Vol. 10: 149–163, 1996 | AQUATIC MICROBIAL ECOLOGY
Aquat Microb Ecol | Published May 9

Dynamics of size-fractionated phytoplankton and trophic pathways on the Scotian Shelf and at the shelf break, Northwest Atlantic

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ABSTRACT: Composition of ultraplankton (<5 µm) and of biomass and primary production of size-fractionated phytoplankton (<5 or >5 µm) were determined during 1 yr at 2 stations off Nova Scotia, eastern Canada. Water temperature was a major factor regulating the abundance of ultraplankton cells, whereas nutrient concentrations and irradiance mainly controlled the relative proportions of procaryotes to eucaryotes. Procaryotes (mainly phycoerythrin-rich cyanobacteria) clearly dominated the ultraplankton throughout the year. Eucaryotes were more severely affected by low nutrient concentrations and high irradiances than procaryotes. The study indicates that ultraplankton assemblages were highly dynamic, with succession among groups in response to seasonal variations in environmental conditions. The spring bloom was dominated by large phytoplankton and ended upon exhaustion of nitrate and silicate. During the remainder of the year, nutrient concentrations were low (although non-limiting) and ultraplankton were the main primary producers. In summer, sporadically enhanced production of large phytoplankton was likely caused by inputs of nutrients and seeding of the euphotic zone by local vertical mixing. This mechanism was effective at the shallow shelf station only. The size structure of the grazer assemblage controlled the fate of primary production, i.e. sinking to depth or export to higher trophic levels. Hence, primary production and standing stock were controlled by bottom-up (nutrient input and seeding of the euphotic zone) and top-down (grazing pressure by micro- or mesozooplankton) processes, respectively. Interactions between these processes determined the nature of the trophic web in the euphotic zone. Differences in hydrodynamics and grazer communities between the 2 sampling sites led to the following model: (1) at the 2 sites, year round, there was a microbial food web, in quasi-steady state; (2) on the shelf, year round, herbivorous and microbial components coexisted, leading to efficient transfer from large and small phytoplankton to large metazoans; and (3) at the shelf break, because of scarcity of mesozooplankton, the microbial food web dominated year round and most of the large spring-bloom phytoplankton could be lost to sedimentation.

KEY WORDS: Ultraplankton composition · Size-fractionation · Chl *a* biomass · Primary production · Trophic pathways

INTRODUCTION

It has been suggested that small phytoplankton mainly prevail in oligotrophic regenerative systems, where new nutrients are scarce and water column stability is high (Cushing 1989). Yet, recent studies in a coastal upwelling area off New Zealand (Vincent et al. 1989, Hall & Vincent 1990) showed that, in nutrient-rich waters, small phytoplankton can also contribute significantly to the total biomass and production. In the present study, the term 'ultraplankton' is used for the size fraction <5 µm (Murphy & Haugen 1985, Cushing 1989, Legendre 1990).

At temperate latitudes, highest abundances of ultraplankton generally occur during summer (Waterbury et al. 1986). These organisms mainly comprise procaryotes (phycoerythrin-rich and phycocyanin-rich cyanobacteria) and small eucaryotes. Most of the published studies concern phycoerythrin-rich cyanobacteria (Waterbury et al. 1979, Glover et al. 1986), which are ubiquitous and dominant. There are few data on the phycocyanin-rich group, which seems to be confined

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mainly to estuaries (Campbell et al. 1983, Affronti & Marshall 1992), or on small eucaryotes. Procaryotes are generally more abundant in coastal waters than offshore (Murphy & Haugen 1985, Olson et al. 1990) and also at low latitudes where water temperature is high (Murphy & Haugen 1985). Their range of abundance is 1 order of magnitude larger than that of eucaryotes (Glover et al. 1985, Joint 1986), especially in coastal waters. Procaryotes and eucaryotes exhibit different responses to irradiance, leading to a competitive advantage of eucaryotes over procaryotes at the bottom of the euphotic zone (Glover et al. 1986, 1987). Adaptation of procaryotes to low irradiance is still debated, some authors considering that these organisms grow better at low irradiance (e.g. Platt et al. 1983) while others found them to be abundant near the surface (Joint & Pomroy 1986, Waterbury et al. 1986, Howard & Joint 1989). The role played by nutrients in determining the relative abundances of procaryotes versus eucaryotes is poorly known.

Given the importance of the small size fraction in primary production, this group should also play a major role in structuring pelagic ecosystems. In oligotrophic areas, the dominant food web is generally microbial. The microbial food web (Azam et al. 1983) is a system in quasi-steady state (Goldman 1988) that includes heterotrophic bacteria, phototrophic ultraplankton and protozoa. In contrast, eutrophic areas often support the herbivorous food chain, which goes from large phytoplankton (>5 µm, mainly diatoms) to copepods and fish larvae (Cushing 1989). Yet, there is evidence that herbivorous protists (i.e. heterotrophic dinoflagellates) graze part of the large blooming of phytoplankton (Hansen 1991, Lessard 1991, Neuer & Cowles 1994). These organisms are thus potential competitors of herbivorous copepods (Sherr & Sherr 1994). Legendre & Rassoulzadegan (1995) suggested that there is a continuum of trophic pathways between the herbivorous food chain and the microbial loop (*sensu* Rassoulzadegan 1993, i.e. a nearly closed system from which small phytoplankton are almost absent). These authors used the term 'multivorous food web' to describe a trophic structure in which the microbial and herbivorous trophic modes both play important roles. Systems dominated by one or the other extreme pathway (i.e. herbivorous chain or microbial loop) would reflect unstable and transient conditions, whereas the 2 intermediate pathways (multivorous or microbial web) would lead to longer-lasting equilibrium in time and space.

The present study was conducted on the Scotian Shelf, a temperate continental shelf. In the first part of the paper, the variability in physical (temperature, irradiance) and chemical (nutrient concentrations) characteristics at 2 stations is used to assess the conditions that control the composition of ultraplankton and shifts among groups of algae. In the second part, we test the hypothesis that interactions between hydrodynamics (which sets the size distribution of primary production) and grazing pressure (which sets the size distribution of biomass) determine the trophic structure of pelagic ecosystems and their changes in time.

MATERIALS AND METHODS

Sampling was conducted on the Scotian Shelf, eastern Canada (Fig. 1). Two stations were visited monthly from March 1991 through March 1992: one on the shelf (SH; ca 70 m deep, northeast of Sable Island) and the other at the shelf break (SB; ca 1000 m deep) off Halifax. At each station, temperature and salinity were recorded with a CTD profiler (Seabird 19), down to the bottom (Stn SH) or to 100 m depth (Stn SB). Underwater irradiance was measured with a 4π Biospherical Instruments meter, every 2 m between 100 and 1% of the photosynthetically available radiation (PAR) at the sea surface. From this profile, 10 sampling depths were chosen at *in situ* light levels corresponding to 10 irradiances available in a linear incubator on board the ship. Water was sampled with 8 l Niskin lever action bottles (in order to avoid contamination; Williams & Robertson 1989). Water was filtered through Nitex 333 µm to remove large grazers and stored in 4 l black thermos containers until the beginning of laboratory deteminations (within 1 h).

The coefficient of diffuse light attenuation (k) was determined as the regression coefficient of the relation

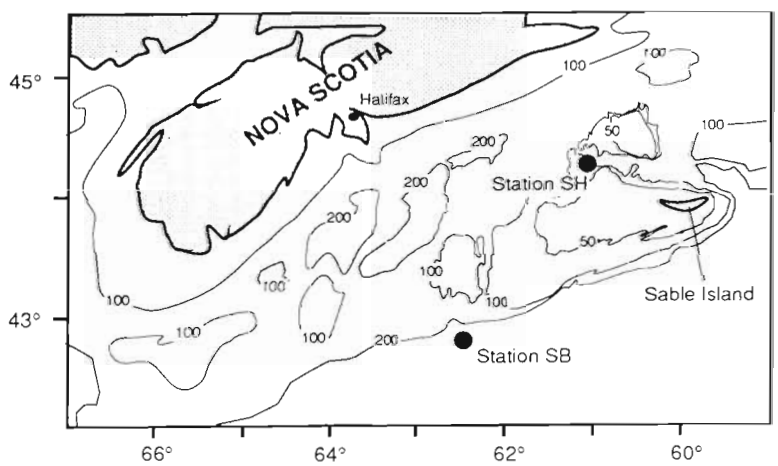

Fig. 1. Location of sampling stations on the Scotian Shelf. Isobaths are in metres

$\ln E_z = \ln E_0 - kz$, where E_z is the underwater irradiance measured at depth z and E_0 is the theoretical irradiance calculated for $z = 0$ m. Coefficient k was taken as homogeneous over the euphotic zone.

Water samples for nutrient analyses were filtered through precombusted GF/F filters into 2 ml cryovials and stored at −40°C for ca 1 mo. Dissolved nutrients (nitrate, phosphate, silicate and urea) were determined (Parsons et al. 1984) with an autoanalyser (Alpkem). Ammonium was not estimated because of problems resulting from freezing and analytical procedure.

For enumeration of ultraplankton (cells <5 µm), a 50 ml water sample was fixed with 0.2% formaldehyde (final concentration) during 20 min at 4°C, then sequentially filtered by gravity onto 5 µm and 0.4 µm Poretics filters. The 0.4 µm filters were laid on microscope slides with immersion oil and stored at −40°C until counting (within 1 mo). Cells were enumerated under a Leitz epifluorescence microscope using the following criteria (Hall & Vincent 1990): under blue excitation, red fluorescent cells were counted as chlorophyll-rich eucaryotes, yellow fluorescent cells as phycoerythrin-rich cyanobacteria (CyPE), and orange fluorescent cells as phycoerythrin-rich cryptomonads; under green excitation, procaryotes exhibited bright orange fluorescence. Numbers of phycocyanin-rich cyanobacteria (CyPC) were obtained by subtracting CyPE from total procaryotes. Samples from at least 3 depths were counted, i.e. in the maximum of total chlorophyll *a* (chl *a*), above the maximum and below. When chl *a* maxima for the total and <5 µm size fraction were at different depths, a fourth slide was enumerated for the latter depth.

Water samples for determination of chl *a* were filtered in parallel through 5 µm and 0.4 µm Poretics filters, which were frozen at −40°C for a maximum of 1 mo. The fluorometric method (Holm-Hansen et al. 1965), as modified by Parsons et al. (1984), was used to determine the concentrations of chl *a*.

Primary production estimates were obtained from simulated *in situ* incubations, conducted during ca 4 h at surface water temperature. Light was provided by a 400 W super metal halide lamp (Tungsten Products Corp.), covered by blue plexiglass to simulate the underwater light. When necessary, neutral density filters were used to screen the light, in order to adjust the highest irradiance in the incubator to 100% of the submarine surface irradiance. Irradiances in the incubator were 100, 55, 33, 22, 14, 8, 5, 3, 2 and 1% of that at the surface. For each photic depth, 2 dark and 2 clear 135 ml Pyrex bottles were filled with sampled water, to which 10 µCi of $NaH^{14}CO_3$ was added. After incubation, the contents of 1 dark and 1 clear bottle were filtered through 0.4 µm Poretics filters and the 2 other bottles were filtered through 5 µm filters. The filters were rinsed twice with filtered seawater (0.4 µm) to eliminate non-incorporated ^{14}C, although avoiding complete drying, and put in vials with 20 ml of scintillation cocktail (Ready Safe, Beckman). Radioactivity was determined within 1 mo with a Beckman LSI liquid scintillation counter using the channel ratio method. *In situ* productivity was calculated following Parsons et al. (1984), with a value (determined from the salinity of the water) of 24.123 g C m^{-3} for dissolved inorganic carbon. Values were corrected for the dark uptake and a discrimination factor of 1.05 was used.

For the biomass and primary production determinations, filtered volumes were slightly less than those clogging the filters under a pressure of ca 100 mm Hg. Size fractionation provided estimates for 3 fractions, i.e. the 0.4 µm filter gave a value for the total assemblage (>0.4 µm), the 5 µm filter for phytoplankton > ca 5 µm (large phytoplankton), and the difference between the 2 filters for phytoplankton between 0.4 and 5 µm (ultraplankton). The <5 µm fraction can in fact include algae up to ca 8 µm diameter because of the plasticity of cell walls (Murphy & Haugen 1985, Stockner & Antia 1986).

RESULTS

Physical characteristics

At the shelf break, stratification of the upper water column was established before August and persisted until the end of October (Fig. 2a). Although no CTD data are available from June through mid-August, stratification likely began at around mid-June, as in temperate oceanic waters. The depth of the euphotic zone varied from 20 to 60 m. Deepest values were in June and from the end of November through March, corresponding to attenuation coefficients (k) between 0.08 and 0.10 m^{-1}.

On the shelf, the overall physical characteristics were similar to those at the shelf break, although stratification of the water column was more pronounced from June through November. Waters were generally less salty than at the shelf break and the surface layer was cooler (not shown). The euphotic zone (20 to 50 m) displayed the same general changes as at the shelf break, except from October through January when it was shallower, with $k > 0.12$ m^{-1}.

Nutrients

In general, the vertical distributions of nutrients were more homogeneous on the shelf than at the shelf break, where the highest concentrations were often

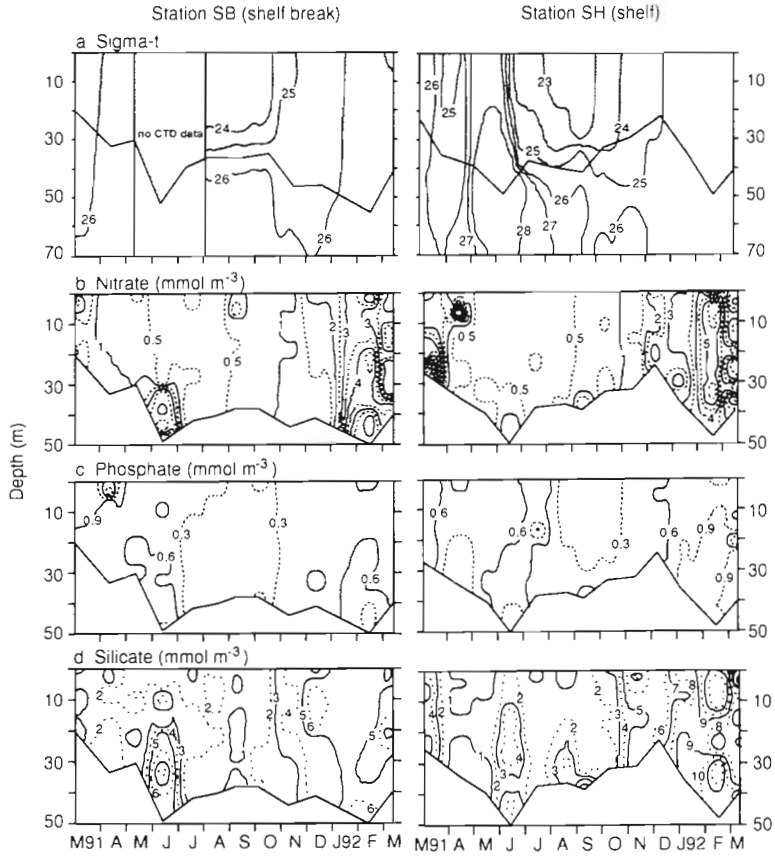

Fig. 2. Seasonal variations in the depths of (a) isopycnals in the upper 70 m of the euphotic zone (shaded) and in the depths of isopleths for (b) nitrate, (c) phosphate, and (d) silicate, in the euphotic zone

observed near the bottom of the euphotic zone. Concentrations of nitrate (Fig. 2b) increased during autumn, to reach maximum values in February. Concentrations of phosphate (Fig. 2c) were generally lower at the shelf break than on the shelf, but the seasonal pattern was similar at the 2 stations, i.e. lowest values were during summer. Concentrations of silicate (Fig. 2d) were >6 mmol m^{-3} at the shelf break during winter only and on the shelf from November through March. Values were minimum during summer, after showing some increase at depth in June. In winter, values were higher on the shelf than at the shelf break. The highest values of urea (not shown) occurred in summer and autumn (6 to 9 mmol m^{-3}), with a strong decline in September. The spatio-temporal distributions of urea were patchy.

The annual cycles of mean concentrations in the euphotic zone (not shown) were quite similar at the 2 stations, with minimum concentrations of silicate and phosphate at the end of summer and low concentrations of nitrate and silicate in March, early in the spring phytoplankton bloom. At all times of the year, concentrations of regenerated nitrogen (i.e. N-urea) were always above detection. In addition, urea made up the bulk of the pool of nitrate + urea (mean concentrations in the euphotic zone; Fig. 3), except from January through March (high nitrate) and in September (low urea). Dissolved nitrogen was always available, as either urea or nitrate.

Ultraphytoplankton cells

At the 2 stations, ultraplankton concentrations exhibited a well-defined peak near the surface (Fig. 4a). High abundances (>30×10^9 cells m^{-3}) occurred for a longer time at the shelf break (4 mo) than on the shelf (1 mo). Fig. 5 shows the percentage contribution of each pigment group to the whole assemblage, in terms of mean concentrations over the euphotic zone. Ultraplankton eucaryotes comprised chlorophyll-rich eucaryotes and phycoerythrin-rich cryptomonads. As the latter played only a minor role (<2%) in the eucaryote assemblage at the sampling stations, chlorophyll-rich eucaryotes are taken here as total eucaryotes. Procaryotes mainly comprised phycoerythrin-rich cyanobacteria (CyPE), with va-

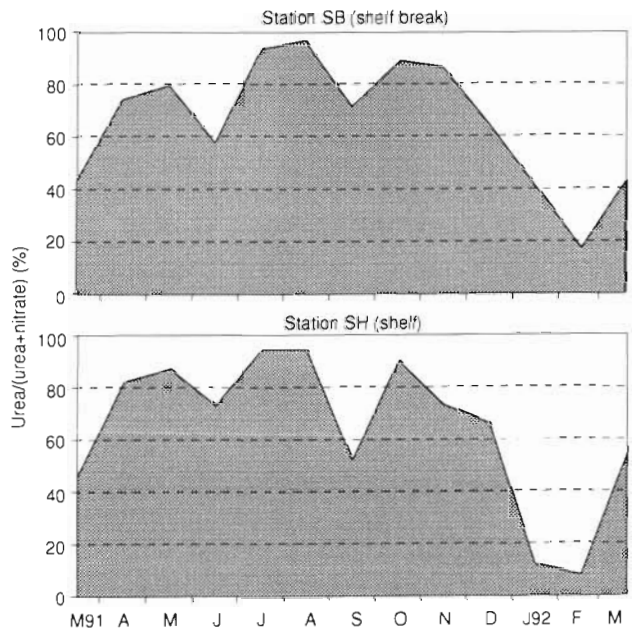

Fig. 3. Seasonal variations in the percentage contribution of N-urea to urea + nitrate. Values are mean concentrations in the euphotic zone

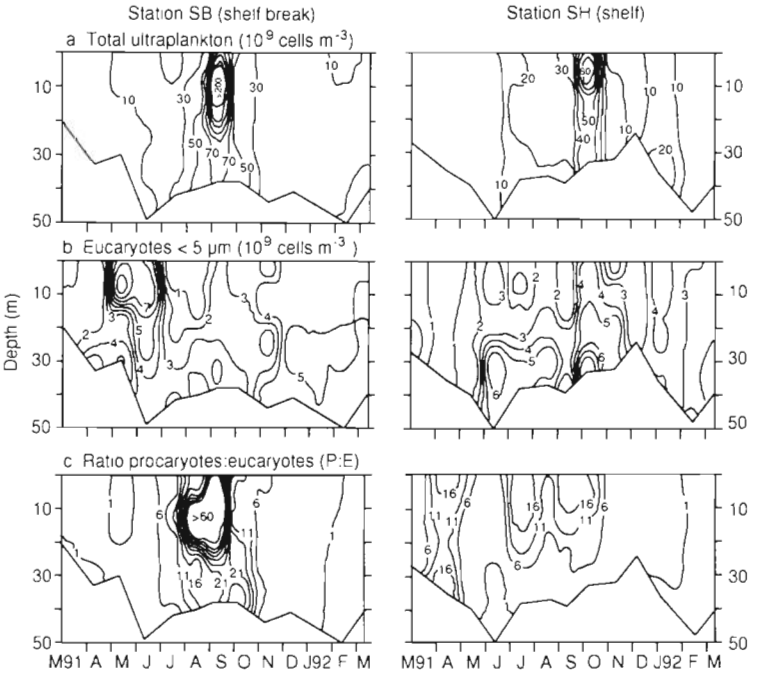

Fig. 4. Seasonal variations in the depths of isopleths for (a) total ultraplankton numbers, (b) eucaryote numbers, and (c) the procaryotes:eucaryotes ratio, in the euphotic zone

rying proportions of phycocyanin-rich cyanobacteria (CyPC). At the 2 stations, procaryotes markedly dominated the total cell numbers in summer and autumn, while eucaryotes contributed to the whole assemblage mainly during winter and spring.

At the 2 sites, the vertical distributions of procaryotes over the euphotic zone (not shown) followed those of total ultraplankton (Fig. 4a). At the shelf break, procaryotes peaked in September at 15 m due to CyPC (ca 130×10^9 cells m^{-3}), and at 35 m due to CyPE (ca 90×10^9 cells m^{-3}). On the shelf, the peak value, in October, was mainly supported by CyPE (>80%; Fig. 5).

At the shelf break, there was a spring outburst of eucaryotes in the upper 20 m (Fig. 4b). In summer, eucaryotes were mainly confined to the bottom of the euphotic zone, whereas their winter distributions ($< 5 \times 10^9$ cells m^{-3}) were vertically homogeneous. On the shelf, counts of eucaryotes were high at the bottom of the euphotic zone from June through November and over the whole zone in January. In spite of different vertical distributions of eucaryotes at the shelf break and on the shelf, their annual patterns, as percentages of ultraplankton cell numbers in the euphotic zone, were quite similar at the 2 stations (Fig. 5).

At the shelf break, the ratio of procaryotes to eucaryotes (Fig. 4c) was generally <10, except in August and September when it rose to 70 in the upper 30 m of the water column. On the shelf, ratios were relatively high (10 to 20) over the whole euphotic zone in April and in the upper 20 m between July and October.

Scatter diagrams of total counts as functions of temperature and nutrient concentrations showed significant linear correlations ($p < 0.01$; Fig. 6a to c). Since the total ultraplankton assemblage was mainly composed of procaryotes (by numbers; Fig. 5), relationships of procaryotes to temperature and nutrients (not shown) were similar to those of total ultraplankton. Total and procaryote counts markedly increased at temperatures >5 to 6°C and, at the 2 stations, there was a general trend for total and procaryote numbers to be low at high concentrations of nitrate and phosphate. Eucaryotes were mainly found at irradiances <200 µmol photons m^{-2} s^{-1}, the relationship between total or procaryote counts and irradiance being non-significant (Fig. 6d). The procaryotes:eucaryotes (P:E) ratios exhibited the same relationship with temperature and nutrients as total ultraplankton, which reflected the high contribution of procaryotes to ultraplankton.

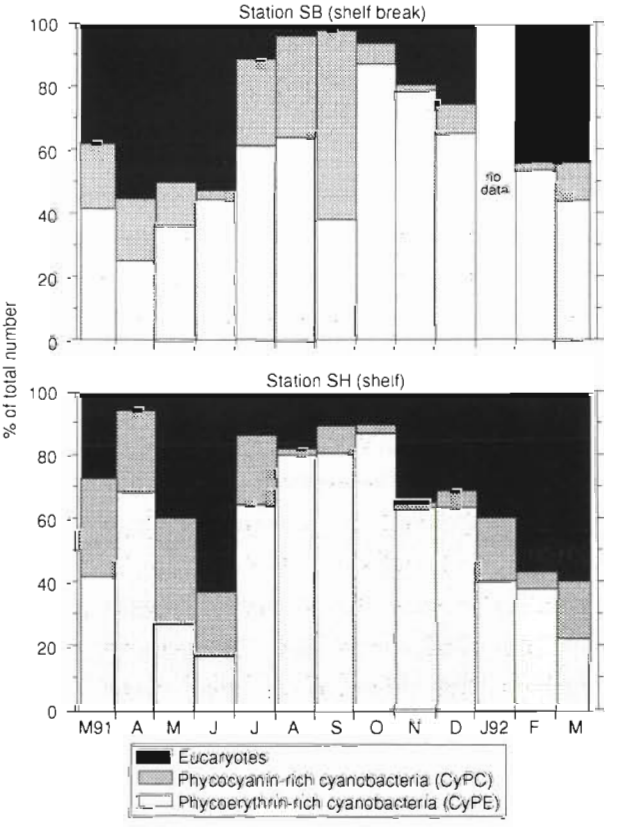

Fig. 5. Seasonal variations in the 3 pigment groups as a percentage of total numbers (average concentrations in the euphotic zone)

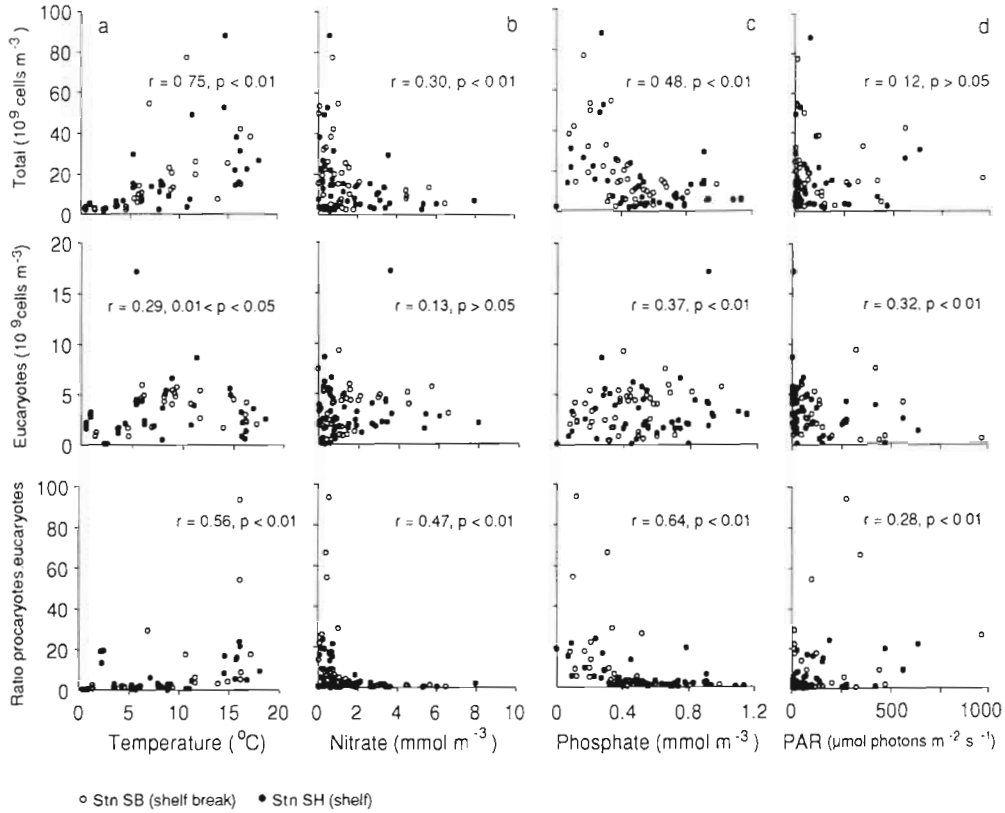

Fig. 6. Scatter diagrams of the abundances of ultraplankton (total and eucaryotes) and the procaryotes:eucaryotes ratio plotted as functions of (a) temperature, (b) nitrate, (c) phosphate, and (d) PAR. Linear correlation coefficients (r) and associated probabilities given. Numbers of observations were 42 at the shelf break and 44 on the shelf

Total and size-fractionated biomass and primary production

The annual variations of depth-integrated chl *a* biomass were similar at the 2 stations, although vertical distributions differed. Total chl *a* values integrated over the euphotic zone were low from June through February, with a transient increase in November (Table 1). The spring bloom occurred from March through May-June, the highest chl *a* concentrations being in March at the shelf break and in April on the shelf. At the shelf break, spring concentrations >4 mg m^{-3} were over the whole euphotic zone, whereas in November chl *a* concentrations >1 mg m^{-3} were limited to the upper 10 m

Table 1. Areal values of phytoplankton biomass (mg chl *a* m^{-2}) and production (mg C m^{-2} h^{-1}) over the euphotic layer at the 2 stations, for the whole assemblage and the 2 size fractions. Bold characters: peak values. ND: no data

Date	Stn SB (shelf break)						Stn SH (shelf)					
	Chl *a* biomass			C uptake rate			Chl *a* biomass			C uptake rate		
	Total	Large	Small	Total	Large	Small	Total	Large	Small	Total	Large	Small
1991 Mar	**130.7**	**112.1**	18.5	**63.3**	**45.7**	17.7	41.5	19.1	22.4	3.3	1.3	2.0
Apr	61.9	7.6	**54.2**	40.9	6.0	**34.9**	**70.8**	**60.7**	10.4	15.3	10.9	4.4
May	55.9	17.2	38.6	31.6	9.7	21.9	47.2	18.3	**28.9**	16.9	5.1	11.8
Jun	27.8	5.0	22.7	59.6	8.2	**51.4**	23.3	11.8	11.5	22.1	9.4	12.7
Jul	12.4	2.7	9.6	20.6	4.3	16.3	29.5	25.7	3.8	29.6	**16.5**	13.1
Aug	21.0	4.2	16.8	29.7	5.4	24.3	21.9	7.1	14.8	**39.9**	7.1	**32.8**
Sep	18.6	3.7	14.9	19.2	3.4	15.8	19.9	7.0	12.9	**38.1**	13.5	**24.6**
Oct	11.1	1.6	9.4	24.2	5.2	18.9	17.4	6.0	11.4	14.7	6.4	8.3
Nov	23.3	3.9	19.3	7.5	2.2	5.3	34.9	7.7	27.9	29.7	12.8	16.9
Dec	17.0	5.6	11.3	9.9	4.6	5.3	10.4	6.5	3.9	8.5	6.5	2.0
1992 Jan	ND	ND	ND	ND	ND	ND	13.4	3.5	9.9	24.5	5.0	19.5
Feb	14.8	4.9	9.9	17.7	6.0	11.6	13.3	7.1	6.2	6.7	3.7	3.0
Mar	**84.8**	**74.3**	10.5	**73.9**	**61.0**	12.8	20.9	13.3	7.6	**32.1**	10.3	21.8

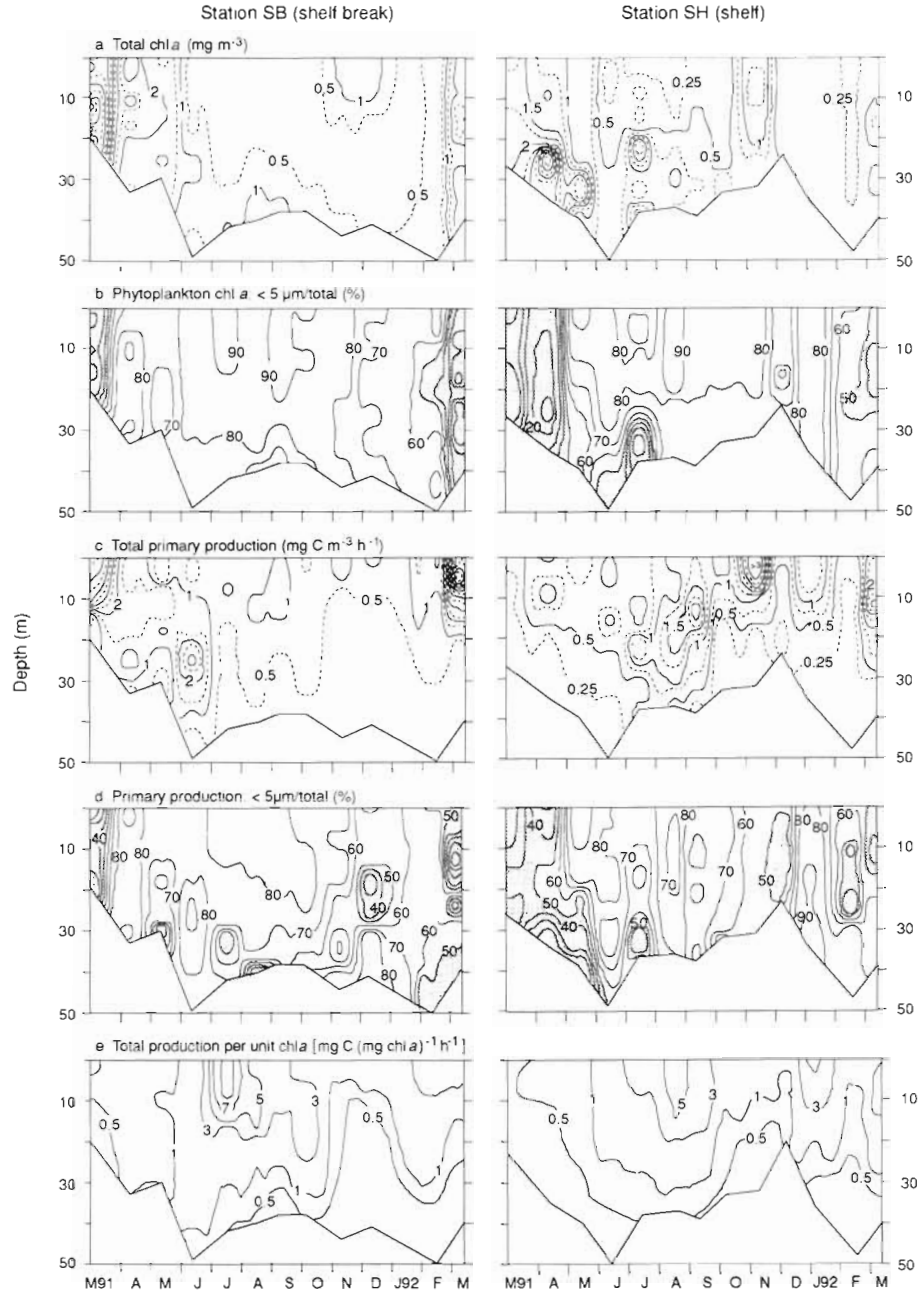

Fig. 7 Seasonal variations in the depths of isopleths for (a) total chl *a* concentration, (b) percentage contribution of <5 µm to total chl *a* (shaded areas: <50%), (c) total primary production, (d) percentage contribution of <5 µm to total primary production (shaded areas: <50%), and (e) total production per unit chl *a*, in the euphotic zone

(Fig 7a). On the shelf, high chl *a* biomasses were at the bottom of the euphotic zone in April-May, at mid-depth in July, and over the upper 25 m in November (Fig. 7a).

Annual variations in areal primary production tended to be reversed at the shelf break compared to the shelf. At the shelf break, total areal production was high from March through June, after which it gradually decreased to <10 mg C m^{-2} h^{-1} (Table 1). Values were >40 mg C m^{-2} h^{-1} in March, April and June. On the shelf, total areal production progressively increased during spring and summer, to peak (ca 40 mg C m^{-2} h^{-1}) in August-September. Spatio-temporal variations of primary production were different at the 2 stations (Fig. 7c). High values at the shelf break were in the upper part of the euphotic zone in March and at depth in June. Yet, from March through June, total production was >1 mg C m^{-3} h^{-1} at all depths. On the shelf, values >1 mg C m^{-3} h^{-1} were within the upper 20 m during summer and autumn, except in July and August when they extended deeper. The only values >2 mg C m^{-3} h^{-1} were in the surface layer in November and at mid-depth in March 1992. At the 2 stations, val-

ues of total production per unit chl *a* (P:B) >1 mg C (mg chl *a*)$^{-1}$ h^{-1} were from June through November and in January-February (Fig. 7e).

Table 1 shows that the small size fraction reached maximum depth-integrated biomass 1 mo after the large phytoplankton. Although less obvious, the same trend existed for primary production. A common feature of the 2 stations was the prevalence of ultraplankton in total biomass and primary production outside the bloom period (Fig 7c, d) At the shelf break, the large size fraction accounted for >80% of the total biomass and production during the bloom, whereas at other times ultraplankton markedly dominated (>80%). The high values of total production recorded in June were mainly due to ultraplankton. On the shelf, the share of ultraplankton in total biomass and production was less consistently dominant. Their contributions to total chl *a* varied between 60 and 80%, except in spring when they were ca 20% The deep chl *a* maximum was supported by large phytoplankton in April and by the small size fraction in May. In spite of the different contributions of each size fraction to the total standing stock, large phytoplankton were the main primary producers during April and May. In July, the high total biomass below 20 m corresponded to a high concentration of productive large phytoplankton, whereas the peaks of subsurface biomass and production in November were mainly due to the small size fraction.

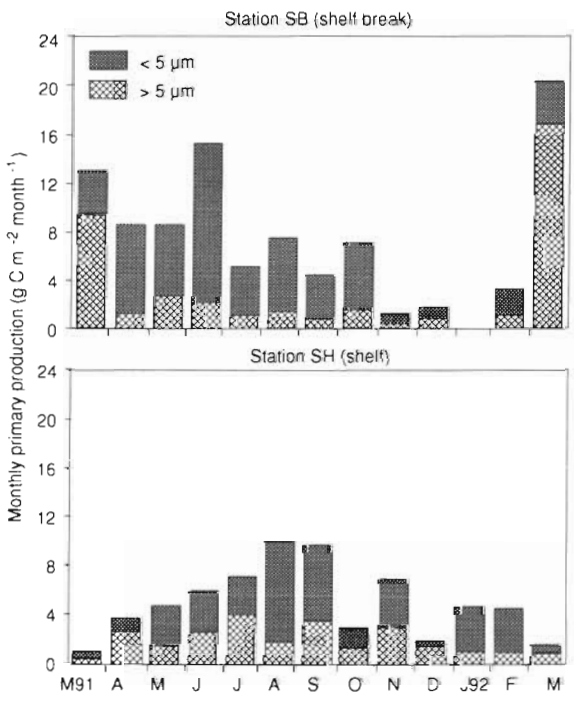

Fig. 8. Estimated monthly primary production. (Calculation is explained in the text)

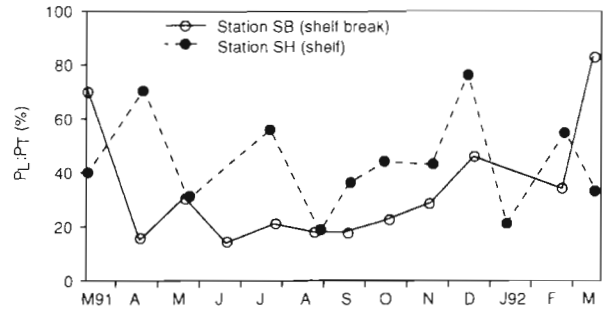

Fig. 9. Seasonal variations of the contribution of the large size fraction (>5 µm) to total primary production (P_L:P_T), calculated as (depth-integrated P_L/depth-integrated P_T)

Daily production rates, calculated as depth-integrated rates during the 4 h incubations divided by the corresponding percentage of daily irradiance, were assumed to be representative of the mean value for a given month (Fig. 8). The estimates of total annual primary production were 102 g C m^{-2} yr^{-1} at the shelf break and 63 g C m^{-2} yr^{-1} on the shelf. Large phytoplankton accounted for 30% of the total annual production at the first site and 37% at the second.

Seasonal variations in the ratio of production by the large size fraction to total production (depth-integrated P_L/ depth-integrated P_T) were not the same at the 2 stations (Fig. 9). At the shelf break, values were low (<20%) during summer They began to increase in late autumn and winter, to reach 80% in spring. In contrast, ratio values on the shelf were variable (20 to 60%) and generally higher than those at the shelf break, with no obvious seasonal trend.

DISCUSSION

Ultraphytoplankton assemblage

On the Scotian Shelf and at the shelf break, cell numbers varied between 10^9 and 10^{11} m^{-3}, which is within the range observed by Murphy & Haugen (1985) in the North Atlantic and by Douglas (1984) on the Scotian Shelf. Highest abundances were during summer and early autumn (Fig. 4a) as typically observed in oceans (Waterbury et al. 1986), with maximum annual values within the upper 25 m of the water column at the beginning of autumn (at the shelf break in September and on the shelf in October). Total cell abundances significantly increased with temperature (Fig 6a). Accordingly, ultraplankton abundances at the shelf break peaked 1 mo before those on the shelf, where surface waters warmed up later than at the shelf break. This is consistent with the general inverse relationships between ultraplank-

ton abundance and temperature reported with latitude for the North Atlantic (Murphy & Haugen 1985) and on the vertical in freshwater (Caron et al. 1985) and with the inhibition of ultraplankton growth by cold temperature found in Woods Hole Harbor (Waterbury et al. 1986).

In general, cyanobacteria were more numerous than small eucaryotes in the ultraplankton assemblage, as also observed in the Gulf of Maine (Glover et al. 1985), in the Pacific Ocean (Blanchot et al. 1992), and in the North Atlantic (Murphy & Haugen 1985). Seasonal variations in the relative abundances of cyanobacteria (Fig. 5), which were also observed in the absolute concentrations (not shown), are similar to those described in the Carmans River estuary (Campbell et al. 1983), Celtic Sea (Joint 1986), Kiel Bight (Jochem 1989), and Davies Reef lagoon (Ayukai 1992). Phycoerythrin-rich cells were the major component of cyanobacteria, except at the shelf break in September when CyPC strongly contributed (>60%) to peak abundance of ultraplankton. A similar percentage of CyPC was observed in the lower Chesapeake Bay during summer by Affronti & Marshall (1992), these authors linking the dominance of CyPC to the influence of environmental factors (e.g. low salinity, high irradiance, high nitrogen concentration). However, these environmental characteristics were not really different at our 2 sampling sites, so that other explanations must be found for the dominance by CyPC at the shelf break in September. Joint & Pomroy (1986) reported different photosynthetic parameters for oceanic and shelf ultraplankton in the Celtic Sea, so that physiological responses could be responsible for the observed difference between bloom assemblages on the shelf and at the shelf break.

Similarly to total ultraplankton abundances (Fig. 6b, c), procaryotes were inversely related to nitrate and phosphate concentrations, which is consistent with the high abundances (Fig. 4a, c) observed in late summer and early autumn when nutrient concentrations were low (Fig. 2b, c). Waterbury et al. (1986) established that cyanobacteria can utilize ammonia or urea as the sole nitrogen source for their growth. Urea, the main form of nitrogen determined in the present study, was available during the ultraplankton bloom in the studied area, so that it could have supported ultraplankton growth at this time. Furthermore, Blanchot et al. (1992) explained high occurrence of CyPE at low nitrate concentration by the ability of these cyanobacteria to store nitrogen in their phycobiliproteins when nitrate is abundant and to mobilize it at time of nitrate depletion (Glover et al. 1988). The ability of cyanobacteria to grow in N-depleted waters could explain the high abundances observed in late summer and early autumn at the 2 sites. However, high abundances of cyanobacteria in NO_3-depleted water are not usual (e.g Glover et al. 1986, Blanchot et al. 1992, Tamigneaux et al. 1995). Procaryotes did grow at phosphate concentrations <0.3 mmol m^{-3} at the shelf break from July through November and on the shelf in September and October (Fig. 2c), and they derived no advantage from the high concentrations of phosphate in winter and spring, contrary to observations reported by Stockner & Antia (1986). It follows that cyanobacteria were abundant under conditions of low nutrient concentrations associated with high water temperature, so that the latter could have been the main factor that controlled the growth of procaryotes.

There was no significant relationship between total ultraplankton numbers (and hence procaryotes) and irradiance (Fig. 6d), so that this factor did not likely influence the vertical distribution of procaryotes. Outside the autumn bloom, when procaryotes were largely dominant at the surface (Figs. 4 & 5), the vertical distributions of their counts did not exhibit any marked variations (not shown). Thus, there is little evidence that procaryotes were preferentially abundant in the deep part of the euphotic zone, on the shelf or at the shelf break.

Eucaryotes were 1 order of magnitude less abundant than procaryotes in summer and autumn, when they were mainly found at the bottom of the euphotic zone (Fig. 4b). In winter, they were distributed over the whole zone. Significant relationships with phosphate concentration and irradiance (Fig. 6c, d) indicate that eucaryotes thrived preferentially in nutrient-replete waters at low irradiance. This is consistent with previous reports on their ability to grow at low light levels because of high light-harvesting capacity (Shapiro & Guillard 1986, Iriarte & Purdie 1993). At the shelf break, high counts in the surface layer during spring could be partly explained by cloudy weather, which caused low daily irradiances during the 2 days before and on the day of sampling. This contrasted with clear sky over the shelf. Ecological preferences can thus explain why eucaryotes did not exhibit very high numbers during any period, contrary to procaryotes.

Variations in the P:E ratio may reflect physiological differences between procaryotes and eucaryotes, e.g. nutrient uptake, growth characteristics, response to light, or tolerance to temperature. Due to the smaller size of procaryotes compared to eucaryotes (Murphy & Haugen 1985, Shapiro & Guillard 1986), the former have a higher surface to volume ratio, which in turn should favour nutrient uptake in nutrient-poor waters. Thus, procaryotes can get the advantage over eucaryotes during periods of low nutrients. It follows that the significant inverse relationships observed between P:E and the concentrations of nitrate and phosphate could

reflect differential effects of nutrients on eucaryotes versus procaryotes (Fig. 6b, c)

In general, P:E values (Fig. 4c) were in the upper range of those reported by Murphy & Haugen (1985), but P:E $\gg$10 found in the present study during summer have not been reported elsewhere. At this time of the year, high P:E ratios were caused by the high contribution, at the 2 stations, of procaryotes to ultraplankton (Fig 5). In September, the very high ratios at the shelf break were due to high CyPC abundances. In contrast, the high spring values on the shelf were caused by low eucaryote numbers, which occurred simultaneously with low nitrate and phosphate concentrations and high irradiances. High P:E ratios, (1) when caused by increased procaryote numbers, could reflect a better adaptation of procaryotes to summer conditions, i.e. low nutrients and high temperature, or, (2) when caused by decreased eucaryote numbers, could indicate that, at low temperature, limitation of growth by low nutrients would not affect the procaryotes as severely as the eucaryotes. In the Southern Ocean, Hall & Vincent (1990) also observed low P:E to be negatively related to nutrients. Since these authors were working in a nutrient-rich area, they associated low P:E to a possible competitive advantage of eucaryotes over procaryotes with regard to nutrients. Furthermore, due to differential grazing effects on eucaryotes and procaryotes (Rassoulzadegan et al. 1988), the P:E ratio could be influenced by grazer assemblages. Differential grazing on cyanobacteria and eucaryotes was also suggested by Ayukai (1992) to explain low P:E in Davies Reef lagoon.

There was no direct relationship between the period of maximum biomass of the small size fraction (Fig. 7b) and the highest numerical abundances of small cells (Fig 4a). The same was reported in an upwelling coastal area for total ultraplankton (Hall & Vincent 1990) and in a highly stable water column of the tropical ocean for cyanobacteria (Li et al. 1983). In contrast, Joint & Pomroy (1986) found similar depth profiles for chl *a* biomass and cyanobacteria numbers in the Celtic Sea. In the present study, the estimation of biomass was in terms of chl *a* (fluorometric method), whose extraction efficiency varies with phytoplankton taxa (Joint & Pomroy 1986). Moreover, measured chl *a* in the small fraction includes fragments of large cells. In contrast, counts under epifluorescence concern pigmented cells only. Thus, the observed discrepancy between the 2 methods may be partly explained by the fact that they do not estimate exactly the same thing. Another explanation for the uncoupling between the 2 methods could be decreased intracellular pigment concentrations with increasing cell numbers, as observed by Glover et al. (1988) and Blanchot et al. (1992) during a bloom of cyanobacteria.

Species succession is a widely recognized phenomenon for large phytoplankton (e.g. Margalef 1978, Levasseur et al. 1984, Bode & Fernández 1992, Lochte et al. 1993). In contrast, shifts in pigment groups of ultraplankton are poorly documented. The present study suggests that ultraplankton are a highly dynamic assemblage, within which seasonal variations in environmental conditions induce succession among pigment groups. Differences observed between the 2 stations, both spatially at the onset of the autumn ultraplankton bloom and in total abundances over the year, support the view that the annual cycle in water temperature is a major factor that controls the distribution and abundance of ultraplankton. In contrast, for a given water mass, nutrient availability and irradiance alter the proportions of procaryotes versus eucaryotes on the vertical. Temperature, irradiance and nutrients seem to exert similar controls on ultraplankton assemblages, in shallow (shelf) and deep (shelf break) waters. Since these factors did not vary similarly in the 2 sampling areas, the resulting ultraplankton communities differed. This could have influenced the structure of the microbial component of the food webs at the 2 stations, as examined in the next section.

Significance of trophic webs on the Scotian Shelf and at the shelf break

Estimates of total annual primary production were higher at the shelf break (102 g C m^{-2} yr^{-1}) than on the shelf (63 g C m^{-2} yr^{-1}). Higher primary production offshore was also found by Mills & Fournier (1979), our estimate at the shelf break being however lower than their value of 128 g C m^{-2} yr^{-1}. The annual contribution of large phytoplankton to total primary production was quite similar at the shelf break (30%) and on the shelf (37%), but seasonal contributions were different (Fig 8). The bulk contribution (>50%) of large phytoplankton to total production was restricted to a shorter period at the shelf break (March-April) than on the shelf (March-July), which stresses the transient nature of the spring bloom at the shelf break. Such seasonality in the production of phytoplankton >5 µm was also noted by Joint et al. (1986) in the Celtic Sea, where the annual calculated contribution of the large size fraction (37 to 40%) corresponded to our upper values. After exhaustion of nitrate in spring, urea was the main N-source determined in the present study that fuelled primary production at the shelf break and on the shelf (Fig. 3). This is consistent with nitrogen uptake measurements on the shelf, which indicate that phytoplankton growth there was mainly supported by regenerated nutrients outside the bloom period (Cochlan 1986).

Interestingly, the contribution of large phytoplankton was never zero, because this size fraction has the ability to grow on regenerated N on the Scotian Shelf (Dauchez et al. in press). These authors found a shift from NO_3-based (new) production mainly by phytoplankton >5 µm in spring to regenerated N-based production by the 2 size fractions during the remainder of the year.

Depending on grazer assemblages, phytoplankton production would be either exported or recycled *in situ*. When herbivorous mesozooplankton are absent, large phytoplankton often undergo massive sinking of aggregated intact cells, as exemplified by some spring blooms (e.g. Peinert et al. 1989). Since mesozooplankton can also feed on microzooplankton, which themselves feed on ultraplankton (e.g. Sherr et al. 1986, Wiadnyana & Rassoulzadegan 1989, Jonsson & Tiselius 1990, Stoecker & Capuzzo 1990, Pierce & Turner 1992), mesozooplankton can grow even when the production of large phytoplankton is low. Therefore, herbivory on large phytoplankton and/or omnivory on microzooplankton result in exporting primary production to either higher trophic levels in the water column (e.g. fish larvae) or eventually to depth as sinking faecal pellets. In contrast, low production of large phytoplankton and scarcity of mesozooplankton would lead to the microbial food web, from which there is little or no export. If dinoflagellates were the dominant herbivorous grazers on large phytoplankton (Neuer & Cowles 1994, Sherr & Sherr 1994), part of the large-sized production would have been channelled towards the microbial component of the food web and part would have potentially been exported towards mesozooplankton.

The ratio of production by large phytoplankton to total production (P_L/P_T) can be used as an index for estimating the potential export of production from the euphotic zone (e.g. Legendre & Rassoulzadegan 1995). Prevalence of the large size fraction in primary production (i.e. high P_L/P_T) is indicative of a system dominated by autotrophy. Such systems have high potential for export, since the large algae are likely to either sink out of the euphotic zone or be grazed by mesozooplankton (directly or through heterotrophic dinoflagellates) in the herbivorous chain. In contrast, low P_L/P_T is indicative of dominance by heterotrophy. In such cases, export of carbon towards higher trophic levels is not very efficient because of multiple steps in the microbial food web between small algae and large zooplankton. Intermediate P_L/P_T ratios and hence intermediate export conditions would correspond to the multivorous food web (Legendre & Rassoulzadegan 1995). As the seasonal patterns of P_L/P_T differed at the 2 stations (Fig. 9), it can be hypothesized that the fate of primary production was not the same, as explained below.

Although there were no marked differences in hydrodynamics (i.e. stratification) or nutrient concentrations between the Scotian Shelf and the shelf break, seasonal changes in biomass and primary production exhibited different patterns and ranges of variation (Figs. 7 & 8). At the shelf break, changes were typical of temperate North Atlantic waters (e.g Joint et al. 1993), i.e. a spring bloom starting in March, dominated (>80%) by large phytoplankton and characterized by high levels of biomass and production over the whole euphotic zone. The bloom led to depletion of nutrients as soon as summer stratification was established, after which the small size fraction dominated the total biomass and production (Table 1, Figs. 7 & 8). The biomass and production of phytoplankton <5 µm varied little over the year, whereas those of phytoplankton >5 µm exhibited large seasonal variations. Exhaustion of silicate over the euphotic zone (Fig. 2d) early in the spring bloom indicates that phytoplankton >5 µm were then mainly diatoms. Replenishment of nitrate and silicate at the bottom of the euphotic zone in June (Fig. 2b, d) suggests upward diffusion of nutrients from deeper waters. However, this nutrient input was not rapidly used by large algae, since there was no major increase in biomass or production. Because large phytoplankton have high sinking rates, and water depth at the shelf break (ca 1000 m) is much greater than the depth of the euphotic zone, sinking particles there are lost to deep waters. Hence, seeding of diatoms in the euphotic zone during local upward mixing events is unlikely. Moreover, because of the scarcity of large grazers at the shelf break (Fournier et al. 1977, O'Boyle et al. 1984), production during the spring bloom (phytoplankton >5 µm) probably did not reach the higher trophic levels. The fate of production by the small size fraction was different. Ultraplankton can maintain themselves in the water column owing to their low sinking rates and they can grow at low nutrient concentration due to their high surface to volume ratios. However, micrograzers are present in large numbers at the shelf break (e.g. protozoa; Fournier et al. 1977) as a consequence of the scarcity of mesozooplankton. Because of their abundances and high reproduction rates, the micrograzers maintained the biomass of ultraplankton at steady levels (Sherr et al. 1991, Riegman et al. 1993), hence *in situ* recycling of primary production <5 µm. This scenario is consistent with the low P_L/P_T (ca 20%) at the shelf break during summer and autumn, which would correspond to the microbial food web, whereas values near 80% in spring likely reflected high export through massive sinking of cell aggregates.

On the shelf, there was also a seasonal shift in the size structure of phytoplankton, but seasonal variations were different than those at the shelf break. The

spring bloom, which occurred in April, was much less productive than at the shelf break (Table 1). The highest concentrations of total chl *a* were at the bottom of the euphotic zone, with values half those observed at the shelf break. Deep maximum chl *a* values did not correspond to high production rates, which could imply that sampling took place at the very end of the bloom, when large phytoplankton were already sinking. Low concentrations of nitrate and silicate (Fig. 2b, d) and low P:B values [<0.5 mg C (mg chl $a)^{-1}$ h^{-1}; Fig. 7e] are consistent with the idea of senescent sinking cells. A second deep chl *a* maximum was observed in July (Fig. 7a, c), associated with enhanced production and corresponding to large phytoplankton (Fig 7b, d). This subsurface maximum followed increases of nitrate and silicate in the water column (Fig. 2b, d). During summer and autumn, increased total production was not reflected in total biomass (Table 1). Since ultraplankton then dominated the whole assemblage, the summer-autumn trend may indicate active *in situ* recycling or export out of the euphotic zone, by grazing, sinking (through aggregation) or advection of this size fraction. The biomass and production of large phytoplankton remained at a steady low level, which was however higher than at the shelf break (Table 1). The shelf station was located in the vicinity of Sable Island Bank, on the border of a clockwise circulation around this bank. The area supports active fishing and secondary producers are found year round, including small zooplankton (Fournier et al. 1977), copepods, suspension feeders (e.g. appendicularians), and fish larvae (O'Boyle et al. 1984, Mousseau 1995). The high concentrations of mesozooplankton and microzooplankton (Fournier et al. 1977, O'Boyle et al. 1984, Mousseau 1995) found there during summer could efficiently use a broad range of algal sizes. Grazing likely prevented increases of the standing stock and was a source of regenerated nutrients and dissolved organic matter. High excretion by micro- or mesozooplankton would allow high *in situ* recycled production, which would keep ultraplankton in active growth phase (Goldman & Caron 1985). Moreover, on the shelf, the bottom of the euphotic zone was close to the sea floor, so that local events of upward mixing could seed diatoms in the upper waters during summer. Such events, combined with excretion by grazers, could have prevented the collapse of primary production, while continuous grazing prevented increase of the standing stock. Hence, variations in P_L/P_T, at values (20 to 60%) which were generally higher than at the shelf break, would reflect dominance of the system by the multivorous food web, in which the microbial and herbivorous grazing modes both played significant, but alternating, roles.

Food web model

Our results on phytoplankton biomass and primary production, combined with available information on micro- and mesozooplankton, lead us to propose a general food web model in which the relative importance of the various pathways varies according to station and season (Fig. 10). In our conceptual model, the trophic pathways are regulated by 2 types of mechanisms, i.e. bottom-up control involving nutrient replenishment by physical processes and leading to enhanced primary production, and top-down control involving regulation of phytoplankton biomass by grazing. These mechanisms operate in concert, but variations in their relative importance favour one or the other phytoplankton size fraction.

Concerning the small size fraction, bottom-up control is weak, because ultraplankton grow well on regenerated nutrients, which were always present in the water column. Grazing by microzooplankton exerts a strong top-down pressure that controls the biomass of ultraplankton and simultaneously recycles nutrients, thus preventing their limitation. This trophic component of the food web, which is nearly closed (i.e. little export), can maintain itself in the euphotic zone. During the bloom period, the microbial component is present at the 2 sampling stations (Fig 10a), where it coexists with high production of large cells, which are exported to depth (at the 2 sites) and are perhaps also grazed by mesozooplankton (on the shelf). The herbivorous and microbial components are then not, or only weakly, connected. During the remainder of the year (Fig. 10b), the microbial system described above persists on its own at the shelf break (i.e. microbial food web), whereas on the shelf, there is some export of the production processed by the microbial component through grazing by mesozooplankton on microzooplankton. The biomass of ultraplankton is largely top-down controlled by microzooplankton grazing, so that it remains quite constant.

In contrast to the small size fraction, the biomass of large phytoplankton largely depends on bottom-up controlled changes in primary production. During winter, deep mixing causes upward seeding of large cells, but vertically mixed phytoplankton are then exposed to an average irradiance which is too low for biomass to build up. The spring bloom occurs in response to the release of the bottom-up controlling factor (i.e. average irradiance in the surface mixed layer), which leads to a transient condition characterized by high export through sinking or grazing (Fig 10a). During summer, large phytoplankton are generally controlled by the availability of allochthonous nutrients (mainly new nitrogen), even if the

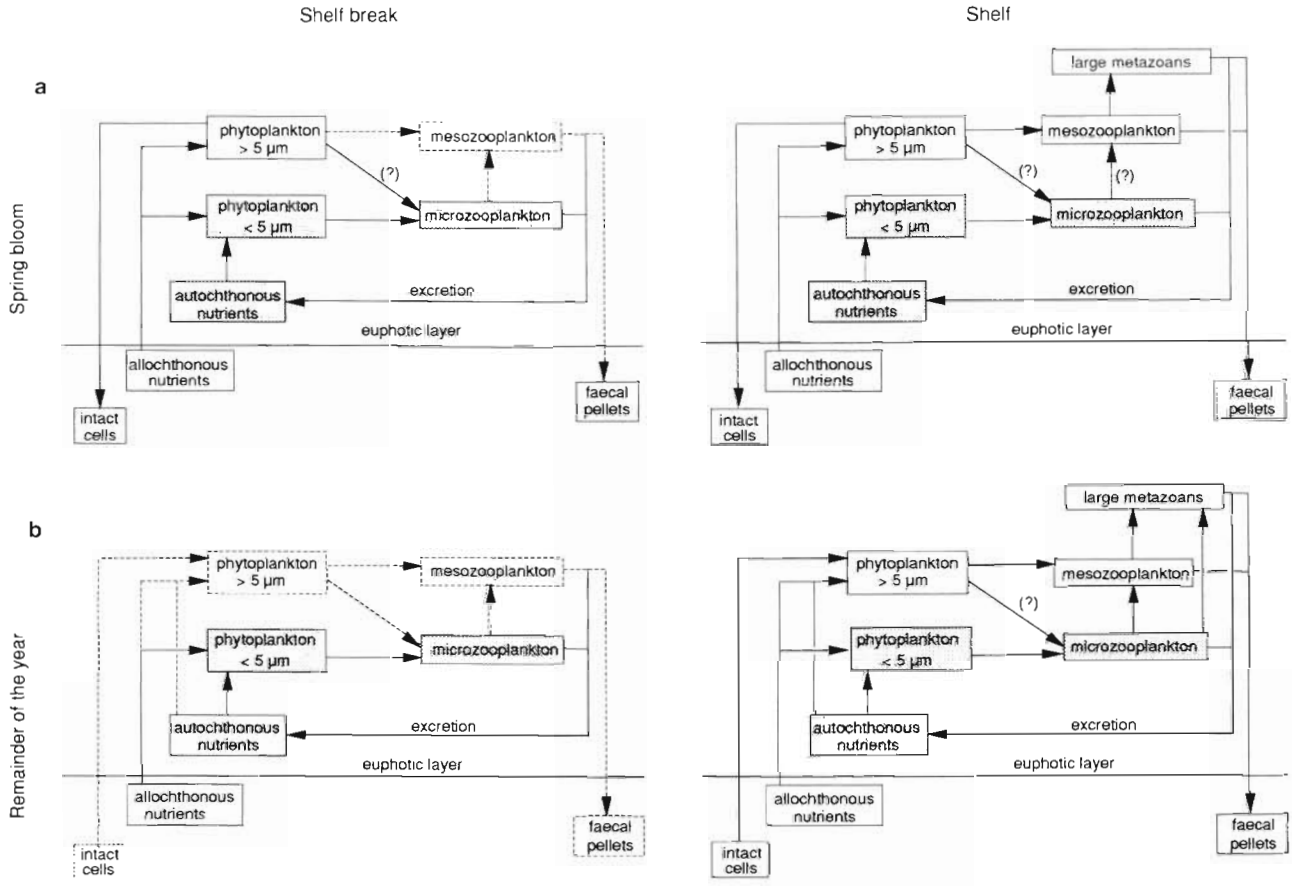

Fig. 10. Schematic representation of trophic pathways in the euphotic zone at the 2 sampling stations, during (a) the spring bloom and (b) the remainder of the year Solid arrows and boxes: actual fluxes and compartments; dashed arrows and boxes: weak or unlikely. Shaded boxes: the microbial food web, which was always present; heterotrophic bacteria and their grazers are not included. Grazing of large phytoplankton by microzooplankton (heterotrophic dinoflagellates) is hypothetical in this study (question mark). At the shelf break: mesozooplankton are scarce, hence grazing on microzooplankton and production of large faecal pellets are probably weak. Outside the spring bloom, seeding of the euphotic layer is unlikely because of great water depth. On the shelf: the spring flux between microzooplankton and mesozooplankton is uncertain (question mark)

large size fraction can use autochthonous nutrients (Fig. 10b). Events of shallow vertical mixing sometimes replenish allochthonous nutrients at the bottom of the euphotic zone. At the shelf break, because of water depth, upward mixing would not normally seed large cells in the euphotic zone, so that the production and biomass of large phytoplankton would generally remain at low levels until the next spring. On the shelf, because of a shallower water column, transient events of upward mixing during summer can replenish the euphotic zone in both new nutrient and seeds of large cells. This would release the bottom-up control and, hence, favour summer growth of large phytoplankton and their grazing by mesozooplankton.

Hydrodynamic events that occur seasonally (e.g. spring stratification of nutrient-rich water) or sporadically at various times of the year (e.g. vertical mixing at the bottom of the euphotic zone) generally favour the production of large phytoplankton. These events and their associated production are transient, whereas the production of ultraplankton appears to be relatively steady. The size structure of grazers mainly controls the biomass of phytoplankton. Hence, hydrodynamics and the size structure of the grazer community determine the functioning of the pelagic system. The relative importance of these 2 factors sets the type of trophic food web (and, thus, the type of export from the euphotic zone) and its duration. It is concluded that, off Nova Scotia: (1) on the shelf, dynamic trophic systems should favour the efficient use of primary production by high level consumers, year round, and (2) the shelf break should experience high direct export of primary production in spring, co-existing with a nearly closed microbial component year round.

Acknowledgements. Funding of the research was provided by OPEN, one of the 15 Networks of Centres of Excellence supported by the Government of Canada. Grants to L.L. and L.F. from the Natural Sciences and Engineering Research Council of Canada and to GIROQ from NSERC and the Fonds FCAR of Québec were instrumental in the completion of the work. We thank the crew of RV 'Petrel V' for their valuable assistance at sea, G. Bergeron, B. LeBlanc and J. Richard for technical support, and 2 anonymous reviewers for useful comments and suggestions. This is a contribution to the programme of GIROQ (Groupe interuniversitaire de recherches océanographiques du Québec).

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Responsible Subject Editor: F. Rassoulzadegan, Villefranche-sur-Mer, France

Manuscript first received: June 7, 1995
Revised version accepted: January 8, 1996