (e.g. Holligan & Harbour, 1977; Colebrook, 1979). Similar studies have described zooplankton dynamics since 1931 thanks to the foundation of the 'Continuous Plankton Recorder Survey' (Rae & Fraser, 1941), as well as more detailed descriptions of seasonal cycles of, e.g. copepods (Beare & McKenzie, 1999), cladocerans (Gieskes, 1971) and chaetognaths (Bainbridge, 1963).

Since the work of Azam et al. (1983) the microbial loop has been the focus of many investigations on the role of bacteria and nanoflagellates (Tuomi & Kuuppo, 1999), cyanobacteria (Murphy, 1985), ciliates (Nielsen & Kiørboe, 1994) and viruses (Bratbak et al., 1995) in the planktonic system. These studies point out the importance of small organisms in the cycling of nutrients and organic matter (Fenchel, 1988; Fuhrman, 1992). However, there are few comprehensive studies of all planktonic components (Holligan et al., 1984; Roman et al., 1995, Richardson et al., 1998) and also accounting for seasonal variations (Bradford-Grieve et al., 1999). In this paper we present the temporal variation of the planktonic system (from viruses and bacteria to mesozooplankton) in a temperate coastal system (English Channel). The chosen sampling station (L4) is situated in summer between stratified and transitional mixed-stratified waters (Figure 1) and on some occasions represents the margin of the tidal front characteristic of this region (Pingree, 1978). We have summarized the observed annual succession of plankton in a series of conceptual trophodynamic models from which the role of biological communities in the cycling of matter can be inferred.

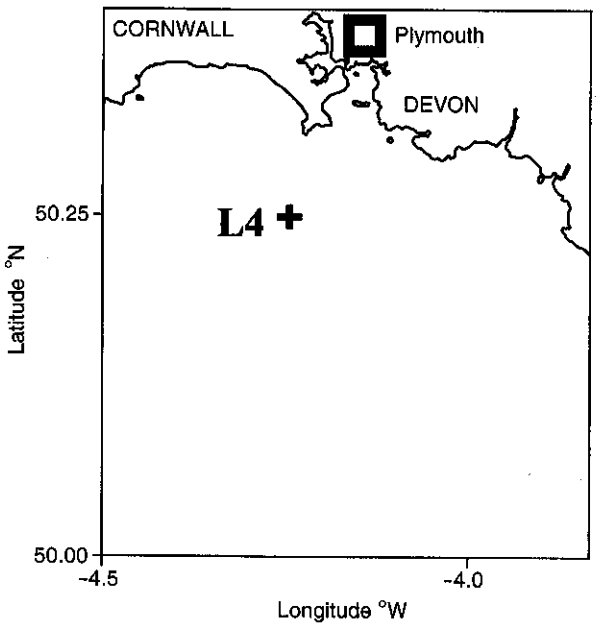

Figure 1. Location of station L4.

MATERIALS AND METHODS

Weekly visits were carried out on-board RV 'Squilla' to station L4, located to the south of Plymouth, UK (50°15'N 04°13'W; depth 51 m) from October 1992 to January 1994 (Figure 1). On each date from May 1993 onwards, the thermohaline structure of the water column was monitored by means of a CTD probe developed from the Undulating Oceanographic Recorder (UOR) (Aiken & Bellan, 1990). Prior to that date measurements were made with a Braystoke TSD probe.

Water samples were collected from 10 m depth using 5-l Niskin bottles for the determination of inorganic nutrients and chlorophyll-*a* (chl-*a*) concentrations and the abundance of viruses, bacteria, cyanobacteria, phytoplankton and microzooplankton populations. Seawater subsamples (100 ml) were drawn from each bottle and filtered inmediately through 0.45 μm Whatman membrane filters. Filtered samples were maintained deep frozen (−20°C) and later analysed for nitrate using the spectrophotometric methods described in Strickland & Parsons (1972). Water samples for the determination of chl-*a* were pre-filtered through 10 and 5 μm Nucleopore membrane filters and Whatman GF/F glass fibre filters. Filters were kept frozen until further fluorometric analysis with a Turner Designs 1000R fluorometer after extraction in 90% acetone overnight.

The abundance of free virus-like particles (VLP) was determined by counting samples preserved with buffered formalin. Suspended particles were harvested by centrifugation (200,000×g) for 1 h, prepared for transmission electron microscopy and counted at ×100,000 magnification following protocols described in Børsheim et al. (1990) and Bratbak et al. (1990). View fields were randomly selected and counted until total counts exceeded 200.

Bacterial and cyanobacterial cells were counted by epifluorescence microscopy. Samples for bacterial counting were stained previously with 4,6-diamidino-2-phenylindole (DAPI) (Porter & Feig, 1980) and filtered through black 0.2 μm polycarbonate filters. Water samples (10–20 ml) were filtered through similar filters and the abundance of cyanobacteria quantified directly under the microscope. Identification and enumeration of phytoplankton cells were performed by inverted microscopy by examining duplicate samples preserved in buffered formalin (to preserve calcium carbonate structures), and Lugol's iodine solution. The bottom of the sedimentation chamber was completely scanned to count large and less abundant cells. Two perpendicular transects were further examined at high magnification (×400) to enumerate smaller specimens.

Cell to carbon conversion factors for VLP, bacteria and cyanobacteria, were 0.08 fg C VLP^{-1} (Bratbak & Heldal, 1992), 20 fg C $cell^{-1}$ (Lee & Fuhrman, 1987) and 53 fg C $cell^{-1}$ (I.R. Joint & A.J. Pomroy, personal communication), respectively. Phytoplankton cell counts were converted to carbon biomass as described in Holligan et al. (1984).

Mesozooplankton samples were collected with a standard 200 μm WP2 mesh. The net was towed vertically from bottom to surface at a speed of ~ 0.5 m s^{-1}. Samples were preserved in 4% formalin in sodium borate-buffered seawater and counted and identified with a binocular microscope.

RESULTS

Thermohaline characteristics and inorganic nutrients

The thermal structure of the upper water column (Figure 2) showed mixed conditions in February. Slight

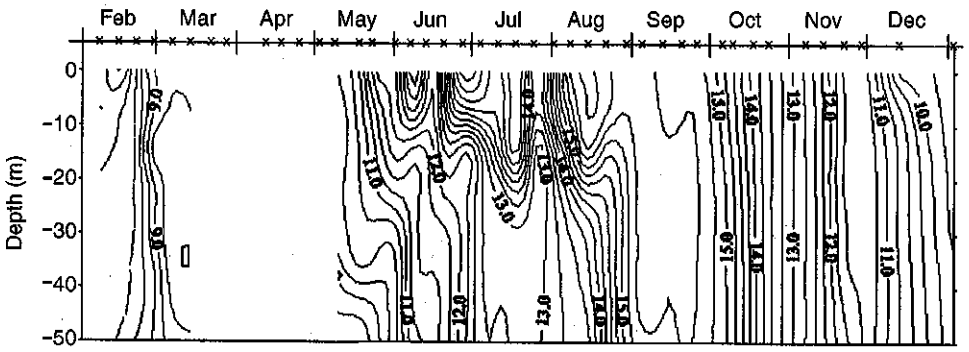

Figure 2. Temporal variation of temperature (°C) (February–December 1993).

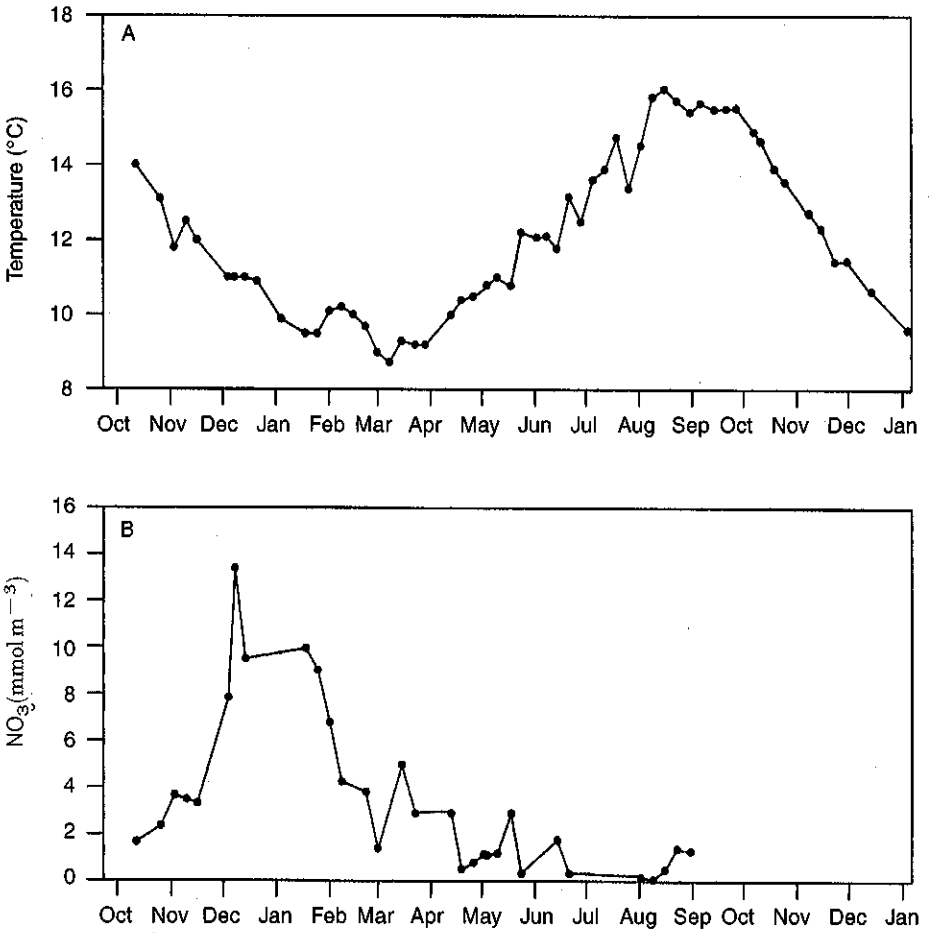

Figure 3. Temporal variation of: (A) temperature at 10 m (°C); and (B) NO_3 concentration (mmol m^{-3}), from October 1992 to January 1994.

stratification developed from March until June, when a 2.5°C gradient in the first 10 m was measured. The thermocline gradually deepened in July and eroded at the end of this month. During August stratification was transiently re-established until complete vertical mixing in late September.

The seasonal cycle of temperature at 10 m depth (Figure 3A) showed a decrease during autumn–winter reaching a minimum of 8.7°C in March. The temperature increased steadily during summer months up to 16°C in August. Available salinity data at 10 m depth showed a maximum in May and a decreasing trend from spring to summer (34.4–34.6 psu in June and August).

NO_3 concentration (Figure 3B) reached values of 13.4 mmol m^{-3} during December 1992 then showing a decreasing trend in spring–summer. Concentrations were lower than 0.4 mmol m^{-3} at the end of June and early August. The lack of a complete vertical distribution of salinity and temperature hinders the interpretation of observations made during winter and early spring.

Temporal distribution of planktonic organisms

Viruses and bacteria

Virus biomass (Figure 4A) increased gradually from an average biomass of 0.47 mg C m^{-3} in winter 1992 to 1.82 mg C m^{-3} in summer, with a maximum in June coinciding with mixing–stratification conditions. Virus biomass was significantly correlated with temperature at 10 m (r=0.61, P<0.001, N=41) and total phytoplankton biomass (r=0.51. P=0.001, N=41).

Bacterial biomass (Figure 4B) showed a pattern similar to that of temperature at 10 m during autumn and winter 1992 (r=0.82, P<0.001, N=14), and increased from spring to summer (average 10 and 21 mg C m^{-3}, respectively). In February, a maximum of bacterial biomass (30 mg C m^{-3}) was observed coinciding with an increase of 1°C in surface temperature and decreasing NO_3 concentrations (Figure 3). From April onwards the correlation between bacterial biomass and surface temperature was not significant, (r=0.23, P=0.4, N=15) but it was found a significant relationship between bacterial and viral biomass during springsummer (r=0.64, P<0.01, N=16).

Autotrophic microplankton

Figure 5A shows the temporal variation of total chl-*a* concentration, and the relative contribution of three size-classes. Chlorophyll-*a* concentration showed two maxima: in April, during a transition phase in water column stability; and in July, during a period of intense stratification (Figure 2). Organisms less than 5 μm were the most important phytoplankton, contributing in April up to 44% of total chl-*a* while in July they represented 65% of chl-*a*.

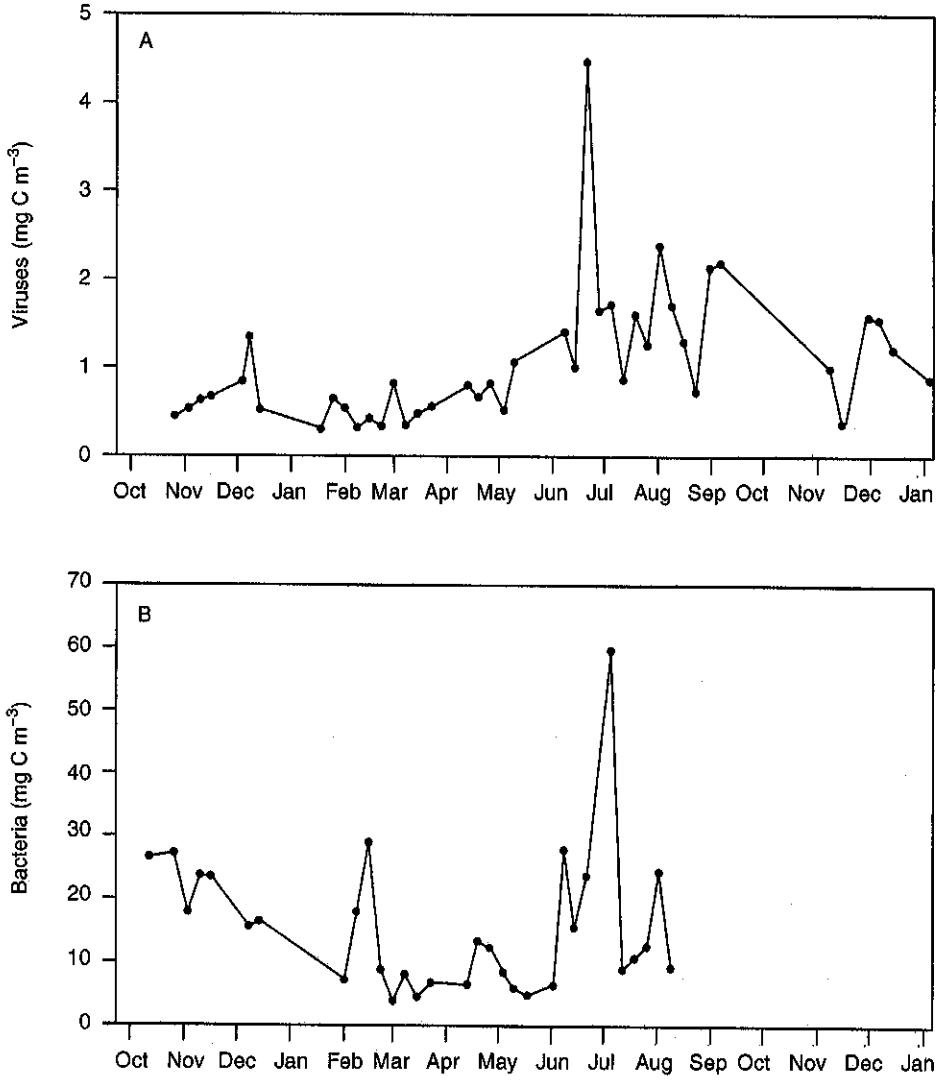

Figure 4. Temporal variation of: (A) virus biomass (mg C m^{-3}); and (B) bacterial biomass (mg C m^{-3}).

Total biomass of autotrophic plankton displayed a sharp maximum of 600 mg C m^{-3} during the stratification period in July (Figure 5B) with lowest values in autumn–winter 1992. A different pattern emerged when phytoplankton abundance was considered (Figure 5C), showing maximum values in April (9000 cells ml^{-1}) and summer (stratification periods in June, July and mixing–stratification in August).

Cyanobacterial biomass (Figure 6A) showed relatively high values in autumn 1992, March and August 1993. The autumn maximum was related to a phase of transition in water column stability, as suggested by the increase in nitrate concentration (Figure 3), while that in March took place after an increase of bacterial biomass and the lowest seawater temperatures monitored during the study. Cyanobacterial biomass was correlated with temperature at 10 m during autumn–winter 1992 (r=0.56, P=0.03, N=15).

Flagellate biomass (Figure 6B) decreased from autumn to winter and sharp fluctuations were observed during spring and summer with maximum values in April, June (in parallel to bacterial and viral maxima) and August. These higher biomasses were due to larger organisms rather than to an increase of abundance during summer.

Diatoms were more abundant between April and October (Figure 6C) and the spring bloom occurred in April due to *Chaetoceros socialis*. This event represented the highest biomass of diatoms (75 mg C m^{-3}) accounting for 56% of autotrophic plankton biomass in that period. Additional maxima occurred in summer (*Thalassionema nitzschoides*, *Leptocylindrus danicus* (August) and *Biddulphia sinensis* (September)).

Autotrophic dinoflagellates (Figure 6D) were mainly present in summer, a *Gyrodinium aureolum* bloom was noted during July with the maximum phytoplankton biomass and chl-*a* concentration (Figure 5A) measured during this study. Coccolithophore biomass (Figure 6E) showed values lower than 1 mg C m^{-3} from October 1992 to June 1993 and its highest values at the diatom bloom in August.

Heterotrophic microplankton

Heterotrophic dinoflagellates (Figure 7A) reached their highest biomass in late spring and summer, being positively correlated with autotrophic biomass (r=0.58, P<0.001, N=50). The dominant organism, *Noctiluca scintillans*, had maximum abundance in June coinciding with the *G. aureolum* outburst.

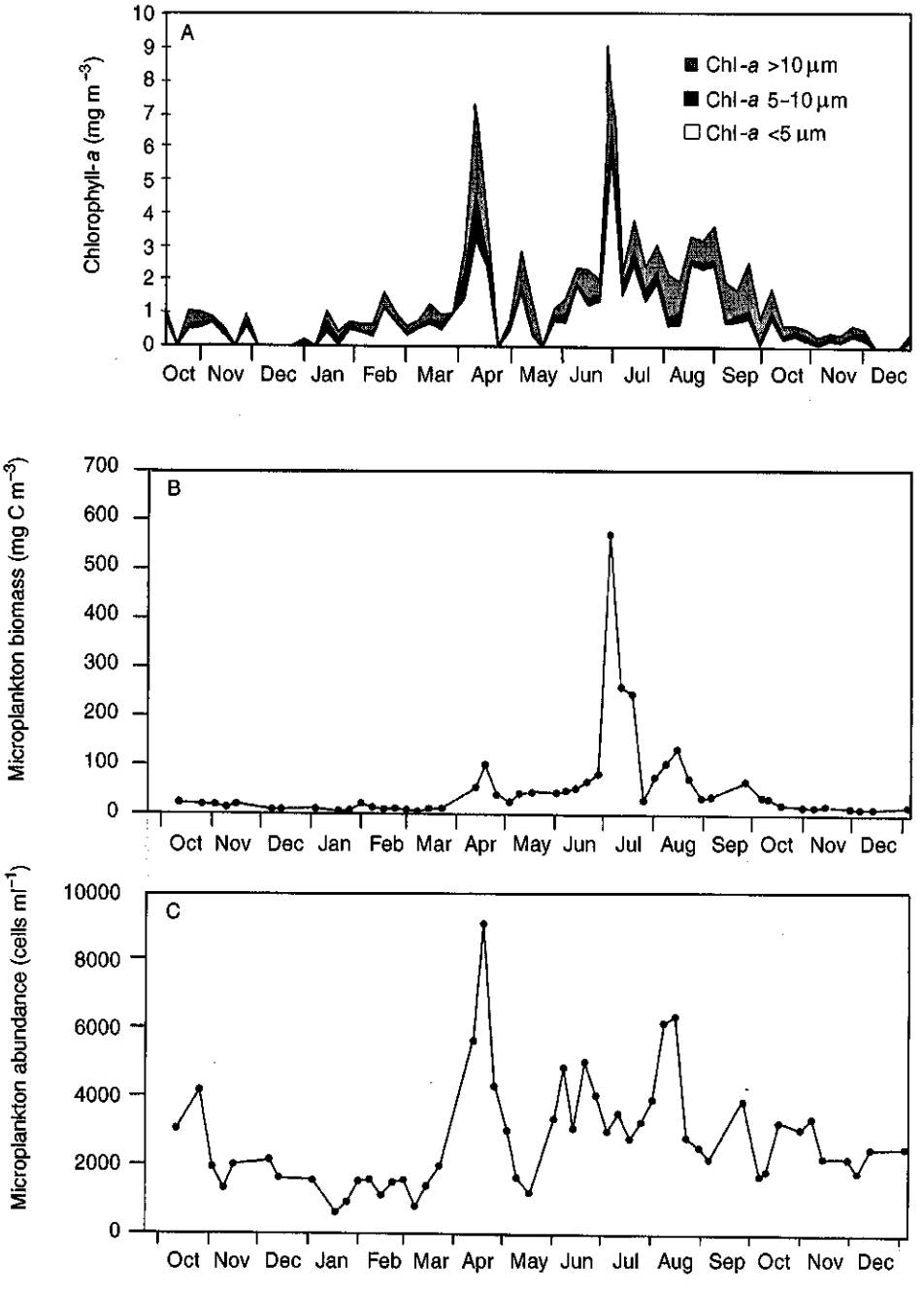

Figure 5. Temporal variation: (A) total, <5, 5–10 and >10 µm chlorophyll-*a* (mg m^{-3}); (B) total microplankton biomass (mg C m^{-3}); and (C) total microplankton abundance (cells ml^{-1}).

Ciliates were not much abundant during autumn and winter (averaged biomass 3.9 ±3.4 mg C m^{-3}, Figure 7B) and reached higher values in spring (averaged biomass of 10.1 ±5.4 mg C m^{-3}) and in summer. The absolute maximum of ciliate biomass was registered in June before the maximum of *N. scintillans* due to small-sized *Strombidium* sp.

Relative contribution of the different microplankton groups

Bacteria and flagellates dominated during autumn and winter 1992 (Figure 8), when they represented 71% of the total biomass. In early spring diatoms were the most relevant group (31%) whereas autotrophic and heterotrophic dinoflagellates accounted for 56% of total microplanktonic biomass from May to August. In the period October 1992–August 1993 the contribution of virus, bacteria and cyanobacterial biomass to total microplanktonic biomass was 1.5, 27 and 0.7% respectively. The ratio phytoplankton:bacterial biomass (an indicator of autotrophic vs heterotrophic processes), was close to 1:1 during autumn and winter 1992. In contrast, in spring and summer it was about 5:1, reaching higher values during the major diatom blooms in spring and August and the *G. aureolum* bloom (10:1 and 30:1, respectively).

Mesozooplankton

Copepod abundance was higher than 1000 ind m^{-3} during most of the study (Figure 9A). Copepod abundance was positively correlated with temperature at 10 m during autumn and winter 1992 (r=0.79, P<0.001,

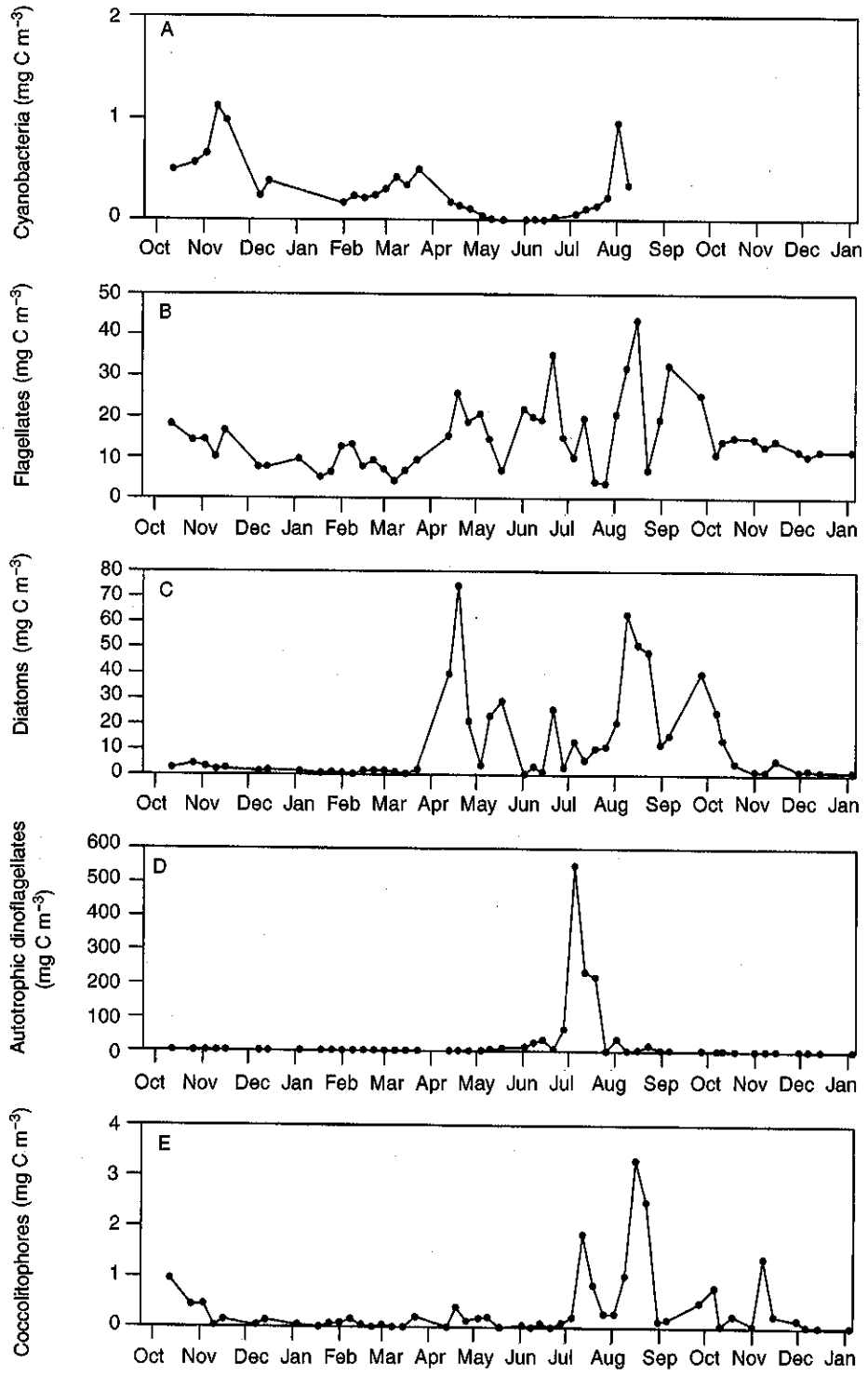

Figure 6. Temporal variation of the biomass (mg C m^{-3}) of autotrophic plankton groups: (A) cyanobacteria; (B) flagellates; (C) diatoms; (D) autotrophic dinoflagellates; and (E) cocolithophores.

N=21); they were abundant in autumn 1992 when large phytoplankton contributed 20% of total autotrophic plankton biomass. *Paracalanus* sp., *Pseudocalanus* sp., *Acartia* spp., and the cyclopoids *Oithona* sp. and *Oncaea* sp. were dominant components during this period. Copepod abundance reached high values in 1993 at the onset and decline of the spring diatom bloom (2500 ind m^{-3}). During summer several maxima were observed associated with diatom blooms: *Temora longicornis* developed in June and July, whereas *Acartia* spp., *Calanus helgolandicus, Oithona* sp. and again *Temora longicornis* reached high values in August. During the *G. aureolum* bloom only *Oithona* sp. showed significant numbers (~250 ind. m^{-3}). After the autumn diatom bloom higher populations of *Oncaea* sp. (1000–2000 ind m^{-3}) occurred.

Cladocerans appeared episodically in spring and summer reaching maximum densities in April–May and

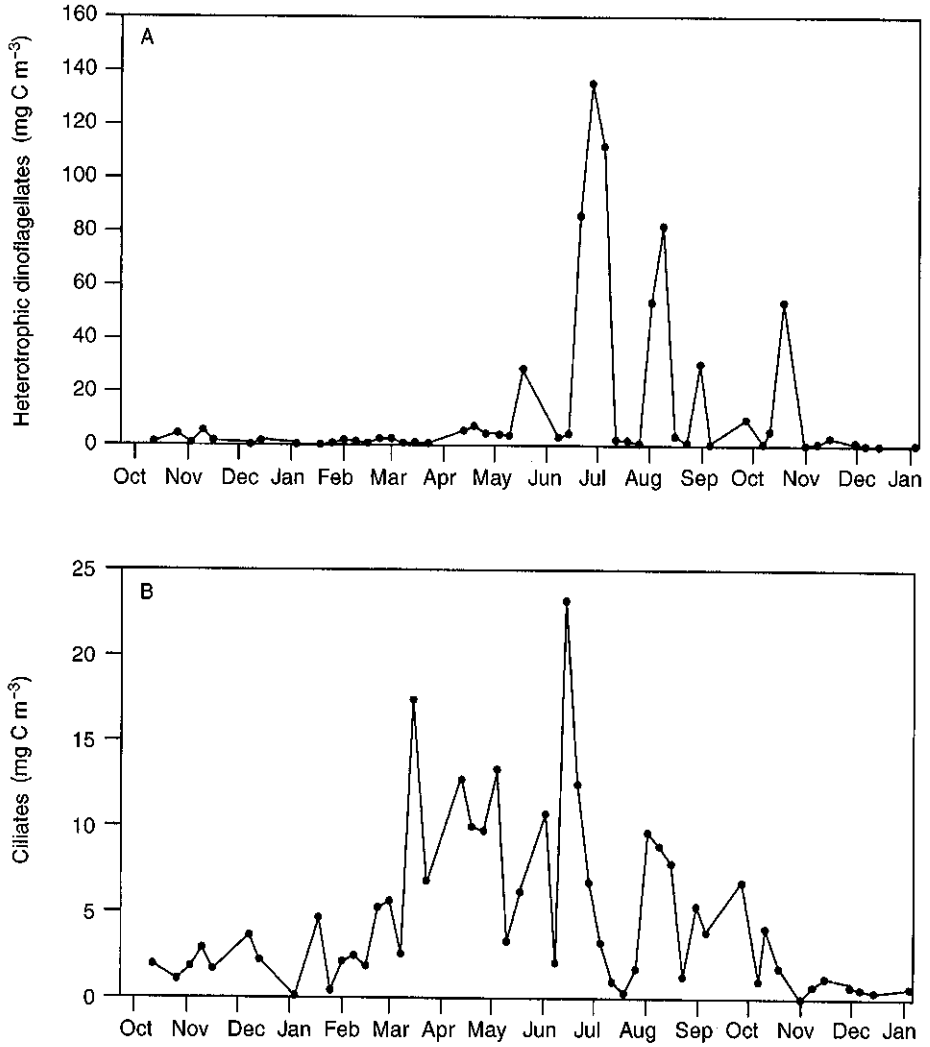

Figure 7. Temporal variation of the biomass of heterotrophic microplankton (mg C m^{-3}): (A) heterotrophic dinoflagellates; (B) ciliates.

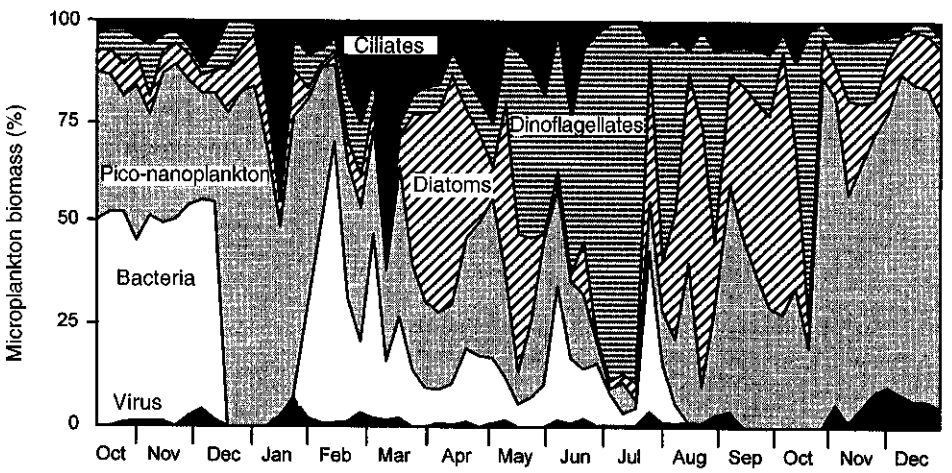

Figure 8. Temporal variation of the total accumulated biomass of virus, bacteria, pico-nanoplankton, diatoms, dinoflagellates and ciliates (mg C m^{-3}).

August (Figure 9B). The abundance of cladocerans showed a statistically significant correlation with autotrophic biomass (r=0.63, P<0.001, N=50).

Larvaceans (Figure 9C) were not present in the water column in winter increasing its abundance in March when bacteria and cyanobacteria reached maximum values. Their highest abundances were measured in April–May. Larvaceans were negatively correlated with bacterial (r=−0.46, P=0.01, N=30) and cyanobacterial biomasses (r=−0.49, P<0.01, N=31). The most abundant species was *Oikopleura dioica*, appearing also *Fritillaria* sp. in March and May.

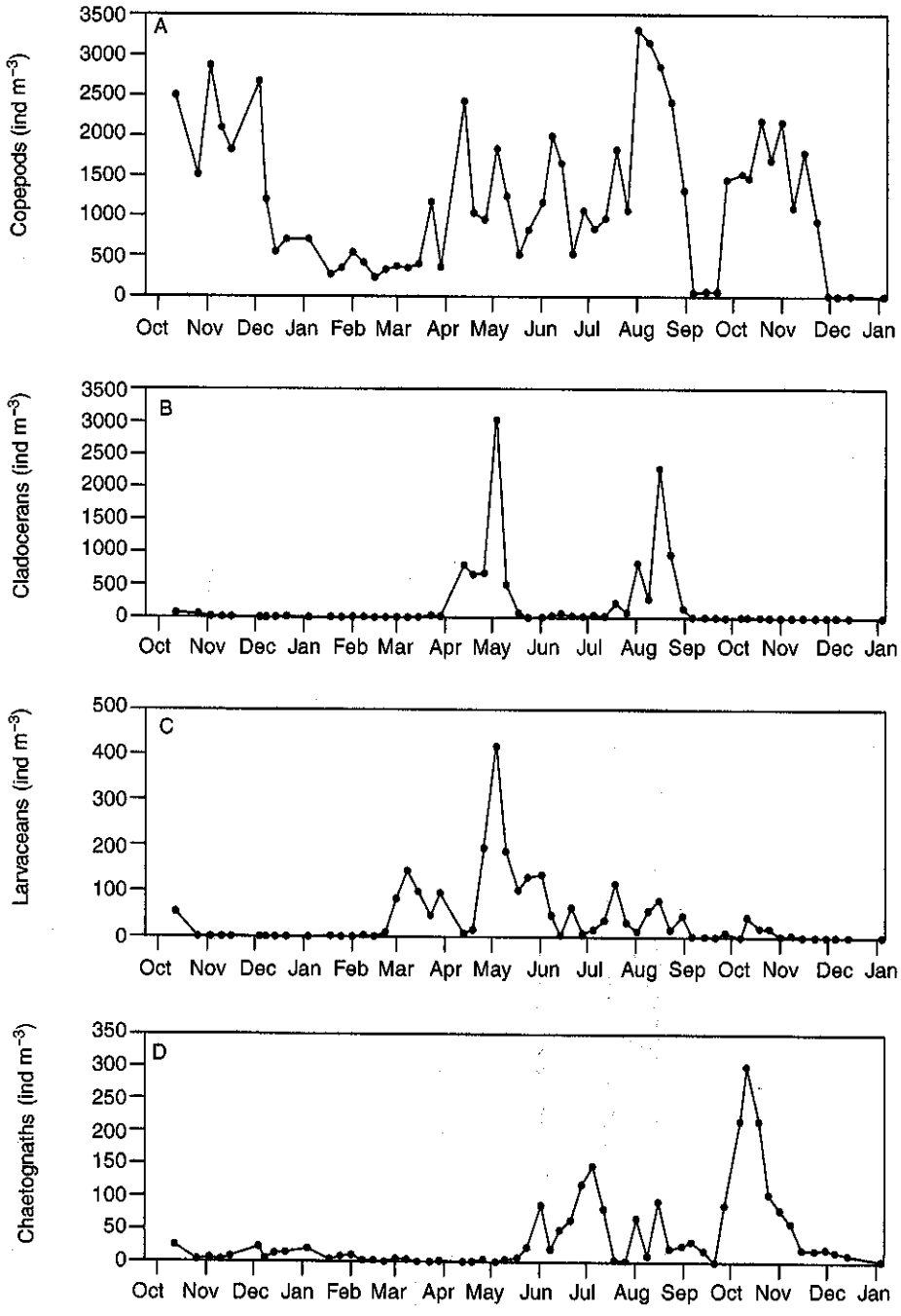

Figure 9. Temporal variation of the abundance (ind m^{-3}) of mesozooplankton: (A) copepod; (B) cladoceran; (C) larvacean; and (D) chaetognath.

Chaetognaths showed two periods of high abundance in July 1993 and October–November 1993, while their lower abundances were recorded in autumn and winter 1992 and early in 1993 (Figure 9D).

Temporal variability of planktonic food webs

The analysis of the seasonal biomass variability of the different planktonic components allowed us to infer changes in the plankton trophic organization. These changes are summarized in a sequence of conceptual models (Figure 10) related to the characterization proposed by Legendre & Rassoulzadegan (1995).

In winter a microbial web was established (Figure 10A). Primary productivity and carbon cycling was probably based on small organisms such as nanoflagellates and bacteria. Viruses showed low densities whereas cyanobacteria were not significant until the end of winter. Nutrient concentrations were high, but low seawater temperatures and vertical mixing prevented the development of high phytoplankton biomass.

A herbivorous web was characteristic of the spring bloom (Figure 10B), where microplankton biomass was mainly formed by large cells like diatoms and ciliates. Nutrients were rapidly depleted and fluxes of organic matter from pico- and nanoplankton (nanoflagellates and bacteria) to micro- or mesozooplankton were important, as is suggested by the high densities of ciliates, cladocerans and larvaceans. The close coupling observed between microplankton and copepods during the spring

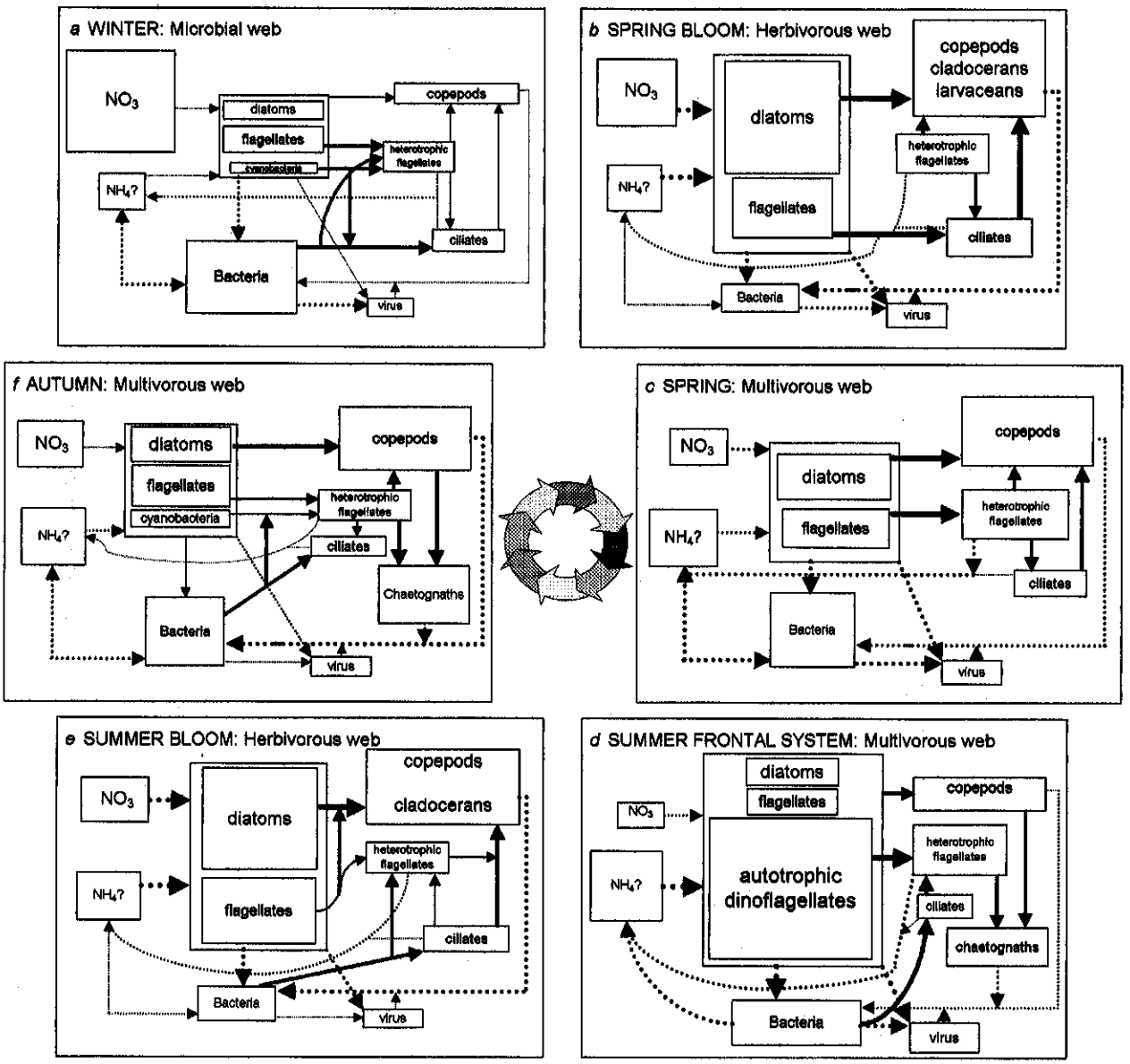

Figure 10. Temporal sequence of conceptual models of trophic webs observed at station L4 throughout the study period. The size of the compartments is proportional to biomasses (abundances in the case of mesozooplankton) measured in this study. Thickness of the arrows represent the magnitude of POC fluxes as inferred from the temporal variation of biomasses (or abundances) of the corresponding source or sink compartments. Dashed lines indicate fluxes of dissolved compounds.

diatom bloom suggests that an important fraction of primary production could be consumed and retained as particulate matter in the upper water column, then available to the subsequent pelagic community based on the regeneration of nutrients during the stratification phase (Kiørboe, 1993).

After the spring bloom (Figure 10C) nitrate concentrations are likely to be limiting phytoplankton growth and heterotrophic processes would play a major role. Therefore, the trophic organization would be a multivorous web. Viruses reached higher biomasses, playing an important trophodynamic role due to their influence on microbial activity, as suggested by the similar pattern of distribution of viruses and bacteria specially in spring and summer.

In the tidal frontal zone in summer the trophic model would be a multivorous web (Figure 10D). The large amount of phytoplanktonic biomass fuelled high rates of bacterial production. Nutrient regeneration is likely to be intense due to the presumably elevated activity of the microbial web, which would favour the subsequent development of viral populations.

A diatom bloom developed in mid-summer, paralell to the breakdown of stratification and input of nutrients in the surface layer (Figure 10E). Thus, a herbivorous food web based on large diatoms (*Thalassionema nitzschioides* and *Leptocylindrus danicus*) was temporarily established. The flux of matter to secondary producers might be important as suggested by the high densities of herbivorous copepods as *C. helgolandicus*.

Autumn would represent a transition between the herbivorous web characteristic of summer and the microbial web typical of winter (Figure 10F), with particularly high densities of mesozooplankton and chaetognaths. The diatom bloom occurring in September allowed the development of high levels of mesozooplankton biomass

followed by a further dominance of pico- and nanoplankton.

DISCUSSION

Seasonal distribution of planktonic groups

Picoplankton and viruses

Abundance of bacteria appears to be determined by the balance between temperature-dependent growth rates and bacterivorous grazing rates. In this study, bacterial biomass showed a pattern of seasonal change similar to that of temperature during autumn and winter, when phytoplankton and microplankton biomasses were low. In spring and summer, when the maximum values of bacterial biomass were measured, the relationship between bacteria and temperature broke down. In June bacteria increased in abundance coinciding with a sharp decrease in ciliate abundance, whereas in July a maximum of bacterial biomass was observed paralleling a bloom of *Gyrodinium aureolum*. Bacterial activity during this bloom may have been favoured by enhanced phytoplankton biomass and also by the reduction in the abundance of predators (Holligan et al., 1984; Heinänen, 1995).

Recent studies have shown that viral-infection mediated mortality should be taken also into account when considering the factors that regulate microbial and phytoplankton dynamics in marine ecosystems (Fuhrman & Noble, 1995; Weinbauer et al., 1995). Viruses seem to be favoured in situations of high biological productivity (Bratbak et al., 1990; Cochlan et al., 1993) when production of dissolved organic matter by phytoplankton exudation, lysis or zooplankton excretion, is significant (Banse, 1992; Maranger & Bird, 1995). In addition, increased temperature in summer leads to enhanced bacterial production and a corresponding increase in viral production (Maranger & Bird, 1995). In this study viral abundance covaried with phytoplankton and bacterial biomass, as well as with surface temperature.

The role of viruses appeared not to be specially important during autumn and winter when phytoplankton biomass was low. From spring onwards, a closer interaction between bacteria, phytoplankton and the viral component was inferred by the coupling of their corresponding biomasses (Figure 4), suggesting that viruses could be a significant cause of bacterial mortality during this period. Selective viral attacks on actively growing bacteria have been suggested as the cause of the high viral abundances that preceed maxima of bacteria (Maranger et al., 1994). In this regard, Murray & Eldridge (1994) postulated that increases in bacterial biomass coinciding with high viral abundance are due to viral-mediated lysis of bacterial cells, thus increasing the concentration of dissolved organic matter taken up by bacteria. In this study, the absolute maximum of viral biomass preceeds the maximum of bacterial biomass by 15 d, an observation that could be explained by these two hypotheses.

Maximum cyanobacterial biomass was measured in August associated with elevated biomasses of bacteria and viruses. Several investigations have reported a positive correlation between cyanobacteria and temperature (e.g. Iriarte, 1994, and references therein). In addition, cyanobacteria are thought to be a significant source of food for protozooplankton (Pernthaler et al., 1996). In this study, a significant correlation between temperature and cyanobacterial biomass was only observed during autumn and winter 1992, suggesting that this factor is not likely to be the main control of cyanobacterial biomass. The development of cyanobacterial populations appear to be favoured during phases of transition in vertical stability (November, March and August) and also during periods of high input of freshwater into the coastal zone (increases in Tamar River run-off paralleled high cyanobacterial biomass during October–November 1992).

Microplankton

The most important episode regarding phytoplankton biomass was the occurrence of the *G. aureolum* bloom in a frontal situation as a consequence of the interaction between stratified and mixed waters, influenced by tidal activity (Pingree et al., 1975; 1978). We observed the co-occurrence of *Noctiluca scintillans* and *G. aureolum* blooms (Figure 7A) which has been previously described in the region (Pingree et al., 1978; Boalch, 1987). These authors observed that in the tidal frontal area, patches of *N. scintillans* were actively consuming *G. aureolum* and other microplankton species. It is therefore likely that heterotrophic dinoflagellates, such as *N. scintillans*, could compete with ciliates for pico- and nanoplankton or even graze on them (Pierce & Turner, 1994). In this sense it should be pointed out that during the *G. aureolum* bloom ciliate biomass was much reduced and there was also a marked decrease in flagellate biomass.

The procceses involved in the regulation of the temporal variability of ciliates have been intensively studied (eg. Nielsen & Kiørboe, 1994). Large ciliates appear to be controlled by predation, principally by copepods (Nielsen & Kiørboe, 1991, 1994), while small-sized ciliates are likely to be controlled by food availability or by predation by heterotrophic dinoflagellates (Nielsen & Kiørboe, 1994).

In this study, the species of ciliates reaching highest densities are oligotrichs, principally small-sized *Strombidium* sp. These are known to be important predators on nanoplankton (Paranjape, 1990), and their maximum abundances were registered between March and June, parallel to increases in cyanobacterial and nanoflagellate biomasses.

Mesozooplankton

Variations in copepod populations are typically controlled by the hydrodynamic characteristics of the water column, the seasonal cycle of microplankton and the ecological characteristics of each species. Some copepods are known to maintain important populations in the pelagic environment during autumn and even winter, despite lower temperatures and primary productivity (Le Fèvre-Lehoerff et al., 1995). Thus, small omnivorous copepods such as cyclopoids (especially *Oncaea* sp.) that reproduce continuously throughout the year, can survive during these unfavourable periods (Le Fèvre-Lehoerff et al., 1995) being abundant in our study during autumn months. *Paracalanus* sp., *Acartia* spp. and *Pseudocalanus elongatus* were also present in this season but their abundance decreased in winter probably due to a migrational

pattern to deeper waters which has been previously reported for species as, e.g. *P. elongatus* (Broekuizen & McKenzie, 1995). The rapid drop observed in copepod abundance during September remains as an unexplained event in our data. We have not observed a similar phenomenon in other years and there is not an obvious hypothesis to it. Finally, it is interesting to point out that a time lag between phytoplankton outbursts and copepod maxima were not detected in this study.

In this study cladocerans showed sharp increases in abundance during spring and summer diatom blooms, when food resources as nanoflagellates and ciliates (references in Schoenberg, 1989) were most abundant. Its seasonal distribution in temperate waters is related to temperature and the vertical stability of the water column (Gieskes, 1971). Their parthenogenetic reproduction confers also this group the ability to exploit efficiently the environment as soon as favourable environmental conditions develop (Viitasalo, 1995).

Larvaceans presented significant negative correlation with biomasses of bacteria and cyanobacteria. This observation is consistent with their capacity to feed on very small particles, even in the submicrometric range, such as viruses (Flood et al., 1992), establishing a tight connection between microbial production and secondary producers.

Temporal variability in the structure of the planktonic community

It is generally accepted that the hydrodynamic characteristics of the marine environment are the most relevant factor which controls the structure of planktonic communities (Kiørboe, 1993; Legendre & Rassoulzadegan, 1995).

Theoretical studies (Legendre & Le Fèvre, 1995, and references therein) and trophodynamic models (e.g. Legendre & Gosselin, 1989) show that the magnitude of export production is determined by the trophic organization of pelagic communities (Michaels & Silver, 1988; Peinert et al., 1989). During the last few decades a dichotomy has been emphasized between the herbivorous food web characterized by high rates of matter export, and the microbial loop which would produce lower rates of vertical flux. However, these are only the extreme situations in a continuum of trophic structures (Legendre & Rassoulzadegan, 1995; Bradford-Grieve et al., 1999). The results obtained in this study (Figure 10) provide an empirical evidence supporting the existence of a temporal sucession of trophic organizations where the classical models appear episodically whereas transition models dominate throughout most of the seasonal cycle.

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