LIMNOLOGY
AND
OCEANOGRAPHY

May 2001
Volume 46
Number 3

Limnol. Oceanogr., 46(3), 2001, 473–485

Size structure and the production/respiration balance in a coastal plankton community

Erik M. Smith[1] *and W. Michael Kemp*
University of Maryland Center for Environmental Science, Horn Point Laboratory, P.O. Box 775, Cambridge, Maryland 21613

Abstract

The quantitative significance of contributions by the picoplankton (<3 μm) to gross primary production (P) and community respiration (R) was investigated seasonally in the plankton community of Chesapeake Bay. Rates of P and R for the total plankton community, integrated over the euphotic zone, ranged from 119–709 μmol O_2 m^{-2} d^{-1} and 41–325 μmol O_2 m^{-2} d^{-1}, respectively. Rates of P and R within the picoplankton community tended to covary with those of the total plankton community, although the strengths of the two relationships were markedly different. The mean proportion of total community R accounted for by the picoplankton averaged 54%, with the two rates being highly correlated. In contrast, the relative contribution of picoplankton to total P was highly variable, ranging from 1 to 77%, with fluctuations in picoplankton production rates explaining only 29% of the variability in total P. Although P and R exhibited a significant positive relationship over the entire data set, individual $P:R$ ratios varied substantially, ranging from 0.95 to 4.73. Seasonal variations in $P:R$ ratios for the picoplankton were out of phase with those of the total community. When the total plankton community was most autotrophic ($P:R > 1$), the picoplankton $P:R$ was net heterotrophic ($P:R < 1$), and as total plankton $P:R$ ratios decreased toward balanced metabolism ($P:R = 1$), picoplankton $P:R$ ratios increased to become net autotrophic. Seasonal and spatial variations in the contributions of picoplankton P and R to total rates had a strong effect on the $P:R$ ratio of the plankton community as a whole. There was a pronounced inverse relationship between the $P:R$ ratio of the total plankton community and the proportion of P attributable to the picoplankton, such that high net autotrophy occurred only when P was dominated by the larger size fractions. These findings indicate an important linkage between the size distribution of the primary producers and the overall balance of P and R in the plankton community, which in turn regulates the potential for organic matter export.

The biological cycle of pelagic ecosystems can be viewed as a coupling between the two fundamental plankton community processes: photosynthesis and respiration. The ratio of gross photosynthesis, or primary production (P), to total community respiration (R) represents a quantitative index of ecosystem trophic status (Odum 1956). This ratio describes the balance between the flow of organic matter required to maintain the metabolic integrity of the community and that available for growth within, or export from, the ecosystem (Platt et al. 1992). Although P and R must converge at long-term global scales, biogeochemical cycling within an ecosystem, or between adjacent ecosystems, is essentially driven by the flux of organic matter that accompanies the uncoupling of P and R.

There is now an increasing recognition of the importance of combined measures of P and R as a means of directly quantifying the ecological functioning of individual communities or ecosystems within the marine carbon cycle (Smith and Hollibaugh 1993; Sherr and Sherr 1996). A growing number of studies have documented relationships between P and R across a variety of marine ecosystems. It is clear from these comparisons that ecosystems exhibiting high rates of P also tend to have high rates of R, although in the largest comparative analysis to date (Duarte and Agustí 1998) R exhibited greater than tenfold variation for any given level of P. Investigations within individual ecosystems have also shown that, although there is often a general relationship between the two variables, the balance between P and R is not static but varies greatly on both temporal (e.g., Hopkinson et al. 1989; Blight et al. 1995) and spatial (e.g., Smith and Kemp 1995; Iriarte et al. 1996) scales. There is

[1] Present address: Dépt. des Sciences Biologiques, Université du Québec à Montréal, CP 8888, succursale Centre-Ville, Montréal, Québec, Canada H3C 3P8 (smith.erik@uqam.ca).

Acknowledgments

We are sincerely indebted to M. E. Mallonee for his generous assistance during research cruises. Earlier versions of this manuscript benefited greatly from discussions with T. C. Malone and W. R. Boynton, as well as from the constructive criticisms of P. J. leB. Williams and one anonymous reviewer. Funding and ship time for this research were provided by the NSF LMER program (DEB-9412113). This is contribution number 3397 of the University of Maryland Center for Environmental Science.

little empirical information, however, regarding what controls the proportion of *P* readily consumed within the plankton community versus that which remains available for export. The substantial unexplained variation common to all published relationships of *P* and *R* (e.g., Duarte and Agustí 1998) suggests that variations in heterotrophic consumption must depend on other factors in addition to simply the magnitude of *P*, per se.

If the type, or source, of *P* plays a role in the variability of *R*, then models of phytoplankton size and the structure of aquatic food webs (e.g., Legendre and Le Fèvre 1995) would suggest that the size of the autotrophs themselves may be an important component of *P* versus *R* relationships in the plankton community. Size-fractionated rate measurements within coastal planktonic communities have consistently shown *R* to be dominated by the microbial fraction (e.g., Williams 1981; Sampou and Kemp 1994), whereas the proportion of *P* due to the picoautotrophs is highly variable (e.g., Malone et al. 1986; Blight et al. 1995). This suggests that the differential partitioning of plankton community *P* and *R* with respect to organism size may strongly influence the fate of that production.

The idea that the structure of pelagic ecosystems is largely dependent on organism size is at the foundation of most conceptual models of biological oceanography (e.g., Ryther 1969; Platt 1985; Legendre and Le Fèvre 1995) and has led to the paradigm of two contrasting modes of carbon flow in pelagic systems (e.g., Goldman 1988; Cushing 1989). In the first mode, the classical grazing food chain, primary production is dominated by large phytoplankton, with a relatively short food web leading directly to zooplankton and fish. In the second, the microbial food loop, production by picoplankton and nanoplankton is largely dissipated within the loop itself, with little capacity to support higher trophic levels or the export of organic matter. These modes of production are expected to dominate under different environmental or hydrodynamic conditions (Margalef 1978) as a result of the size-dependent physiological properties of the phytoplankton, such as nutrient uptake, photosynthetic efficiency, and sinking rates (e.g., Malone 1980; Chisholm 1992). If variability between the two production modes is a major factor in the fate of production within plankton communities (Boyd and Newton 1999), this should be reflected by the $P:R$ ratio within these communities.

Although oceanic plankton communities are often assumed to operate near steady state (e.g., Fenchel 1988), short-term physical events, providing the right combination of mixing and new nutrient input, allow rapid bursts of growth by larger plankton (Goldman 1988). The coastal zone certainly cannot, at any time, be considered in steady state, and temporal variability across a range of scales effects the associated plankton communities (Lewis and Platt 1982). For example, estuarine production can be driven on annual scales by the spring freshet (e.g., Harding 1994), on lunar scales by spring-neap tidal cycles (D'Elia et al. 1981), and on event scales by wind-driven lateral seiching and pycnocline tilting (Malone et al. 1986). To the extent that physical–chemical differences influence variability between the two previously mentioned modes of organic carbon flow, coastal and estuarine plankton should experience widely varying community structure and metabolic balance.

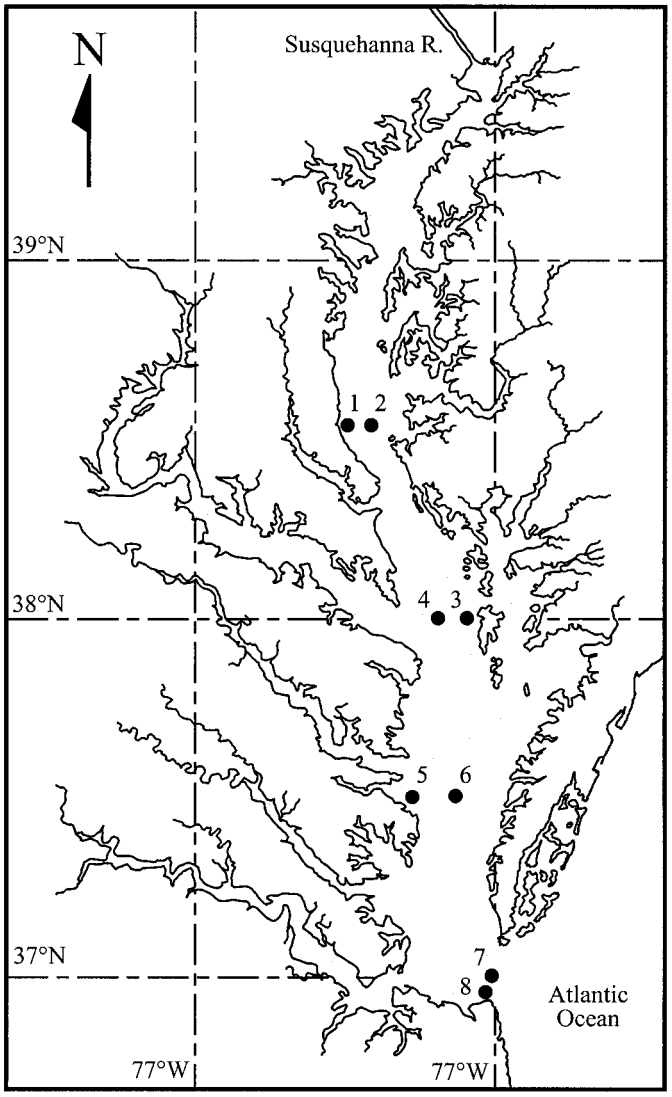


Fig. 1. Map of Chesapeake Bay, USA, showing nominal location of paired channel and flank stations. Station numbers refer to those given in Table 1.

Although there are numerous reports of size-fractionated phytoplankton productivity measurements (e.g., Malone 1980), systematic plankton community investigations of both *P* and *R* with respect to organism size distribution are few (e.g., Smith et al. 1986; Blight et al. 1995). The aim of this study was to relate seasonal and spatial differences in plankton community *P* and *R* rates to their variability within the picoplankton community, as operationally defined by that within the <3-μm size fraction. Assuming that the $P:R$ ratio represents an integrated index of export potential, we then tested for a relationship between size distribution of primary production and the ratio of autotrophy to heterotrophy within the plankton community. Finally, in an attempt to deduce processes governing these relationships, we examine temporal and spatial variability in the partitioning of rates and $P:R$ ratios among the two size fractions. This study was

conducted in the surface waters of the mesohaline to polyhaline region of Chesapeake Bay, which is characterized by a wide range of *P* and *R* rates in the plankton community (Smith and Kemp 1995) and by high overall net autotrophy (Kemp et al. 1997).

Methods

Sampling protocol—In 1996 and 1997, water samples were collected from the euphotic zone at eight stations within the middle to lower portion of the mainstem Chesapeake Bay (Fig. 1). Sampling was conducted during three cruises each year, representing the spring, summer, and fall seasons. Specific cruise dates were, for 1996, 28 April–02 May, 17–21 July, and 27 October–01 November, and for 1997, 20–23 April, 11–14 July, and 31 October–3 November. Owing to logistical constraints, only four stations were sampled during the spring cruise of 1996, and only six stations were sampled during the fall cruise of 1997.

At each station, water was collected for rate measurements, nutrient concentrations, and algal biomass. Water samples at these stations were obtained from approximately 2 m below the surface during morning (0700 to 1000 h) hydrocasts using an array of Niskin bottles (10 liters) mounted on a General Oceanics rosette, with a CTD (Neil Brown Instruments) providing concurrent surface to bottom vertical profiles of temperature, salinity, dissolved oxygen, and in situ fluorescence.

Size fractionation—Water samples at each station were fractionated through 142 mm, 3.0-μm pore-size polycarbonate membrane filters (Poretics). Filtration was accomplished using a custom made, low-flow, gravity driven, reverse flow filtration system (e.g., Williams 1981; Sampou and Kemp 1994). All fractionations were done indoors under low light and initiated immediately after completion of the hydrocast. To ensure homogeneity among sample incubation bottles, the filtrate was not subsampled until the required volume had been obtained (approx. 2 liters). The resulting concentrate of sample water was discarded. Filtration was generally completed within an hour after sampling. During times or locations with high concentration of the larger phytoplankton, membrane filters were changed periodically to prevent overloading of filters, and thus avoid potential problems involving the rupturing of cells (Malone et al. 1991).

Production and respiration rate measurements—Rates measurements of plankton community gross primary production and respiration were based on light–dark bottle oxygen incubations. All oxygen concentrations were determined by precise Winkler titration of whole samples in the incubation bottle, with an automated photometric endpoint detection system (Sensoren Instrumente Systeme). All incubations were performed using standard, clear, acid-washed, glass biological oxygen demand (BOD) bottles. For total community rate measurements, 300 ml volume BOD bottles were used. For the $<$3-μm size-fraction measurements, 60 ml volume BOD bottles were employed to reduce the amount of filtering required. Preliminary experiments showed no difference in rates of production or respiration for the $<$3-μm fraction when incubated in either 60-ml or 300-ml bottles. Thus, the 60-ml bottles were adopted for all subsequent $<$3-μm fraction incubations.

Immediately after completion of the sampling hydrocast, unfiltered water was gently combined, via siphon, from several Niskin bottles into a low-density polyethylene (Nalgen) carboy (50 L) to ensure homogeneity of the sample. Water was then siphoned from the carboy into BOD bottles, which were filled and allowed to overflow to twice the sample volume, and then capped with ground-glass stoppers. Four replicate bottles were fixed immediately after collection for initial O_2 concentrations. This same filling procedure was employed for the size-fractionated samples, except that bottles were filled by siphoning directly from the reverse-filtration apparatus.

Production rates were measured in BOD bottles incubated for 4–6 h in an on-deck flow-through incubator ($\pm$1°C of in situ temperatures), with one bottle at each of seven irradiance levels (from 3 to 100% ambient light) established using neutral-density screening of individual bottles. Ambient incident photosynthetically active radiation (PAR, 400 to 700 nm) was measured on shipboard using an integrating PAR sensor. Light reaching each bottle was expressed as a percentage of mean integrated ambient PAR (Ein m^{-2} d^{-1}) for the day of incubation. Rates of gross primary production (*P*) were estimated as the difference between dissolved oxygen concentrations in clear and opaque bottles. Vertically integrated rates of *P* were calculated using a photosynthesis versus irradiance (*P-I*) relationship modeled as a hyperbolic tangent function (Jassby and Platt 1976). The specific *P-I* relationship for each station-date was estimated by least-squares fit using the nonlinear regression techniques of SAS statistical software (SAS Institute). Gross production (μmol O_2 m^{-2} h^{-1}) was integrated over the depth of the euphotic zone (to 1% surface irradiance) based on the vertical attenuation of light. Values for diffuse downwelling irradiance attenuation coefficient (K_{par}) were estimated as 1.5/Secchi disk depth (Harding 1994). Daily integrated rates (μmol O_2 m^{-2} d^{-1}) were then calculated by extrapolating the hourly production rates based on the fraction of total daily PAR occurring during the course of the incubation.

Plankton community respiration rates (*R*) were calculated as the difference in O_2 concentration between initial bottles and four replicate opaque bottles at the end of incubation. Bottles were incubated in removable opaque sleeves for a period of either 6 h (summer cruises) or 12 h (spring and fall cruises). As with *P* measurements, bottles were incubated in shipboard flow-through water baths maintained at in situ temperatures ($\pm$1°C). Daily integral rates of total community respiration were then calculated as hourly rates multiplied by 24 h d^{-1} and vertically integrated by multiplying volumetric rates by the depth of the euphotic zone. This integration step assumes respiration rates are uniform with depth, which previous work (Smith and Kemp 1995) has shown to be valid for the relatively shallow, well-mixed surface layer of Chesapeake Bay. The integrated value is thus the total community respiration rate within the euphotic zone (μmol O_2 m^{-2} d^{-1}), and it can be directly compared to *P* for estimating the metabolic balance for the plankton community of the euphotic zone.

Table 1. Station locations and surface water temperatures, and production, respiration and chlorophyll *a* data for the total community and for the <3 μm size fraction. Z_{max} equals total station depth. $Z_{1\%}$ equals depth of the euphotic zone. Data not available = nd.

Season	Station	Latitude (°N)	Longitude (°W)	Temperature (°C)	Z_{max} (m)	$Z_{1\%}$ (m)	P_T (μmol O_2 m^{-2} d^{-1})	R_T	Chl_T (μg L^{-1})	P_3 (μmol O_2 m^{-2} d^{-1})	R_3	Chl_3 (μg L^{-1})
Spring 1996	1	38.50	76.50	13.3	6.2	4.3	246.6	71.0	15.2	15.3	32.9	1.0
Spring 1996	2	38.50	76.41	13.6	22.4	6.1	336.6	87.5	17.4	11.5	38.2	0.8
Spring 1996	3	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Spring 1996	4	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Spring 1996	5	37.50	76.25	13.8	6.6	3.4	383.4	81.1	46.2	4.6	33.2	1.4
Spring 1996	6	37.50	76.03	13.8	15.7	5.5	474.7	149.3	44.4	48.0	74.3	3.7
Spring 1996	7	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Spring 1996	8	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Summer 1996	1	38.50	76.50	24.4	5.4	5.4	311.6	105.3	7.7	58.4	82.7	1.8
Summer 1996	2	38.50	76.40	25.5	22.3	6.1	605.3	201.3	19.0	98.4	141.1	5.2
Summer 1996	3	38.00	76.21	25.8	12.0	7.1	665.4	324.8	14.7	212.9	142.0	8.2
Summer 1996	4	38.00	76.30	25.8	22.5	7.1	603.5	314.2	13.9	229.0	181.9	6.8
Summer 1996	5	37.50	76.25	26.1	6.8	5.8	708.6	261.0	17.6	336.0	210.3	5.1
Summer 1996	6	37.50	76.03	26.1	12.2	6.8	438.0	224.4	14.5	120.2	187.0	nd
Summer 1996	7	37.03	76.00	23.8	7.7	7.7	483.3	173.3	13.1	52.6	129.9	2.1
Summer 1996	8	36.95	76.00	25.9	22.0	8.0	244.3	240.0	8.9	161.3	187.8	4.2
Fall 1996	1	38.50	76.50	17.5	7.5	6.1	292.4	100.7	16.3	49.6	45.8	4.7
Fall 1996	2	38.50	76.40	17.5	22.6	6.4	366.9	124.8	19.3	83.9	52.0	9.2
Fall 1996	3	38.00	76.10	17.5	6.7	6.1	270.6	91.5	20.1	97.3	82.0	5.1
Fall 1996	4	38.00	76.20	17.6	24.6	8.6	201.3	148.4	11.4	107.9	91.4	4.2
Fall 1996	5	37.50	76.25	17.0	6.6	5.8	213.7	78.3	14.7	70.9	56.2	5.1
Fall 1996	6	37.50	76.17	17.0	10.3	5.8	209.4	78.3	10.6	16.9	30.8	3.7
Fall 1996	7	37.04	76.00	17.0	8.0	4.6	154.0	62.1	10.5	12.6	10.1	2.1
Fall 1996	8	36.95	76.00	17.0	25.5	4.6	117.1	62.1	7.7	48.4	34.5	3.9
Spring 1997	1	38.50	76.49	10.6	4.5	4.3	323.8	116.1	17.8	138.8	71.2	10.4
Spring 1997	2	38.49	76.41	10.4	22.9	4.3	188.4	93.5	17.0	97.9	55.1	8.3
Spring 1997	3	38.00	76.08	10.8	4.3	4.3	398.4	109.7	71.0	3.5	25.5	4.4
Spring 1997	4	38.00	76.21	10.7	25.1	5.2	199.1	70.2	33.9	9.2	39.0	5.3
Spring 1997	5	37.50	76.25	12.1	6.2	5.8	133.4	56.6	23.9	9.8	25.4	3.6
Spring 1997	6	37.50	76.05	11.6	16.5	5.8	130.9	60.9	13.6	24.6	25.4	2.8
Spring 1997	7	37.02	76.00	12.2	6.5	5.6	295.6	79.8	8.0	5.9	24.5	1.2
Spring 1997	8	36.98	76.00	12.3	14.0	7.1	281.3	74.6	8.1	28.4	42.2	0.7
Summer 1997	1	38.50	76.49	25.4	7.3	4.9	336.3	162.0	17.8	175.5	128.9	6.6
Summer 1997	2	38.50	76.41	25.9	22.2	7.7	361.6	247.7	19.5	236.0	168.0	6.9
Summer 1997	3	38.00	76.08	25.9	6.0	4.9	274.4	173.1	36.9	145.7	136.6	7.9
Summer 1997	4	38.00	76.20	26.0	23.0	6.8	305.3	227.8	32.5	180.6	46.4	6.3
Summer 1997	5	37.50	76.26	26.6	5.0	5.5	360.0	174.2	23.9	158.6	148.6	6.2
Summer 1997	6	37.50	76.05	26.1	16.8	6.5	262.8	275.7	13.6	201.2	133.0	7.8
Summer 1997	7	37.02	76.00	25.7	9.2	5.5	232.1	136.9	8.7	124.4	115.8	1.3
Summer 1997	8	36.97	76.00	25.8	13.9	5.5	191.4	149.3	7.2	101.3	95.0	3.2
Fall 1997	1	38.50	76.49	14.6	4.3	10.4	226.6	58.1	6.6	13.3	32.6	2.5
Fall 1997	2	38.50	76.40	14.6	20.5	10.8	211.3	104.8	9.2	43.6	23.5	1.7
Fall 1997	3	38.00	76.09	14.6	6.2	4.1	131.3	40.4	9.0	2.7	18.1	1.0
Fall 1997	4	38.00	76.20	15.2	21.4	10.4	238.1	148.8	10.6	105.5	45.7	4.2
Fall 1997	5	37.50	76.26	15.4	6.0	5.8	176.6	56.8	8.7	25.9	40.1	2.9
Fall 1997	6	37.50	76.05	15.7	16.2	6.1	508.1	133.5	28.8	69.4	26.9	6.5
Fall 1997	7	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Fall 1997	8	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd

Whole and size-fractionated water samples were also collected for phytoplankton biomass determinations. Biomass was estimated fluorometrically as chlorophyll *a* (Chl *a*) concentration. Samples were collected by filtration onto 25-mm GF/F glass fiber filters (Whatman, nominal pore size of 0.7 μm), and stored frozen until processed (<2 months). Chl *a* was extracted by grinding in cold aqueous acetone (90%), filtered to remove residue, and quantified before and after acidification (Parsons et al. 1984) on a Turner Fluorometer. The fluorometer was calibrated with spectrophotometric measurements on pure Chl *a* (Sigma) using a dilution series and the equations of Jeffrey and Humphrey (1975).

Results and discussion

Rates of plankton community gross production (*P*) and respiration (*R*) were highly variable, both seasonally and spatially. *P* ranged from 119 to 709 μmol O_2 m^{-2} d^{-1}, whereas *R* ranged from 41 to 325 μmol O_2 m^{-2} d^{-1} (Table 1). These ranges are comparable to those reported previously for this highly productive system (Kemp et al. 1997) and tended to bracket the range of rates reported for most coastal marine systems. Seasonal patterns in phytoplankton productivity and biomass tended to be out of phase with one another; highest Chl *a* concentrations occurred during the spring, whereas highest rates of *P* occurred during the summer sampling periods. Most of the seasonal and spatial variability in Chl *a* was represented by total community Chl *a* (Chl_T), rather than that in the <3-μm size fraction (Chl_3), which, on average, represented 30% (±19%) of Chl_T. Temporal and spatial patterns in rates of planktonic *P* and *R*, as well as Chl *a* biomass, are consistent with those reported previously for Chesapeake Bay (Smith and Kemp 1995; Kemp et al. 1997).

Whole and size-fractionated P *and* R *rates*—For this study we define picoplankton as those organisms passing through 3-μm pore-size polycarbonate membrane filters. The choice of this filter pore size for the size fractionation was based on the fact that the average retention size of these filters is somewhat smaller than their rated pore size (Sheldon et al. 1972; Williams 1981). As such, our protocol was generally consistent with the convention of Sieburth et al. (1978), who defined the picoplankton as organisms smaller than 2 μm in spherical diameter. Our size-fractionation technique, therefore, tends to separate free-living bacterioplankton, cyanobacteria and other small autotrophs, and the smaller heterotrophic flagellates from larger organisms and detrital particles (plus attached bacteria). Within the regions of Chesapeake Bay sampled during the present study, free-living cells largely dominate total bacterial numbers and metabolic activity. Particle-attached cells have been shown to generally account for less than 10% of bacterial abundance and metabolism within these regions (Griffith et al. 1994). Thus, our estimates of *R* for the <3-μm size fraction account for the vast majority of the bacterial metabolism within the plankton community.

Although the prefiltration methods for size fractionation of plankton metabolism have been widely used (e.g., Williams 1981; Smith et al. 1986; Biddanda et al. 1994; Blight et al. 1995), this approach may cause changes in cell physiology (Malone et al. 1991) or predator–prey interactions (Sherr and Sherr 1988; Pomeroy et al. 1994). In the later case, actual microbial rates tend to be overestimated due to the removal of predators, sometimes resulting in size-frac-

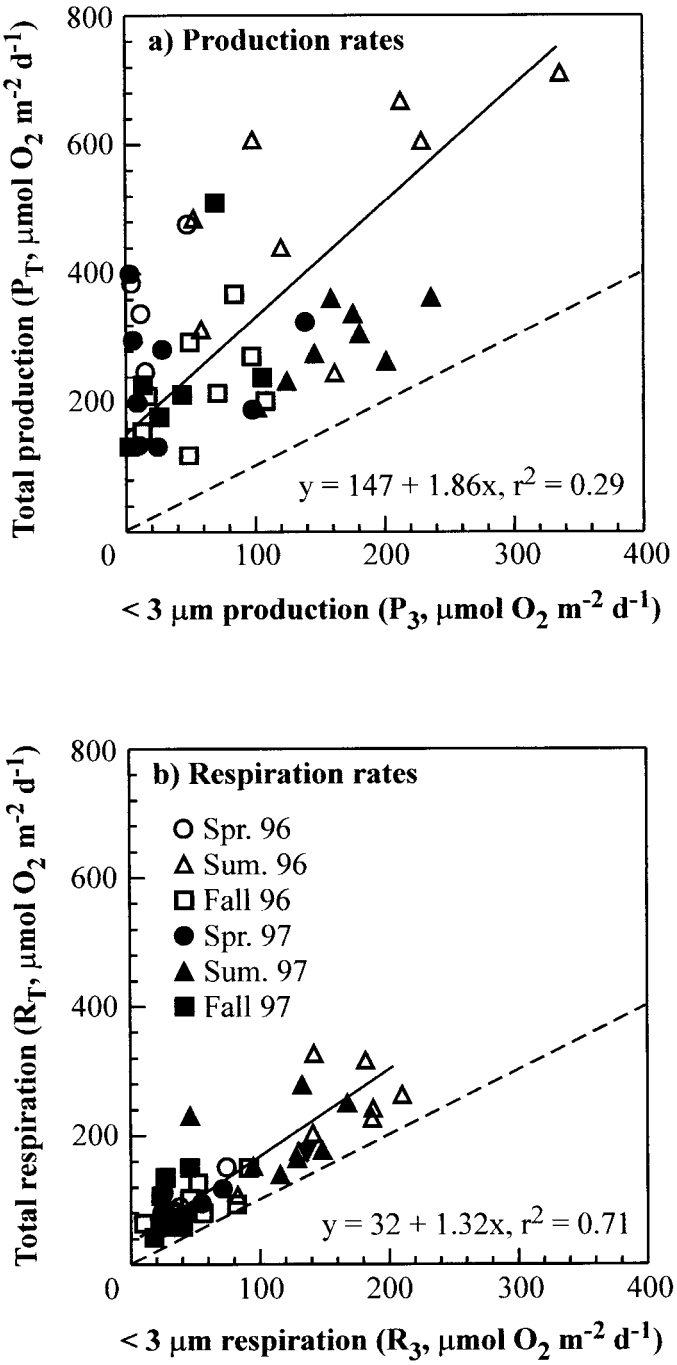


Fig. 2. Relationships between (a) rates of gross production within total plankton (P_T) and <3-μm size fraction (P_3) communities, and (b) rates of community respiration within total plankton (R_T) and <3-μm size fraction (R_3) communities. Respiration rates are integrated over the depth of the euphotic zone, comparable to that of gross production. Solid lines represent best fit of model II regression. Dashed lines represent 1 : 1 lines.

tionated rates exceeding those of the unfiltered water (e.g., Hopkinson 1985). In general, these artifacts of prefiltration methods would result in significant changes in metabolic rates over the course of the incubation (e.g., Pomeroy et al. 1994). Where rates are linear over long (24–36 h) incubations, it is reasonable to infer that these problems are relatively unimportant (Williams 1981; Sampou and Kemp 1994; Blight et al. 1995). In the present study, initial time-course respiration experiments revealed linear changes in oxygen concentration for incubations up to 30 h (data not shown). Actual incubation times for rate determinations were kept relatively short (4–6 h for P, 6–12 h for R), however, to minimize effects of food-web disruptions. At no time did the <3-μm rates exceed the corresponding total community rates.

For both P and R, picoplankton rates tended to covary with those of the corresponding total plankton community, although the strength of the two relationships differed greatly (Fig. 2). Although the relationship between primary production rates for picoplankton (P_3) and total plankton community (P_T) was statistically significant, it exhibited considerable scatter (Fig. 2a). Variation in P_3 explained only 29% of the variability in P_T, with P_3 accounting for 1–77% (mean 28%) of P_T. There was a significant seasonal component to this variation, as well. Picoplankton contribution to P_T averaged 13% during spring, but increased to 45% during summer. This is consistent with the seasonal trend reported previously for size-fractionated ^{14}C productivity in Chesapeake Bay (Malone et al. 1991), and it reflects a general spring to summer transition in plankton community structure typical of temperate coastal environments (Kiørboe 1993). Although picoplankton productivity rates and contributions to P_T tended to peak in summer, over the entire sampling period most of the total gross primary production was generally attributable to larger cells.

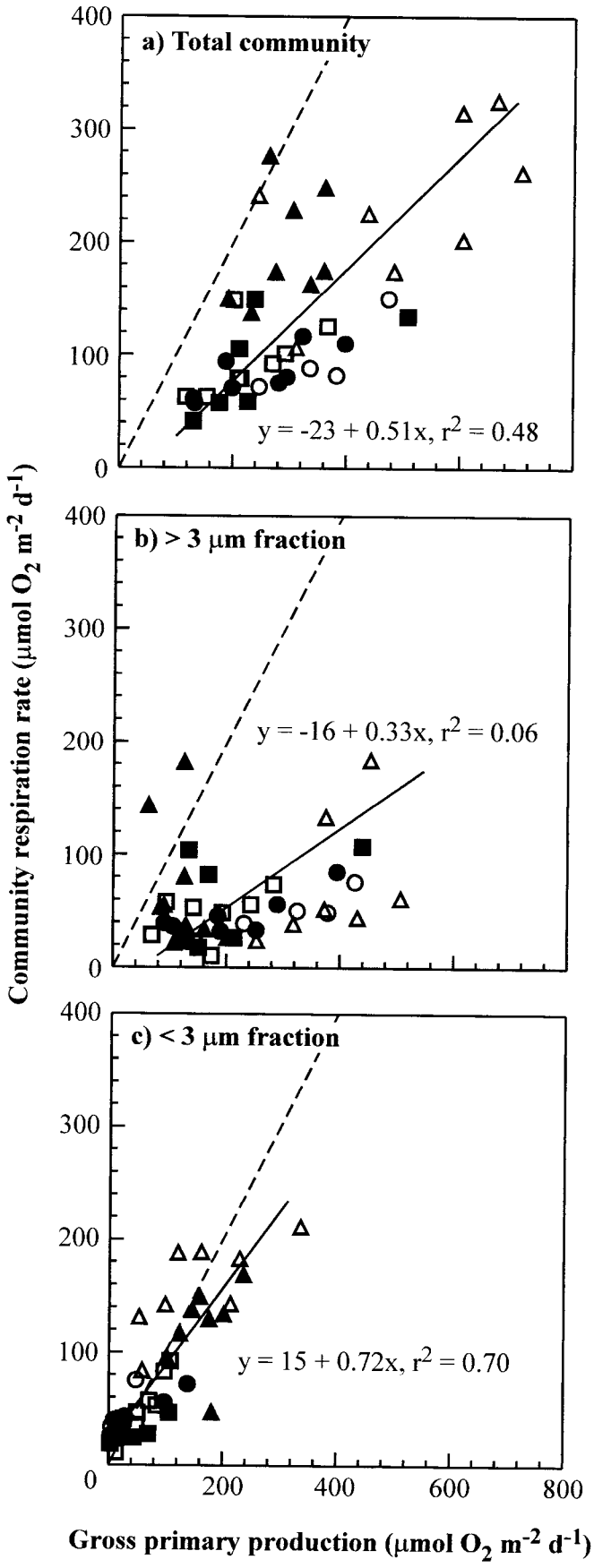
In contrast, picoplankton respiration rates (R_3) were strongly correlated with respiration rates of the total plankton community (R_T), explaining 71% of the variability in R_T (Fig. 2b). Furthermore, the ratio of $R_3:R_T$ was consistently larger than $P_3:P_T$, with picoplankton respiration averaging 54% of R_T (range 16–90%), but only 28% of P_T. This mean ratio of $R_3:R_T$ is similar to previous estimates for Chesapeake Bay (Sampou and Kemp 1994). Additionally, the strong relationship between R_3 and R_T suggests that the variability in total plankton respiration was largely attributable to respiration in the picoplankton. Within the <3-μm size fraction, respiration rate showed no significant correlation with Chl a biomass ($r^2 = 0.19$, $P > 0.01$). This suggests that variations in autotrophic biomass within the <3-μm size fraction were not controlling variations in R_3, and thus the autotrophic component was not a major contributor to the respiration rate of this size fraction. This is consistent with the findings of a previous study for the Chesapeake Bay, which estimated the mean contribution of picoautotrophs to total respiration within the <3-μm size fraction to be less than 15% (Smith 1998). In the present study, picoplankton respiration exhibited some seasonal pattern, accounting for 46% R_T in spring and 68% during summer. The variability in $R_3:R_T$, however, was substantially less (C.V. = 38%) than that for $P_3:P_T$ (C.V. = 76%).

Relationships between P *and* R—When integrated over annual and Bay-wide scales, Chesapeake Bay is net autotrophic ($P > R$), both for the plankton community (Smith and Kemp 1995) and the whole ecosystem (Kemp et al. 1997). This pattern of P exceeding R is particularly pronounced in the lower, polyhaline regions of the Bay (Smith and Kemp 1995; Kemp et al. 1997). During the present study, rates of P exceeded R for the plankton community in all but one case, and the mean $P_T:R_T$ ratio was 2.5. The euphotic zone was therefore a net source of organic production for the ecosystem. Comparisons between P and R may differ depending on whether rates are normalized to water volume or surface area (Williams 1998), and here we used vertically integrated rates to consider metabolic balances over the euphotic zone. Perspectives on metabolic balance may also be influenced by whether P versus R relations are modeled as linear or power functions (cf., Duarte and Agustí 1998; Williams and Bowers 1999). As is the convention for analyzing plankton metabolism data from a single coastal environment (e.g., Hopkinson 1985; Jensen et al. 1990; Iriarte et al. 1996), we used a linear model for our analysis of P versus R relationships. As both P and R include associated measurement error, however, linear regressions were performed using model II regression techniques following the equations of Ricker (1973).

A significant ($p < 0.001$) relationship between total community rates (P_T and R_T) was observed for the entire data set (Fig. 3a), although variations in P_T explained only 48% of the seasonal and spatial variability in R_T. Significant positive relationships between P_T and R_T appear to be common features of aquatic systems, both within individual systems (e.g., Jensen et al. 1990) and across a range of systems (e.g., Duarte and Agustí 1998; Williams 1998). A relationship between P_T and R_T is commonly taken as evidence of the importance of autochthonous production in supplying the organic matter to sustain heterotrophic activity within the ecosystem (Hopkinson 1985; Blight et al. 1995). The lack of a significant intercept ($p > 0.19$) for the relationship between P_T and R_T seen here is also consistent with the idea that, at least for this area of Chesapeake Bay, allochthonous inputs of organic matter do not significantly contribute to the heterotrophic respiration in the euphotic zone (Smith and Kemp 1995).

Although significant relationships between P_T and R_T were observed over the seasonal and spatial scales sampled in this study, the substantial unexplained variation in R_T suggests that plankton respiration was regulated by more than substrate supply alone. Ratios of $P_T:R_T$ integrated over the euphotic zone ranged greatly, from 0.95 to 4.73. The absence of a relationship between $P_T:R_T$ and P_T ($r^2 = 0.03$, $P = 0.31$) suggests that, over the range of observed rates, the balance of autotrophy and heterotrophy was independent of the magnitude planktonic production, per se (cf., Duarte and Agustí 1998), and other factors need to be considered.

Patterns of $P:R$ ratios for the >3- and <3-μm size fractions differed dramatically (Fig. 3b,c). For the picoplankton community, there was a highly significant ($p < 0.001$) relationship between P_3 and R_3 (Fig. 3c), with variations in P_3 explaining 70% of the variability in R_3. Rates of picoplankton production and respiration tended to approach balanced



conditions, with a mean $P_3:R_3$ ratio of 1.08 and a relatively small range (0.14–3.89). In contrast, for the larger (P_L = >3 μm) size fraction (Fig. 3b), there was no significant relationship ($p > 0.05$) observed between production (P_L) and respiration (R_L). Although estimates of P_L varied over a relatively large range (comparable to that of P_T), the bulk of the estimates of R_L showed substantially less variability. The plankton community in this larger fraction tended to be strongly autotrophic, with a mean $P_L:R_L$ ratio of 5.14 (ranging from 0.43 to 18.17). Although rates for the larger size fraction were calculated by difference between direct measurements for picoplankton and total community and are therefore subject to error propagation, the weak relationship between P_L and R_L again suggests that community respiration was regulated by factors other than substrate availability.

Organism size distributions and the balance between P *and* R—The contrast in relationships between P and R for the picoplankton and the larger (>3 μm) size fractions suggests that variations in the size structure of organisms in the plankton community may determine the balance between autotrophy and heterotrophy within that community. We tested this hypothesis by examining the relationship between the ratio $P_T:R_T$ and the proportion of P_T attributable to the <3-μm size class ($P_3:P_T$). A strong inverse relationship between the two variables was evident (Fig. 4). Differences in $P_3:P_T$ explained 70% of the variability in plankton community $P_T:R_T$ ratios. This relationship is markedly stronger than that between P and R for the total plankton community (Fig. 3a). In fact, measurements of P_3 served as an excellent predictor for deviations from the regression line relating P_T and R_T, such that R_T(predicted) $-$ R_T(observed) = $59 - 209 \times P_3$ ($r^2 = 0.71$, $P < 0.001$). That is to say, in those cases where R_T was above the value predicted by the regression equation in Fig. 3a, P_T tended to be dominated by P_3. The mean ratio of $P_3:P_T$ for data where R_T (observed) exceeds R_T (predicted) was 0.51, with 60% of the data having a value for $P_3:P_T$ greater than 0.50. On the other hand, for all observed values of R_T that were below the regression line (higher than predicted net autotrophy), associated values of $P_3:P_T$ were all less than 0.50, with a mean ratio of $P_3:P_T = 0.16$. As a result, when production by the picoplankton was only a minor component of the total production, the plankton community as a whole was highly autotrophic. Conversely, as the relative contribution of picoplankton increased, net metabolism of the plankton community declined toward a balance between autotrophy and heterotrophy. This relationship between $P_T:R_T$ and $P_3:P_T$ therefore supports the hypothesis that the balance between planktonic production and consumption of organic matter is regulated, in large part, by the community size structure. In this respect, events that stim-

←

Fig. 3. Relationships between euphotic zone production and respiration for (a) total plankton community, (b) >3-μm size fraction, and (c) <3-μm size fraction. Solid lines represent best fit of model II regression. Dashed lines represent 1 : 1 lines. Symbols are as in Fig. 2.

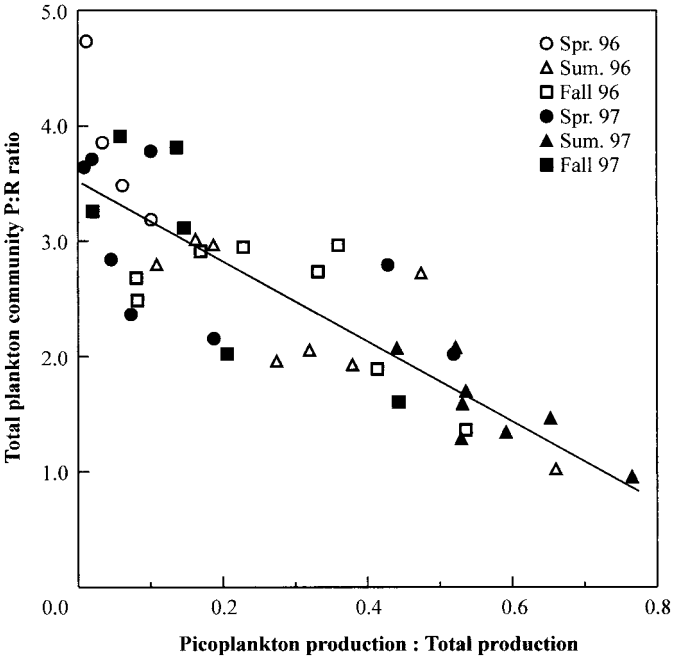


Fig. 4. Relationship between proportion of total plankton production attributable to that of the <3-μm size fraction ($P_3:P_T$) and the $P:R$ ratio of the total plankton community ($P_T:R_T$). Solid line represents best fit of model II regression.

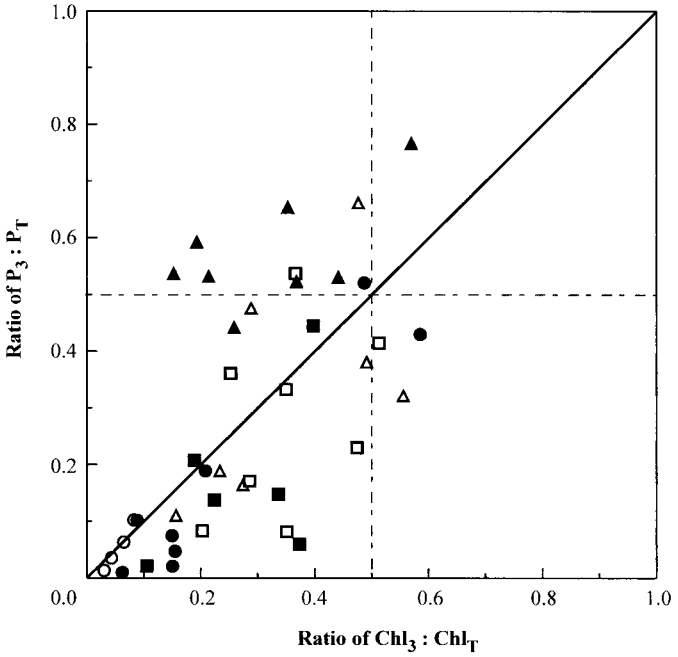


Fig. 5. Production–biomass diagram showing the relationship between proportion of <3-μm Chl *a* to that of total Chl *a* ($Chl_3:Chl_T$) and <3-μm *P* to that of total *P* ($P_3:P_T$). On the main diagonal (solid line) $P_3:P_T = Chl_3:Chl_T$. Dashed lines provide visual references to point where small algal cells represent 50% of biomass and production. *See text for details.*

ulate production of the larger phytoplankton will result in temporal or spatial pulses of enhanced net autotrophy and the concurrent potential for organic export from the plankton community.

Because the $P:R$ is related to the *f* ratio (Quiñones and Platt 1991), which is, in turn, related to the relative availability of primary production for export (Epply and Peterson 1979), the present results support the hypothesis that export from the euphotic zone is proportional to the ratio of large to small phytoplankton cells (e.g., Legendre and Le Fèvre 1995; Boyd and Newton 1999). Results here also suggest that the dominance of one size class over another is more important in a relative, rather than absolute, sense. As there was only a weak relationship between P_3 and total plankton, P_T (Fig. 2a), the relationship between $P_3:P_T$ and the absolute level of *P* also showed a great deal of scatter, particularly at the higher end ($r^2 = 0.17$). As a consequence, the relationship between $P_T:R_T$ and P_3 ($P_T:R_T = 3.55–0.11 \times P_3$, $r^2 = 0.35$, $P < 0.01$), although statistically significant, was substantially weaker than that between $P_T:R_T$ and $P_3:P_T$ (Fig. 4).

The above arguments are based on the relative difference between size fractions in *P*, rather than the relative abundance, or biomass, of large versus small phytoplankton. There was also a significant relationship between $P:R$ ratio and the proportion of total plankton community Chl *a* comprised by picoplankton cells ($Chl_3:Chl_T$), where $P_T:R_T = 3.33–2.62 \times Chl_3:Chl_T$, $r^2 = 0.30$, $P < 0.01$, suggesting that $P:R$ ratio could also be predicted simply by the relative abundance of phytoplankton biomass (as measured by Chl *a*) in each size fraction. The strength of the relationship was weaker than that seen in Fig. 4, however, with $Chl_3:Chl_T$ explaining only 30% of the variation in $P:R$ ratio (relative to 70% for that of $P_3:P_T$). This difference was due to the fact that the relationship between $Chl_3:Chl_T$ and $P_3:P_T$ was not constant across the data set. The two parameters were only weakly related to one another ($r^2 = 0.33$), suggesting a highly dynamic balance existed between production and loss terms within the picoplankton community. In fact, there is no reason to expect a direct equivalence between picoplankton contributions to algal biomass and to primary production. Relative differences in productivity of small compared to large phytoplankton result from allometric differences in physiological rate functions, which vary with nutrient and light availability (e.g., Malone 1980). In contrast, the size distribution of standing stock is also influenced by losses to grazing and sinking, in addition to variations in primary production (e.g., Peinert et al. 1989). Thus, it has been suggested that the relationship between the size distribution of phytoplankton production and standing stocks is an intrinsic property of the overall structure of pelagic ecosystems (Legendre and Le Fèvre 1995).

Tremblay and Legendre (1994) introduced the use of phytoplankton production versus biomass (*P-B*) plots to characterize potential export (sedimentation, grazing, or advection) from the euphotic zone, considering the proportions of production and biomass in two algal size fractions (<5 and >5 μm). Here, we present a slight variation of their *P-B* plot, using the ratio of picoplankton to total Chl *a* ($Chl_3:Chl_T$) and *P* ($P_3:P_T$), as *x* and *y* axes, respectively (Fig. 5). In theory, if production and loss terms were equal between the two size fractions, the data would all fall along the di-

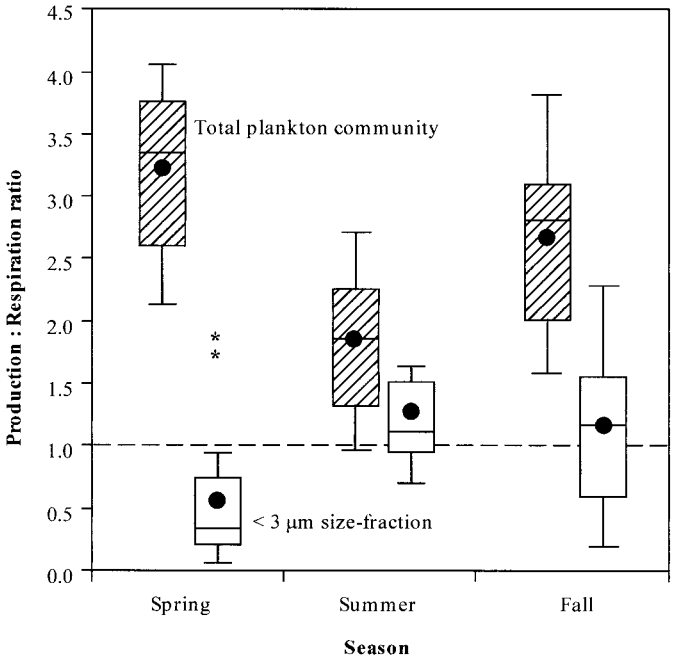


Fig. 6. Box plot of $P:R$ ratios within total plankton community (hatched boxes) and <3-μm size-fraction community (open boxes) for each season. The bottom and top edges of the box are the sample 25th and 75th percentiles. The center horizontal line is the sample median, and the central filled circle is the sample mean. Vertical lines represent 1.5 interquartile ranges. Any values more extreme than this are marked with an asterisk (*). Horizontal dashed line at $P:R = 1$ provides visual reference. Spring = late April–early May, summer = mid-July, fall = late October–early November.

agonal ($P_3:P_T = \text{Chl}_3:\text{Chl}_T$). Deviations below the diagonal indicate that, relative to total phytoplankton, the standing stock of small cells is higher than expected from their share of the primary production. This suggests a net accumulation of picoplankton biomass within the euphotic zone. By the same logic, deviations above the diagonal represent a loss of small cells disproportionate to their share of the production.

In the present study, data points fell above the diagonal for all observations in which picoplankton production dominated ($P_3:P_T > 0.50$). These data points also correspond to those for which the picoplankton $P:R$ balance was significantly net autotrophic, as will be discussed below. Since small cells do not appreciably sink (e.g., Smayda 1970), this loss represents either grazing or horizontal advection. For the summer data (seven of the ten observations above the diagonal at $P_3:P_T > 0.5$), however, spatial variations in picoplankton abundance were relatively minor, leaving grazing as the most direct explanation for this deviation. Thus, these data suggest that when picoplankton contribution to P_T was greatest, this production was being rapidly consumed to fuel secondary production at higher trophic levels. In this case, we expect a relatively tight coupling of P and R within the total plankton community, such that the ratio $P_T:R_T$ approaches unity (Fig. 4).

Variability in size-fractionated P *versus* R *relationships*—The relative proportion of P_T attributable to P_3 served as a significant predictor of the residual variability in the plankton community P versus R relationship over the entire data set. The distribution of data points in Fig. 4, however, indicates a pattern of both temporal and spatial differences in the overall relationship. In the following section we examine these two types of variability in the data as a means of exploring the substantial range in $P:R$ ratios observed within the plankton community of Chesapeake Bay.

Seasonal patterns in $P_T:R_T$ ratios have been reported previously for plankton communities of Chesapeake Bay (Smith and Kemp 1995), as well as for other coastal systems (e.g., Lefevre et al. 1994; Blight et al. 1995). In all these studies there was a documented progression from high $P:R$ ratios during winter/spring to lower values during summer. When data from the present study are pooled by season, this same pattern for $P_T:R_T$ ratios is evident (Fig. 6). Like most temperate latitude estuaries, the seasonality in phytoplankton dynamics in Chesapeake Bay is characterized by a prominent spring bloom, consisting largely of diatoms and supported by riverine input of allochthonous nutrients, and a summer phytoplankton community of lower biomass, supported primarily by regenerated nutrients and dominated by more diverse community of picoplankton and smaller nanoflagellates (Boynton et al. 1982; Malone et al. 1991). Thus, the annual cycle in $P_T:R_T$ ratio closely corresponds to previously described taxonomic shifts in the seasonal succession of the phytoplankton community in Chesapeake Bay.

The seasonal trend of $P_3:R_3$ ratios for the picoplankton, on the other hand, followed exactly the opposite pattern as that of the whole water community. On average, the springtime metabolism of this <3-μm community was decidedly net heterotrophic, with a mean $P_3:R_3$ ratio of 0.56. Picoplankton production in spring tended to be low, such that consumption of organic matter by small heterotrophs, and the net heterotrophy of the picoplankton, was apparently being supported by the relatively high net production of larger phytoplankton in the spring bloom community (Fig. 7a). This differential partitioning of P and R between larger cells ($P > R$) and smaller cells ($P < R$) has been observed in previous studies comparing size-fractionated metabolic rates (Williams 1981; Smith et al. 1986; Blight et al. 1995). A different pattern was observed, however, for the summer period, when the average metabolic balance of the picoplankton community shifted to that of net autotrophy, with a mean $P_3:R_3$ ratio of 1.26. This finding appears to be without precedent in the literature, but is consistent with previous observations of a spring to summer decrease in the ratio of bacterioplankton to picophytoplankton productivities in Chesapeake Bay (Malone et al. 1991). As carbon flux through picoautotrophs increased to its summer maximum, increases in P_3 were greater than increases in R_3 such that this community became a net source of organic matter potentially available to fuel the secondary production of the larger heterotrophs (Fig. 7b). This is consistent with the *P-B* plot for this time period, which shows high production but low standing stock of this size fraction (Fig. 5), thereby supporting the possibility that picoplankton production was being grazed by the larger heterotrophs during summer.

Observations in this study also suggest substantial interannual variability in the relative contribution of picoplankton

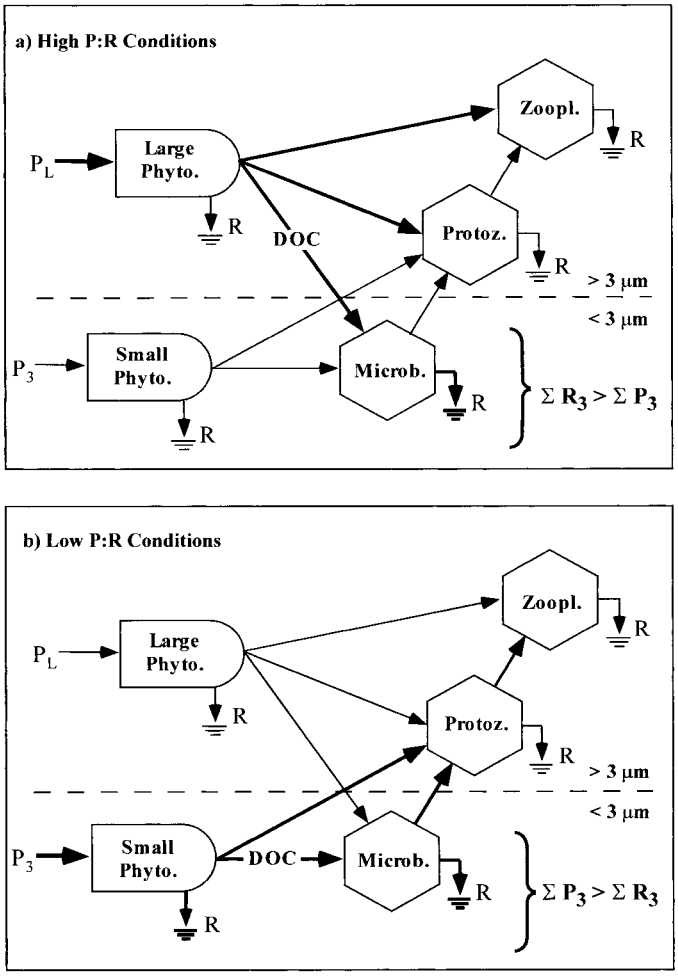


Fig. 7. Conceptual diagram depicting hypothesized relationships between plankton community structure and $P:R$ balance. Bold lines depict dominant flow paths. (a) When production is dominated by larger phytoplankton, $P:R$ balance is highly net autotrophic for the community as a whole, but net heterotrophic for the <3-μm size fraction. (b) When production is dominated by the smaller phytoplankton, $P:R$ balance of the total plankton community decreases, but the <3-μm size fraction becomes net autotrophic.

production and its effect on community level $P:R$ ratio ($P_T:R_T$). This pattern is seen by comparing the individual data (Table 1 and Fig. 4) by year. Interannual variability in the magnitude and seasonality of plankton production and biomass are largely driven by variations in river flow to Chesapeake Bay (Harding 1994). Riverine inputs of freshwater and associated nutrient loading to Chesapeake Bay exhibited record high levels throughout most of 1996 (USGS monitoring data, http://chesapeake.usgs.gov). A vast spring bloom of diatoms extended throughout the length of the estuary and, in contrast to typical seasonal patterns, diatom abundance and productivity remained high throughout the bay during the summer months as well (E. M. Smith, unpubl. data). Hydrographic conditions in 1997, on the other hand, were more typical. The contrast in summer conditions between these two years is reflected in both mean $P_T:R_T$ ratios and the contribution of P_3. The mean summer $P_T:R_T$ ratio during 1996 was 2.30 ($\pm$0.69), compared to that of 1.56 ($\pm$0.39) for 1997. Although P_T during summer (Fig. 3) was significantly higher in 1996 than in 1997 (ANOVA, $P < 0.001$), the contribution by the picoplankton community was, in fact, lower in 1996 relative to 1997 ($p < 0.005$). As a result, $P_3:R_3$ ratios for the picoplankton community tended toward net heterotrophy during the summer of 1996, with a mean of 0.90 and a range of 0.40–1.60. It was only during the summer of 1997, when the picoplankton dominated P_T rates (mean $P_3:P_T = 0.57$), that this community was observed to be consistently net autotrophic, with $P_3:R_3$ ratios ranging from 1.07 to 3.89. In comparison, the absolute levels of P within the picoplankton size class showed no difference, on average, between the two summer sampling periods (158 $\pm$ 97 and 165 $\pm$ 43 μmol O_2 m^{-2} d^{-1} for 1996 and 1997, respectively). It would appear that higher nutrient loading to the Bay during the wet year of 1996 preferentially stimulated production within the larger size classes of phytoplankton. It was this production that resulted in higher levels of P_T during 1996 (comparing data points in Fig. 2a). As there was no commensurate difference in levels of R for either the picoplankton (R_3) or total plankton (R_T) communities, the integrated $P_T:R_T$ ratio was also shifted higher in 1996 (2.30 $\pm$ 0.69), relative to that of 1997 (1.56 $\pm$ 0.39). This observed interannual pattern is consistent with the general trend of new nutrient inputs stimulating large phytoplankton and total phytoplankton biomass accumulation (Epply and Peterson 1979; Malone 1980; Tamigneaux et al. 1999).

In addition to the temporal variability seen in the relationship between size structure and $P:R$ ratio, there was a substantial amount of spatial variability observed within any given sampling period. This variation was often almost as large as that observed seasonally (Table 1). Within each cruise there were no consistent patterns in $P_T:R_T$ ratio with respect to distance along the portion of the estuarine gradient sampled during this study. The largest and most consistent variations in $P_T:R_T$ occurred laterally, between stations in the deep central channel and in the shallower lateral flank regions. In 16 out of 21 paired station comparisons (Fig. 8a), metabolic ratios for the flank station [$(P_T:R_T)_{fl}$] were greater than those of the corresponding channel station [$(P_T:R_T)_{ch}$]. There was a weak, but significant, trend to the comparison that showed this lateral difference tended to decrease with increasing $P:R$ ratios [$(P_T:R_T)_{fl} = 1.71 + 0.51(P_T:R_T)_{ch}$, $r^2 = 0.37$, $P < 0.05$]. On average, therefore, it was during summer that differences were most pronounced, with the lateral flank stations being substantially more net autotrophic than the central channel stations. A similar comparison for the picoplankton, however, did not show any relative enhancement of $P_3:R_3$ for the flank stations, compared to the channel stations (Fig. 8b). Ratios of $P_3:R_3$ were largely equivalent among these stations pairs, except for the four occasions in which $P_3:R_3$ ratios were, in fact, greater in the channel station.

Horizontal gradients are a common feature of estuarine environments. Lateral gradients in both phytoplankton biomass and productivity have been reported previously for Chesapeake Bay (Malone et al. 1986; Weiss et al. 1997), as well as other estuaries (e.g., Caffrey et al. 1998). Within the Chesapeake, these lateral gradients in biomass and produc-

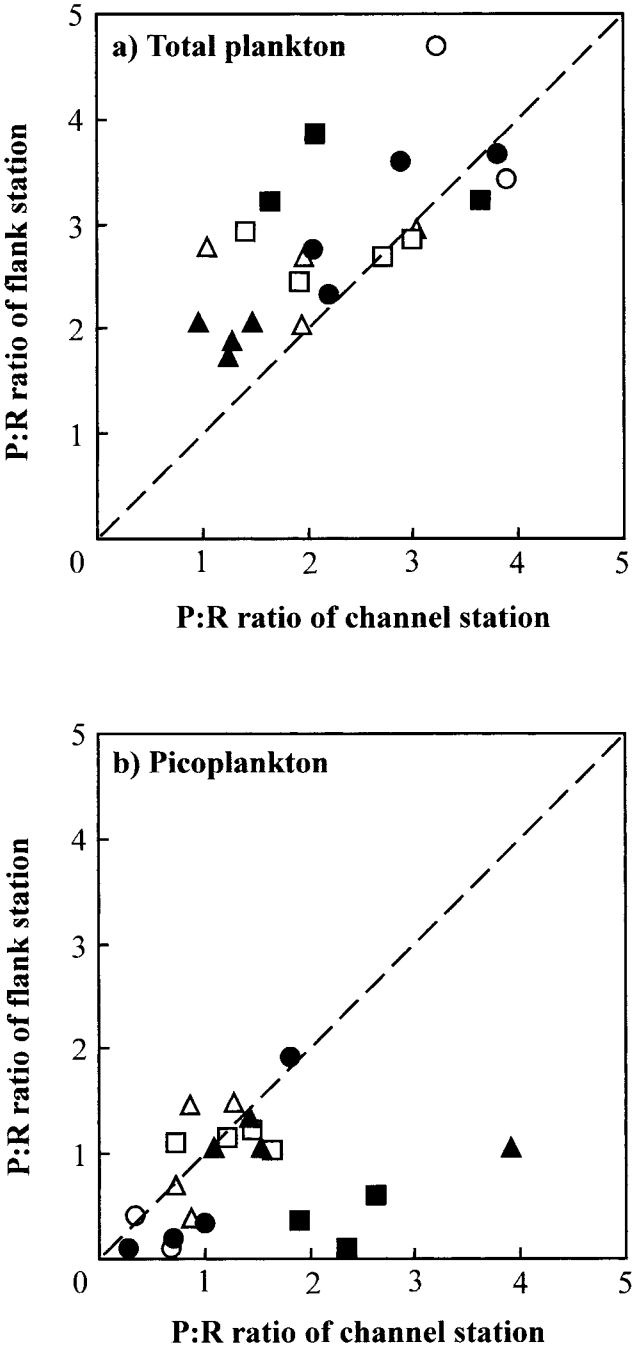


Fig. 8. Property–property plots of $P:R$ ratio of channel and flank station pairs for (a) total plankton community ($P_T:R_T$) and (b) <3-μm size-fraction community ($P_3:R_3$).

tivity have been related to gradients in nutrient concentrations and vertical density structure. The shallow mean depths of the flank stations result in a well-mixed water column, in contrast to the two-layer stratification typical of the central channel. In addition, by virtue of the close vertical proximity of the euphotic zone and benthos on the flanks, enhanced benthic-pelagic coupling within these regions could also act to stimulate higher production relative to the deeper channel region. The results here suggest that lateral differences represent a substantial shift in phytoplankton community structure, which result in significant gradients in $P:R$ from shallow to deep regions. During the summer, when $P_T:R_T$ ratios within the euphotic zone are closest to balance (Smith and Kemp 1995; and Fig. 6), phytoplankton tend to be dominated by a community of nanoflagellates and cyanobacteria (Malone et al. 1986). Under these conditions, the majority of the carbon flow is channeled through a microbial type of food web (e.g., Malone et al. 1991). This was certainly the case for the channel stations of the present study. By comparison, samples taken from the flanks, not more than a few kilometers away, revealed a phytoplankton community dominated by large cells with a highly net autotrophic $P:R$ balance (Fig. 7a). This is more what might be expected for spring (high nutrient) conditions.

Essentially, this small-scale lateral pattern in the estuary is analogous to the larger scale trend from neritic to oceanic waters, where large phytoplankters tend to dominate inshore waters while picoplankton dominate offshore to the oligotrophic open ocean (Malone 1980; Fenchel 1988). In both cases, the gradient in phytoplankton community structure from large cells inshore to small cells offshore suggests hydrodynamic control over phytoplankton size structure (e.g., Cushing 1989; Legendre and Le Fèvre 1995). Small-scale spatial variations in picoplankton contributions to production were highly correlated to the degree of mixing and surface layer stratification in the lower St. Lawrence estuary (Tremblay et al. 1997; Tamigneaux et al. 1999). This general pattern may, in fact, be a feature of all aquatic systems, related to the relative depth of the mixed layer and strength of stratification. An important consequence of this trend in Chesapeake Bay is that plankton communities of the lateral flanks contribute a disproportionately large fraction to the ecosystem net production, supporting the characteristic net heterotrophy of the deeper channel regions (Kemp et al. 1997).

In summary, variability in the partitioning of P and R between size fractions played an important role in driving observed patterns in the overall metabolic balance of the plankton community as a whole. Variations in R_T were largely determined by variations in R_3, as R_3 was a major contributor to R_T. The contribution of P_3 to P_T, on the other hand, was less and highly variable, both seasonally and spatially. P and R were tightly coupled within the picoplankton community, but not so in the larger size fraction. As a result, variations in the $P:R$ balance of the total plankton community were highly related to the relative production attributable to the picoplankton. This strongly argues that heterotrophic metabolism of in situ production is dependent not only on the overall magnitude of P, but also by the size of the algal cells responsible for that production. There is thus a strong interdependence between structure (size) and function (integrated metabolic balance) within the overall plankton community. This relationship was robust over a variety of temporal and spatial scales and particularly useful in understanding small-scale lateral variability within the estuary.

References

BIDDANDA, B., S. OPSAHL, AND R. BENNER. 1994. Plankton respiration and carbon flux throughout bacterioplankton on the Louisiana shelf. Limnol. Oceanogr. **39:** 1259–1275.

BLIGHT, S. P., T. L. BENTLEY, D. LEFEVRE, C. ROBINSON, R. RODRIGUES, J. ROWLANDS, AND P. J. LEB. WILLIAMS. 1995. Phasing of autotrophic and heterotrophic plankton metabolism in a temperate coastal ecosystem. Mar. Ecol. Prog. Ser. **128:** 61–75.

BOYD, P. W., AND P. P. NEWTON. 1999. Does planktonic community structure determine downward particulate organic carbon flux in different oceanic provinces? Deep-Sea Res. I **46:** 63–91.

BOYNTON, W. R., W. M. KEMP, AND C. W. KEEFE. 1982. A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production, p. 67–90. *In* V. S. Kennedy [ed.], Estuarine comparisons. Academic Press.

CAFFREY, J., J. CLOERN, AND C. GRENZ. 1998. Changes in production and respiration during a spring phytoplankton bloom in San Francisco Bay, California, USA: implications for net ecosystem metabolism. Mar. Ecol. Prog. Ser. **172:** 1–12.

CHISHOLM, S. 1992. Phytoplankton size, p. 213–238. *In* P. A. Falkowski and A. Woodhead [eds.], Primary productivity and biogeochemical cycles in the sea. Plenum.

CUSHING, D. H. 1989. A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. J. Plankton Res. **11:** 1–13.

D'ELIA, C. F., K. L. WEBB, AND R. L. WETZEL. 1981. Time-varying hydrodynamics and water quality in an estuary, p. 597–606. *In* B. J. Neilson and L. E. Cronin [eds.], Estuaries and nutrients. Humana.

DUARTE, C., AND S. AGUSTÍ. 1998. The CO_2 balance of unproductive aquatic ecosystems. Science **281:** 234–236.

EPPLEY, R. W., AND B. J. PETERSON. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature **282:** 677–680.

FENCHEL, T. 1988. Marine plankton food chains. Annu. Rev. Ecol. Syst. **19:** 19–38.

GOLDMAN, J. C. 1988. Spatial and temporal discontinuities of biological processes in pelagic surface waters, p. 273–296. *In* B. J. Rothschild [ed.], Toward a theory on biological-physical interactions in the world ocean. Kluwer.

GRIFFITH, P., F.-K. SHIAH, K. GLOERSEN, H. DUCKLOW, AND M. FLETCHER. 1994. Activity and distribution of attached bacteria in Chesapeake Bay. Mar. Ecol. Prog. Ser. **108:** 1–10.

HARDING, L. W. 1994. Long-term trends in the distribution of phytoplankton in Chesapeake Bay: Roles of light, nutrients and streamflow. Mar. Ecol. Prog. Ser. **104:** 267–291.

HOPKINSON, C. S. 1985. Shallow-water benthic and pelagic metabolism: Evidence of heterotrophy in the nearshore Georgia Bight. Mar. Biol. **87:** 19–32.

———, B. SHERR, AND W. J. WIEBE. 1989. Size fractionated metabolism of coastal microbial plankton. Mar. Ecol. Prog. Ser. **51:** 155–166.

IRIARTE, A., I. DE MADARIAGE, F. DIEZ-GARAGARZA, AND M. REVILLA. 1996. Primary plankton production, respiration and nitrification in a shallow temperate estuary during summer. J. Exp. Mar. Biol. Ecol. **208:** 127–151.

JASSBY, A. D., AND T. PLATT. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. **21:** 540–547.

JEFFREY, S., AND G. HUMPHREY. 1975. New spectrophotometric equations for determining chlorophylls *a, b, c1,* and *c2* in higher plants, algae, and natural phytoplankton. Biochem. Physiol. Pflanz. **167:** 191–194.

JENSEN, L. M., K. SAND-JENSON, S. MARCHER, AND M. HANSEN. 1990. Plankton community respiration along a nutrient gradient in a shallow Danish estuary. Mar. Ecol. Prog. Ser. **61:** 75–85.

KEMP, W. M., E. M. SMITH, M. MARVIN-DIPASQUALE, AND W. R. BOYNTON. 1997. Organic carbon balance and net ecosystem metabolism in Chesapeake Bay. Mar. Ecol. Prog. Ser. **150:** 229–248.

KIØRBOE, T. 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. Adv. Mar. Biol. **29:** 1–72.

LEFEVRE, D., T. L. BENTLEY, C. ROBINSON, S. P. BLIGHT, AND P. J. LEB. WILLIAMS. 1994. The temperature response of gross and net community production and respiration in time-varying assemblages of temperate marine micro-plankton. J. Exp. Mar. Biol. Ecol. **184:** 201–215.

LEGENDRE, L., AND J. LE FÈVRE. 1995. Microbial food webs and the export of biogenic carbon in oceans. Aquat. Microb. Ecol. **9:** 69–77.

LEWIS, M. R., AND T. PLATT. 1982. Scales of variability in estuarine ecosystems, p. 3–19. *In* V. S. Kennedy [ed.], Estuarine comparisons. Academic.

MALONE, T. C. 1980. Algal size, p. 433–464. *In* I. Morris [ed.], The physiological ecology of phytoplankton. Univ. California Press.

———, H. W. DUCKLOW, E. R. PEELE, AND S. E. PIKE. 1991. Picoplankton carbon flux in Chesapeake Bay. Mar. Ecol. Prog. Ser. **78:** 11–22.

———, W. M. KEMP, H. W. DUCKLOW, W. R. BOYNTON, J. H. TUTTLE, AND R. B. JONAS. 1986. Lateral variation in the production and fate of phytoplankton in a partially stratified estuary. Mar. Ecol. Prog. Ser. **32:** 149–160.

MARGALEF, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanol. Acta **1:** 493–509.

ODUM, H. T. 1956. Primary production in flowing waters. Limnol. Oceanogr. **1:** 102–117.

PARSONS, T. R., Y. MAITA, AND C. M. LALLI. 1984. A manual of chemical and biological methods for seawater analysis. Pergamon.

PEINERT, R., B. VON BODUNGEN, AND V. SMETACEK. 1989. Food web structure and loss rate, p. 35–48. *In* W. Berger, V. Smetacek, and G. Wefer [eds.], Productivity in the ocean: Present and past. Wiley.

PLATT, T. 1985. Structure of the marine ecosystem: Its allometric basis, p. 55–64. *In* R. E. Ulanowicz and T. Platt [eds.], Ecosystem theory for biological oceanography. Can. Bull. Fish. Aquat. Sci. 213. NRC Research Press.

———, P. JAUHARI, AND S. SATHYENDRANATH. 1992. The importance and measurement of new production, p. 273–284. *In* P. Falkowski and A. Woodhead [eds.], Primary productivity and biogeochemical cycles in the Sea. Plenum.

POMEROY, L. R., J. E. SHELDON, AND W. M. SHELDON. 1994. Changes in bacterial numbers and leucine assimilation during estimations of microbial respiratory rates in seawater by the precision Winkler method. Appl. Environ. Microbiol. **60:** 328–332.

QUIÑONES, R. A., AND T. PLATT. 1991. The relationship between the *f*-ratio and the $P:R$ ratio in the pelagic ecosystem. Limnol. Oceanogr. **36:** 211–213.

RICKER, W. E. 1973. Linear regression in fisheries research. J. Fish. Res. Board Can. **30:** 409–434.

RYTHER, J. H. 1969. Photosynthesis and fish production in the sea. Science **166:** 72–76.

SAMPOU, P. A., AND W. M. KEMP. 1994. Factors regulating plankton community metabolism in Chesapeake Bay. Mar. Ecol. Prog. Ser. **110:** 249–258.

SHELDON, R. W., W. H. SUTCLIFFE, AND M. A. PARANJAPE. 1972. The size distribution of particles in the ocean. Limnol. Oceanogr. **17:** 327–340.

SHERR, E. B., AND B. F. SHERR. 1988. Role of microbes in pelagic food webs: A revised concept. Limnol. Oceanogr. **33:** 1225–1227.

———, AND ———. 1996. Temporal offset in oceanic production and respiration processes implied by seasonal changes in atmospheric oxygen: The role of heterotrophic microbes. Aquat. Microb. Ecol. **11:** 91–100.

SIEBURTH, J. M., V. SMETACEK, AND J. LENZ. 1978. Pelagic ecosystem structure: Heterotrophic compartments of the plankton and their relationship to plankton size fractions. Limnol. Oceanogr. **23:** 1256–1263.

SMAYDA, T. 1970. The suspension and sinking of phytoplankton in the sea. Oceanogr. Mar. Biol. Annu. Rev. **8:** 353–414.

SMITH, E. M. 1998. Coherence of microbial respiration rate and cell-specific bacterial activity in a coastal planktonic community. Aquat. Microb. Ecol. **16:** 27–35.

———, AND W. M. KEMP. 1995. Seasonal and regional variations in plankton community production and respiration for Chesapeake Bay. Mar. Ecol. Prog. Ser. **116:** 217–231.

SMITH, R. E., W. G. HARRISON, B. IRWIN, AND T. PLATT. 1986. Metabolism and carbon exchange in microplankton of the Grand Banks (Newfoundland). Mar. Ecol. Prog. Ser. **34:** 171–183.

SMITH, S. V., AND J. T. HOLLIBAUGH. 1993. Coastal metabolism and the oceanic organic carbon balance. Rev. Geophys. **31:** 75–93.

TAMIGNEAUX, E., L. LEGENDRE, B. KLEIN, AND M. MINGELBIER. 1999. Seasonal dynamics and potential fate of size-fractionated phytoplankton in a temperate nearshore environment (Western Gulf of St. Lawrence, Canada). Estuar. Coast. Shelf Sci. **48:** 253–269.

TREMBLAY, J.-E., B. KLEIN, L. LEGENDRE, R. RIVKIN, AND J. THERRIAULT. 1997. Estimation of the *f*-ratios in oceans based on phytoplankton size structure. Limnol. Oceanogr. **42:** 595–601.

———, AND L. LEGENDRE. 1994. A model for the size-fractionated biomass and production of marine phytoplankton. Limnol. Oceanogr. **39:** 2004–2014.

WEISS, G. W., L. W. HARDING, E. C. ITSWEIRE, AND J. W. CAMPBELL. 1997. Characterizing lateral variability of phytoplankton chlorophyll in Chesapeake Bay with aircraft ocean color data. Mar. Ecol. Prog. Ser. **149:** 183–199.

WILLIAMS, P. J. LEB. 1981. Microbial contribution to overall marine plankton metabolism: Direct measures of respiration. Oceanol. Acta **4:** 359–364.

———. 1998. The balance of plankton respiration and photosynthesis in the open ocean. Nature **394:** 55–57.

———, AND D. BOWERS. 1999. Regional carbon imbalances in the oceans. Science **284:** 1735.

Received: 17 July 2000
Accepted: 2 January 2001
Amended: 12 January 2001