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Proportion of plankton biomass in particulate organic carbon in the northern Baltic Sea

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ABSTRACT: In many quantitative studies of the oceanic carbon cycle, measurements of particulate organic carbon (POC) in seawater are used for making budgets of planktonic food webs. In order to evaluate the seasonal changes of the constituents of POC in a temperate sea area, the proportion of autotrophic and heterotrophic plankton biomass in POC was measured for different seasons. At both a coastal and an offshore station in the northern Baltic Sea, POC was dominated by unidentified detritus material. Autotrophic microplankton dominated the plankton biomass in spring, and free-living heterotrophic bacteria in autumn and winter. The remaining plankton groups were of minor importance. The ratio of autotrophic plankton carbon to chlorophyll *a* (chl *a*) was determined by frequent sampling, and varied between 5 and 70 ($\mu g\ l^{-1}/\mu g\ l^{-1}$), lowest in autumn-winter and highest in spring. Such variability makes it difficult to use constant conversion factors of chl *a* and POC to quantify plankton biomasses, and emphasizes the need for careful determination of conversion factors for specific environments and seasons.

INTRODUCTION

Relatively small changes in the oceanic carbon cycle may have large atmospheric consequences (JGOFS 1990). In recent years the interest in understanding the ocean carbon cycle has therefore increased. Measurements of biological rates are used in models describing, for example, the carbon flow in food webs (Hessen et al. 1990, Suttle et al. 1990), and/or the vertical transport and mineralisation of carbon (Smith et al. 1992). In such studies, measurements of particulate organic carbon (POC) in the sea are central, and the composition of POC has therefore been a subject of much interest (Smetacek & Hendrikson 1979, Cho & Azam 1990). However, the groups of organisms included in earlier studies have differed widely. Focus has been on large autotrophic plankton, disregarding the significance of heterotrophic plankton and cyanobacteria. Some recent papers though emphasise the importance of heterotrophic bacterial carbon contribution to POC (e.g. Cho & Azam 1990).

The nutrient status of the sea generally influences the species composition of algae (e.g. Malone 1980); in oligotrophic waters, smaller cells dominate over larger, while the opposite prevails in eutrophic waters. This fact may explain the various results of the composition of POC in different seas. In some nutrient-rich seas, eukaryotic phytoplankton have been reported to account for over 80% of the POC (Hobson et al. 1973, Laws et al. 1988). In contrast though, Cho & Azam (1990) found that in oligotrophic waters almost half the POC was composed of bacterial carbon. In many other studies, the non-living particulate carbon fraction has been shown to dominate (Valiela 1984).

In coastal environments, there is a large seasonal fluctuation in autotrophic plankton populations, with spring blooms of microplankton and summer blooms of nano- and picoplankton (Malone 1980). These fluctuations along with a varying river run-off give rise to a dynamic POC-pool in the water. The purpose of this study was to investigate the seasonal variation of microbial plankton carbon (PC) in relation to the POC-pool in a coastal and shallow sea area in the northern Baltic Sea. All organisms ranging in size from small heterotrophic bacteria to relatively large autotrophic plankton and zooplankton were examined, with the aim of obtaining a complete picture. The ratio of autotrophic biomass to chl *a* was also determined. The

northern Baltic Sea is a sea area influenced by allochthonous material. Since there is larger influence from rivers on nearshore localities, the investigation was conducted at both a nearshore and an offshore station.

MATERIALS AND METHODS

Study site. During 1991 and 1992 a coastal station (NB1: 19° 48' 07" E , 63° 31' 00" N) and an offshore station (US5B: 19° 58' 05" E, 62° 35' 00" N) in the Bothnian Sea, northern Baltic Sea (Fig. 1), were investigated. The water depths at the near- and offshore stations are 24 and 225 m, respectively. The euphotic zone was determined to 0 to 20 and 0 to 14 m at the offshore and nearshore station, respectively.

Sample collection and analytical methods. POC, chl *a* and PC (eukaryotic and prokaryotic plankton), were examined vertically in the euphotic zone. Sampling was performed 4 times at each station; during the early stage of the spring bloom (April), in summer (July), in autumn (October) and in winter (February). At the nearshore station, additional experiments were also carried out during the different stages of the spring bloom. Water (4 l) was collected with a bottle sampler (Hydro-Bios) from the surface to a depth of 20 m at 4 m intervals. The standard errors reported are based on mean values of the depth profiles and standard deviations of triplicate samples.

In addition to the vertical profiles, integrated samples for autotrophic plankton and chl *a* from the respective euphotic layer were taken every second week during the productive season (May to September) and every fourth week during other seasons, starting in February 1991. These samples were obtained by using plastic hoses, 25 mm diameter and 14 m (nearshore) and 20 m (offshore) long, respectively. This sampling technique gave similar results to the mean values calculated from discrete depths sampling (linear regression of chl *a*; slope = 0.92, $r^2 = 0.99$, n = 11).

Chl *a*. Seawater samples (500 to 1000 ml) were filtered onto a 47 mm, 0.45 µm Millipore HA-filter. The chl *a* retained on the filter was extracted for 24 h in darkness at room temperature with 4 ml of 95% ethanol and measured spectrophotometrically (750, 665 and 663 nm) after centrifugation. Chl *a* concentration was then calculated according to Wintermans & Demots (1965), using the absorption coefficient 83.4 l g^{-1} cm^{-1}.

POC. Seawater (300 to 500 ml) was filtered through a precombusted (450°C for 3 h) 18 mm glass fibre filter (Whatman GF/F). After filtration, the filters were dried at 40 °C overnight and prior to analysis, they were cut into halves. On each sampling occasion, blank filters

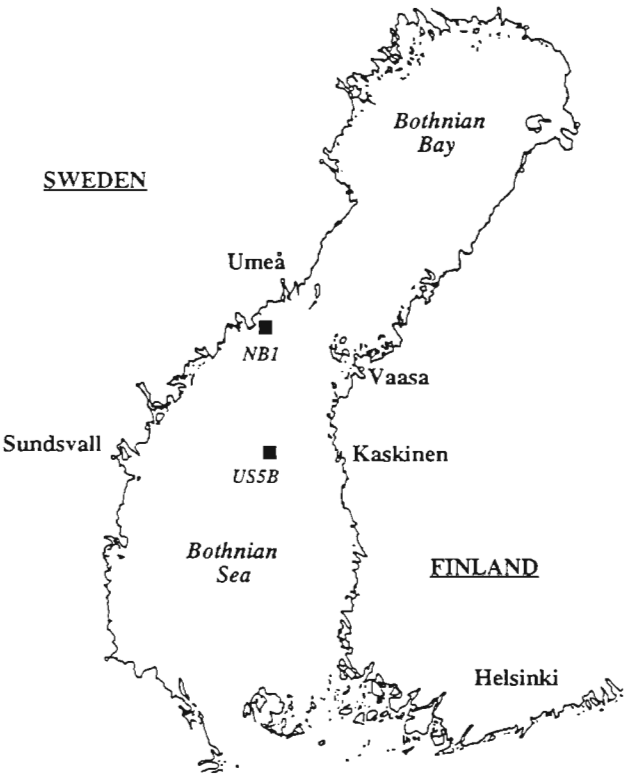

Fig. 1. Northern Baltic Sea showing the positions of the 2 sampling stations

were treated the same way. POC was determined with a Carlo Erba 1106 Elemental Analyzer. The measurements obtained from the 2 filter halves were added, the blank value was subtracted and POC per unit volume was calculated. The standard error for POC samples was about 2.4%. The heterotrophic bacterial carbon (H_{pico}) share of POC was corrected for a 30% filtration loss. All other identified organisms were retained on the GF/F filter and no further adjusting was needed.

Eukaryotic plankton. A subsample (100 ml) was preserved in Lugol's solution (KI 0.1 g ml^{-1}, I_2 0.05 g ml^{-1}) and acetic acid (0.1 g ml^{-1}) to a final concentration of 2%. Each sample (10 to 50 ml) was settled overnight in a sedimentation chamber. Pigmented and non-pigmented plankton were classified, enumerated and measured using an inverted microscope. One-half of the sedimentation chamber (265 mm^2) was scanned, counting plankton larger than 10 µm at 250× magnification. For smaller cells (<10 µm), a magnification of 500× was used and one diameter (2.7 mm^2) of the chamber was scanned. At least 50 cells of the most common species and in total >200 cells $sample^{-1}$ were counted. Cell volume was converted to cell carbon using the conversion factor 0.11 pg C μm^{-3} for all plankton, except for armoured dinoflagellates, where the corresponding factor was 0.13 pg C μm^{-3} (Edler

1979). The vacuole volume (90 %) was subtracted from the cell volume of diatoms. The standard error for estimation of the biomass of autotrophic microplankton, heterotrophic microplankton, autotrophic nanoplankton and heterotrophic nanoplankton was 10.9, 9.3, 7.5 and 9.9 %, respectively.

Prokaryotic plankton. A subsample was fixed with formaldehyde, to a final concentration of 4 %. Cyanobacteria were quantified and measured with an epifluorescence microscope using a green excitation light with a 1200× magnification, after collecting 10 to 20 ml on a 25 mm, 0.2 µm polycarbonate MSI-filter. Heterotrophic bacteria were treated similarly: 3 to 15 ml were filtered, stained with DAPI and counted in UV excitation light (Porter & Feig 1980). For both autotrophic and heterotrophic bacteria, at least 15 microscopic fields per slide were scanned. The mean volume of heterotrophic bacteria was measured (>50 cells slide^{-1}) by image analysis and determined to ca 0.18 µm^3. The conversion factor 0.11 pg C µm^{-3} resulted in a cell carbon content of ca 20 fg C bacterium^{-1} (for comparison, see Lee & Fuhrman 1987). The standard error for enumeration of autotrophic and heterotrophic bacteria was ca 2.4 and 3.7 %, respectively.

RESULTS

The seasonal variation of autotrophic and heterotrophic plankton was investigated at a coastal and an offshore station in the Baltic Sea. The plankton were grouped according to size and pigmentation and showed the following composition. Microplankton (10 to 200 µm) were found to be a widespread heterogeneous group: e.g. dinoflagellates, diatoms, green algae (A_{micro}), ciliates (H_{micro}) and others. The nanoplankton group (2 to 10 µm) contained pigmented (A_{nano}) and nonpigmented (H_{nano}) flagellates; the picoplankton group (<2 µm) contained unicellular cyanobacteria (A_{pico}) and heterotrophic bacteria (H_{pico}).

At both stations, a marked seasonal variation of the plankton biomasses was observed (Table 1). The plankton biomass ranged from less than 10 µg C l^{-1} in winter to ca 300 µg C l^{-1} during the spring bloom maximum. The major part of the plankton biomass in spring was accounted for by dinoflagellates (55 to 62 %) and diatoms (11 to 24 %). Heterotrophic free-living bacteria dominated in autumn and winter, contributing 50 to 60 % of the total biomass. In summer, the biomasses of autotrophic microplankton and heterotrophic free-living bacteria were similar at the coastal station, each constituting ca 20 % of the total biomass, while at the offshore station, heterotrophic bacteria dominated (43 % of the biomass). Ciliates and other heterotrophic microplankton accounted for at most 18 % of the plankton biomass in winter and only about 1 % in summer. Their biomass maximum, 19 µg C l^{-1}, was found in May, at the same time as the spring bloom. Autotrophic pico- and nanoplankton reached their peaks in summer and autumn, contributing 10 to 20 % of the biomass. At both stations, heterotrophic nanoplankton never exceeded 1 % of the total plankton biomass.

Composition of POC

The highest concentration of POC (668 µg l^{-1}) was found at the peak of the spring bloom at the coastal station. Minimum values of 99 and 160 µg l^{-1} were detected in winter, offshore and nearshore, respectively. More POC was present at the nearshore station

Table 1. Seasonal variation of POC, detritus and plankton carbon (PC), offshore and nearshore in the northern Baltic Sea. Autotrophic (*A*) and heterotrophic (*H*) plankton carbon, as percentage of PC. Plankton are size-divided in pico-, nano- and microplankton

Season	POC (µg l^{-1})	Detritus (µg l^{-1})	PC (µg l^{-1})	A_{pico}	H_{pico}	A_{nano} (% of PC)	H_{nano}	A_{micro}	H_{micro}
Offshore									
Spring	267	168	99	1	6	2	<1	88	3
Summer	231	148	83	21	43	14	<1	21	1
Autumn	166	133	33	6	61	8	1	18	5
Winter	99	91	8	3	49	5	<1	24	18
Nearshore									
Early spring	248	191	57	1	6.9	2	<1	80	10
Spring	568	375	193	1	4.2	2	<1	89	4
Spring bloom	668	343	325	1	3.3	3	<1	87	6
Summer	340	282	58	8	36	19	1	36	1
Autumn	181	151	30	16	54	6	1	19	3
Winter	161	151	9	5	49	3.0	<1	31	12

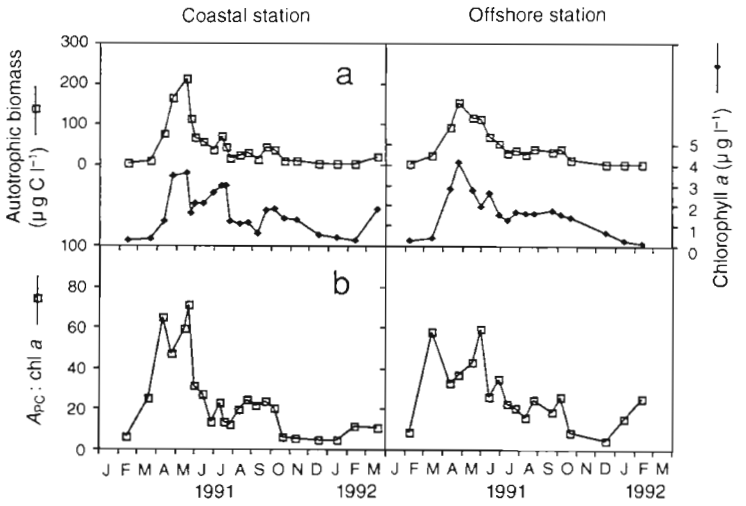

Fig. 2. (a) Variation of autotrophic plankton carbon (A_{PC}) and chl *a* and (b) the ratio of A_{PC}/chl *a* at the coastal and offshore stations during 1991 and 1992

on all sampling occasions, except in early April just before the ice break-up. The difference was mainly due to more detrital material nearshore (Table 1).

As the spring bloom progressed, the POC concentrations increased rapidly (Table 1, Nearshore). Detrital material decreased successively, while the proportion of 'living carbon' increased and formed a peak at the spring bloom maximum. At this point, plankton biomass composed almost half of the total POC at the nearshore station. In summer, POC decreased as did the fraction of plankton biomass, which was by then approximately 20%. In autumn, and particularly in winter, POC was dominated by non-living detritus. In February, the living organisms contributed only to ca 6% of the POC-pool. At the nearshore station, autotrophic and heterotrophic organisms made up an equal proportion of POC in autumn and winter, while the heterotrophic fraction was somewhat larger at the offshore station.

Seasonal changes of phytoplankton and chlorophyll *a*

The ratio of autotrophic plankton carbon (A_{PC}) to chl *a* varied seasonally (Fig. 2). The highest A_{PC}/chl *a* ratio was detected during the development of the spring bloom with a distinct peak after the spring bloom culmination [59 and 71 (µg l^{-1}/µg l^{-1}), offshore and nearshore, respectively]. The ratio rapidly decreased in post-bloom periods, and was nearly constant (ca 20) during the summer and early autumn, with the exception of a small peak in July caused by a diatom bloom of *Chaetoceros* spp. A marked reduction occurred in October and early winter with minimum ratios around 5. Starting in February, the ratio increased again. In the vertical profiles, the highest values were found at 4 to 8 m. No significant differences were found between the near- and offshore stations.

Vertical profiles

The vertical distributions of autotrophic micro-, nano- and picoplankton at the nearshore and offshore stations were similar. Some typical profiles from the coastal station representing the 4 seasons are shown in Fig. 3a, c, e & g. During the spring bloom, nanoplankton biomass was negligible compared to that of microplankton. In July, the distribution of autotrophic plankton was more or less homogeneous throughout the water column. Nano- and microplankton dominated in the upper half of the euphotic layer and each accounted for about 50% of the autotrophic biomass. At the lower half of the euphotic zone, there was a clear dominance of microplankton, mainly *Chaetoceros* spp. Picoplankton decreased slightly with depth. In autumn, the relative importance of picoplankton increased markedly, and together with nanoplankton contributed the same as microplankton to the total biomass. The lowest biomasses were detected in February for all 3 size-classes. Compared to autumn, the fraction of microplankton increased, while the proportion of smaller autotrophic plankton (< 10 µm) decreased.

The vertical profiles of POC show little or no covariation with those of chl *a* (Fig. 3b, d, f & h), nor are they similar to the biomass profiles. Thus, changes in the autotrophic plankton biomass do not seem to reflect the POC values in the vertical profiles.

DISCUSSION

A marked seasonal variability of the constituents of the POC pool was observed. Autotrophic microplankton and free-living heterotrophic bacteria formed the bulk of 'living carbon'. A_{micro} dominated the plankton biomass throughout spring and H_{pico} during autumn and winter, while other plankton groups, e.g. nanoplankton, were of less importance. Previous productivity and biomass estimates indicate that phytoplankton and free-living heterotrophic bacterioplankton mediate most of the flow of carbon and associated nutrients from dissolved inorganic and organic pools to particulate organic pools, available to particle grazers

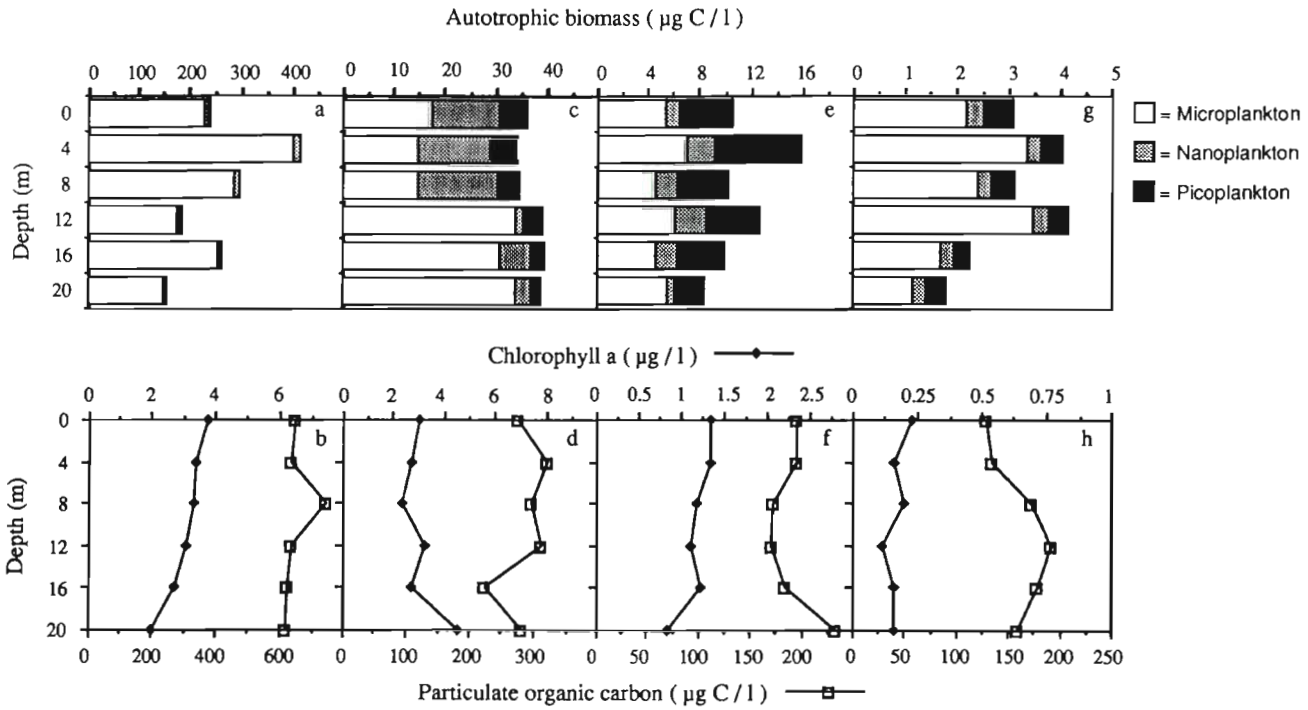

Fig. 3. Vertical distribution of autotrophic plankton carbon (micro-, nano- and picoplankton), chl *a* and POC at the coastal station during: (a, b) spring bloom; (c, d) summer; (e, f) autumn; and (g, h) winter

in the water column (Williams 1984). Thus, both groups represent the 'lowest' trophic levels in marine food webs. The base of a food chain, with several pyramidal trophic levels, may have relatively large biomass and/or rapid turnover time. Other groups of organisms, e.g. autotrophic and heterotrophic nanoplankton, represent intermediate trophic levels. They are carriers of organic material up through the food chain, and do not necessarily contribute largely to biomass.

The spring phytoplankton bloom represents a pulsed source of organic carbon which is important to productivity and carbon flux in marine ecosystems (Laws et al. 1988). In agreement with this, the proportion of plankton biomass in POC was observed to be highest during this time of the year. Maximum POC values occurred during the spring bloom. This pattern corresponds to other coastal areas, whose spring maxima sometimes exceed 1000 µg l^{-1} of POC (Holligan et al. 1984, Mayzaud et al. 1989). However, compared to oceanic concentrations (e.g. ca 20 µg l^{-1}; Sharp et al. 1980), the POC concentrations turned out to be high (nearshore: 160 to 668 µg l^{-1}). During autumn and winter, the particulate detritus made up as much as 85 to 95 % of the POC. The dominance of non-living particles in the POC in this area may be an effect of high river input of allochtonous material and/or resuspended material (Forsgren & Jansson 1992). The detrital part of POC was generally higher at the nearshore station than at the offshore station.

The plankton biomasses were calculated by microscopic analysis of plankton volumes. Recommended conversion factors were used to obtain cell carbon estimates. These compared well to chemical measurements from earlier studies: for equally sized cells of *Thalassiosira* spp., *Gymnodinium* spp. and *Skeletonema costatum* we estimated 1620, 56 and 5 pg C $cell^{-1}$, while Chan (1980) and Strathmann (1967) obtained 1750, 55 and 10 pg C $cell^{-1}$, respectively. The estimations of the biomass of different plankton groups have standard errors of ca 10 % or less. Such variations do not affect the main conclusions of this study.

Besides estimating autotrophic biomass, chl *a* was also measured. Some of the environmental factors which are known to regulate the ratio of A_{PC} to chl *a* are growth rate, light conditions and species composition (Table 2). These factors can be inter-dependent; the photosynthetic rate, and thus the growth rate, may be a function of nutrient status (Eppley 1972). Furthermore, the photosynthetic rate is also connected to the amount of irradiance. The degree of influence of each factor is not obvious. Moreover, the factors may not influence the A_{PC}/chl *a* ratio levels consistently throughout the year. In this area, where there is almost 24 h of daylight in the summer, one would expect maximum ratios to occur during this time. In fact, this was

Table 2. Factors suggested to influence the autotrophic plankton carbon (A_{PC}) to chlorophyll *a* (chl *a*) ratio in seawater

Factor		A_{PC} : chl *a*	Source
Temperature	⇓	⇑	Eppley (1972)
Growth rate	⇓	⇑	Sakshaug et al. (1989)
Irradiance	⇑	⇑	Cullen (1982), Holligan et al. (1984)
Nutrients (phosphate, nitrogen, ammonium)	⇓	⇑	Tett et al. (1975), Sakshaug et al. (1989)
No. of Dinophyceae	⇑	⇑	Chan (1980)
Cell size of eukaryotes	⇑	⇑	Malone (1980), Furuya (1990)

not the case at either of the stations for this study (Fig. 2b). In accordance with this theory though, minimum ratios occurred simultaneously with minimum irradiance between October and December. Thus, the high A_{PC}/chl *a* ratio in spring was a result of the bloom mainly consisting of dinoflagellates and other large eukaryotes (Chan 1980, Malone 1980, Furya 1990). The peak of A_{PC}/chl *a* appearing immediately after the spring bloom culmination would most likely be due to stress caused by nutrient depletion (Jonge 1980). The A_{PC}/chl *a* ratio also varied somewhat vertically in the water column because of differences in species composition, light and nutrient conditions. Thus, it is not obvious that the carbon biomass maxima coincides with the chl *a* maxima.

The values of A_{PC}/chl *a* presented here are mainly within the range of earlier published values (Hobson et al. 1973, Bodungen et al. 1975), except for the low values in winter. In the attempts to find conversion factors for estimating plankton carbon from chemical measurements of chl *a* , we are encouraged by the fact that relatively few autotrophic plankton species are dominant in the northern Baltic Sea. In spring bloom situations, for example, when 1 or 2 groups dominate the algal community, acceptable estimations should be possible (Riemann et al. 1982). This study covers 1 yr (1991) and 2 separate stations, and similar fluctuations of A_{PC}/chl *a* were found at both stations. Furthermore, the variations were found to be repeated during 1992. The ratio after the spring bloom culmination, in summer and autumn was 80, 17 and 4 respectively, at the nearshore station. From these results it is clear that the A_{PC}/chl *a* ratio varies with season in the studied area. Similar seasonal variations in the A_{PC}/chl *a* ratio may also occur in other temperate seas.

The data presented here stress the seasonal variability of the constituents of the POC pool and ratio of autotrophic biomass and chl *a*. Such fluctuations make it difficult to use constant conversion factors for estimating pools of biomasses from chl *a* or POC measurements, except for given environments and seasons. The use of a fixed conversion factor of 50, for example, to obtain phytoplankton carbon from chl *a*, may imply an over-estimation of the phytoplankton carbon by a factor of ca 10. Thus in quantitative studies, like in modelling of the carbon flow in food webs, we suggest that careful determination of the conversion factors should be made on a seasonal basis.

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