Biomass distribution in marine planktonic communities

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Abstract

Patterns in primary production and carbon export from the euphotic zone suggest that the relative contribution of planktonic heterotrophs to community biomass should decline along gradients of phytoplankton biomass and primary production. Here, we use an extensive literature data survey to test the hypothesis that the ratio of total heterotrophic (bacteria + protozoa + mesozooplankton) biomass to total autotrophic biomass (H:A ratio) is not constant in marine plankton communities but rather tends to decline with increasing phytoplankton biomass and primary production. Our results show that the plankton of unproductive regions are characterized by very high relative heterotrophic biomasses resulting in inverted biomass pyramids, whereas the plankton of productive areas are characterized by a smaller contribution of heterotrophs to community biomass and a normal biomass pyramid with a broad autotrophic base. Moreover, open-ocean communities support significantly more heterotrophic biomass in the upper layers than do coastal communities for a given autotrophic biomass. These differences in the biomass structure of the community could be explained by the changes in the biomass-specific rates of phytoplankton production that seem to occur from ultraoligotrophic to eutrophic marine regions, but other factors could also generate them. The patterns described suggest a rather systematic shift from consumer control of primary production and phytoplankton biomass in open ocean to resource control in upwelling and coastal areas.

One of the earliest tenets in community ecology is the pyramidal distribution of biomass in increasing trophic levels, with a broad autotrophic base supporting increasingly smaller strata of heterotrophs (Elton 1927). Planktonic communities in the ocean, however, are the textbook example of “inverted pyramids” (Odum 1971; Jumars 1993). There is evidence that the biomass of zooplankton (Eppeley et al. 1977; Holligan et al. 1984; Alcaraz et al. 1985) and bacteria (Fuhrman et al. 1989; Cho and Azam 1990; Simon et al. 1992) can exceed or at least be equivalent (Li et al. 1992; Buck et al. 1996) to that of phytoplankton in the ocean. The high biomass of bacteria and zooplankton, together with the substantial biomass of heterotrophic protists (e.g. Sorokin 1977), form an inverted pyramid in which the compounded biomass of heterotrophs exceeds that of autotrophs. The question that is yet unresolved is the generality of the phenomenon of inverted biomass pyramids in marine plankton and whether it can be extended to all marine pelagic communities.

The existence of communities where heterotrophic biomass exceeds autotrophic biomass has been explained by the high turnover rate of the autotrophic pool (Odum 1971;

O'Neill and DeAngelis 1981). Hence, the biomass of heterotrophs relative to that of autotrophs (H:A ratio) is expected to increase as the rate of phytoplankton-specific production or turnover increases. The highest growth rates of phytoplankton appear to occur in oligotrophic areas of the oceans (Goldman et al. 1979; Harris 1984; Laws et al. 1984; Baines et al. 1994), whereas they appear to be lower in eutrophic areas. Moreover, the fraction of primary production lost to sinking (export ratio) appears to be lowest in oligotrophic areas (Wassmann 1990; Baines et al. 1994).

The combination of high turnover of the phytoplankton, low phytoplankton standing stocks, and low export ratios suggest a very tight and efficient coupling between phytoplankton and heterotrophs within the oligotrophic ocean in contrast to what occurs in richer areas. This would suggest the existence of a tendency toward increasing planktonic H:A ratios from eutrophic to oligotrophic areas of the ocean. The existence of this tendency is supported by a pattern of decreasing total adenylate pool to chlorophyll ratios (Campbell et al. 1979), electron transport system activity per unit chlorophyll (Packard 1985), and protein-to-chlorophyll ratio (Dortch and Packard 1989) with increasing chlorophyll concentration. Moreover, the suggested pattern of declining H:A ratio with increasing chlorophyll concentration has already been demonstrated for lake plankton (del Giorgio and Gasol 1995).

The existence of such a regular pattern in the partitioning of biomass between autotrophs and heterotrophs in the ocean would suggest differences in biomass structure and ecosys-

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Table 1. Mean, range, number of data points (N), and standard error (SE) for coastal and open ocean data of integrated phytoplankton biomass (AutoB, mg C m^{-2}), bacterial biomass (BB, mg C m^{-2}), protozooplankton biomass (ProtB, mg C m^{-2}), mesozooplankton biomass (ZooB, mg C m^{-2}), total heterotrophic biomass (HB, mg C m^{-2}), chlorophyll concentration (Chl, mg m^{-2}), phytoplankton production (PP, $\text{mg C m}^{-2} \text{ d}^{-1}$), phytoplankton-specific production [P_B , $\text{mg C mg C}^{-1} \text{ d}^{-1}$], and the ratio of heterotrophic to autotrophic biomass (Ratio).

	Coastal			Open ocean		
	N	Mean $\pm$ SE	Range	N	Mean $\pm$ SE	Range
AutoB	163	$2,921 \pm 335$	52–31,860	279	$1,966 \pm 126$	22–17,500
BB	82	541 ± 63	27–2,850	206	$1,132 \pm 71$	111–11,725
ProtB	86	313 ± 39	6–1,952	119	489 ± 116	3–13,475
ZooB	104	$1,096 \pm 146$	6–7,400	208	847 ± 202	20–41,825
HB	70	$1,535 \pm 196$	136–8,260	138	$2,521 \pm 479$	413–67,025
Chl	82	78 ± 13	5–637	130	67.4 ± 7	2–438
PP	67	794 ± 136	60–8,608	146	$1,300 \pm 79$	141–5,886
P_B	67	0.48 ± 0.09	0.07–5.6	144	1.0 ± 0.11	0.1–8.6
Ratio	70	0.98 ± 0.10	0.05–3.2	122	1.85 ± 0.16	0.17–10.2

tem functioning between oligotrophic and eutrophic areas of the ocean. Dominance of heterotrophs in the oligotrophic ocean would be consistent with consumer regulation of autotrophic biomass and production in the oligotrophic oceans, compared to resource regulation of autotrophs in more eutrophic areas (Agustí et al. 1992). Moreover, a consistent pattern in H:A ratios would also be indicative of similar patterns in the relative contribution of heterotrophs and autotrophs in key biological processes, such as plankton metabolism (Pomeroy and Wiebe 1993), material transfer (Cho and Azam 1988), and light absorption (Agustí 1994).

In this paper we use a compilation of published reports on biomass distributions of open-ocean and coastal plankton communities to test the hypothesis that the proportions of heterotrophic and autotrophic biomass change systematically along gradients of autotrophic biomass and production. We also tentatively explore whether these changes can be attributed to systematic differences in the turnover rate of autotrophs, as could be expected from theory.

Materials and methods

We searched the literature for simultaneous reports on the biomass of phytoplankton, bacteria, metazoan mesozooplankton, and, whenever possible, heterotrophic protists for as wide a range of marine systems as possible, from the open ocean to coastal and estuarine environments. In doing so, we screened all of the work published over the past 20 yr in the major journals on the area (*Limnology and Oceanography*; *Marine Ecology Progress Series*; *Marine Biology*; *Deep-Sea Research*; *Journal of Plankton Research*; *Journal of Marine Research*; *Progress in Oceanography*; *Science*; *Nature*; *Polar Biology*; *Marine Sciences Communications*; *Advances in Marine Biology*; *Canadian Journal of Fisheries and Aquatic Sciences*; *Continental Shelf Research*; *Estuarine, Coastal and Shelf Sciences*) and books as well, and then searched for additional papers cited within the literature screened. We have no doubt that there must be many more values measured, but these either lie in field books, have not been pub-

lished in a usable format, or were overlooked by us. In our first scan we selected those reports that presented simultaneous data of bacteria, phytoplankton, protozoans, and macrozooplankton biomass. We found a total of 10 open-ocean and 24 coastal studies with data on all components (a total of 236 data points). We subsequently relaxed our criteria so as to include papers lacking data on protozoan biomass. This process added 12 studies and 164 data points to the dataset. Finally, and for the construction of the biomass pyramids, we also considered those reports that presented the biomass of one heterotrophic component of the plankton along with that of phytoplankton biomass. This last process, less exhaustive than the two previously described, added 38 studies and 258 data points to the global dataset.

About 70% of the data corresponded to surface-integrated values and the other 30% to volumetric values. The depths of integration were different among studies. Most used the depth receiving 1% of surface irradiance as the integration depth, but others used a fixed depth. We did not attempt to integrate data reported volumetrically to avoid conversion errors. Table 1 presents the number of data points and some statistics for the surface-integrated data considered. The entire dataset is available from the authors upon request or via anonymous FTP at cucafera.icm.csic.es/pub/gasol.

The coastal zone was defined as the area between the land margin and the shelf slope (200-m depth in general). Accordingly, most (>80%) of the data on coastal communities derive from relatively deep areas (>100 m), where benthic organisms are not in contact with the mixed-layer planktonic communities. In four studies, biomass values of plankton development in mesocosms were provided. We grouped all mesocosm data with those of estuaries and coastal oceans, as the source of water for mesocosm experiments is usually coastal water. Surface-integrated data were more or less equally spread between coastal and open-ocean sites, whereas only 18% of the open-ocean studies provided data in volumetric units.

Whenever reported, we also added the primary production and chlorophyll concentration of the sites to the dataset. We

did not attempt to recalculate any data, except for the phytoplankton-specific production, P_B ($\text{mg C mg C}^{-1} \text{ d}^{-1}$), obtained from the data reported by the authors. Most studies presented phytoplankton biomass data combining Chl *a* concentrations with a variety of conversion factors. We did not attempt to correct any of these values even though it is likely that older studies of open-ocean communities used a too low C:Chl factor, which is now thought to be ~ 100 (Welschmeyer and Lorenzen 1984; Hewes et al. 1990; Verity et al. 1996a; Buck et al. 1996). In the few cases (7% of all the points) where the authors had not attempted such conversion, we used a C:Chl value of 55. We also credited the carbon conversion factors used by the different authors. In the few cases where we had to transform the data, we used the following conversion factors: Dry weight was assumed to contain 40% of carbon (Båmstedt 1986; Wiebe 1988). Bacterial biovolume was converted to carbon with a very conservative factor of $120 \text{ fg C } \mu\text{m}^{-3}$ that corresponds to a content of 6 fg C for a $0.05\text{-}\mu\text{m}^{-3}$ cell, the lowest prediction of the different carbon-to-volume volume-dependent conversion factors for bacteria (discussed in Psenner 1990). Microzooplankton wet weight was converted to carbon with a factor of 0.1 (Børsheim and Bratbak 1987), and zooplankton wet weight to carbon with a factor of 0.068 (Båmstedt 1986).

In addition to the variability about the carbon conversion factors used, two other methodological limitations have to be acknowledged. As mentioned above, biomass data for heterotrophic protists (protozoans) was not always reported. In most of the cases where these data were available, one or more of the following groups were not included: nanoflagellates, ciliates, dinoflagellates, radiolarians, and tintinnids. Protozoan biomass was often estimated as all heterotrophic organisms retained on a $35\text{-}\mu\text{m}$ net. Whenever reported by the authors, we considered as phytoplankton biomass that of zoochlorellae-bearing protists (*see* discussion on mixotrophy later on). Zooplankton biomass refers here to metazoan mesozooplankton plus copepodites and nauplii, and we did not attempt to include the larger zooplankton in this compartment. Mesozooplankton is defined by different authors as that material being collected by a net of a variable pore size, from 120 up to $300 \mu\text{m}$. Gelatinous zooplankton is typically undersampled by these nets, and even though they can at times be important consumers of phytoplankton and play an important role in the particle flux to the deep sea, their biomass share is usually small [compare our data set to fig. 4 in Pagès et al. (1996) as an example]. This variability in how protozoan and zooplankton biomass data are defined by different authors is certainly a significant source of scatter in the patterns that we describe and that likely reflect stronger regularities in the structure of the ocean ecosystem.

The dataset assembled includes data from many well-studied estuaries and coastal sites, such as the Skagerrak, the North Sea, the Nova Scotia shelf, or sites in the Benguela and Peru upwellings as well as some data for coastal sites off the Antarctic Peninsula. The open-ocean dataset is also quite well spread, as it includes data from the Mediterranean, the tropical Pacific, the North Atlantic bloom area, the Sargasso Sea, the Indian and the Japan Oceans, as well as some high-nutrient-low-chlorophyll ocean sites as the Weddell Sea and the equatorial and subarctic Pacific.

Data were $\log_{10}$ -transformed prior to statistical analysis to stabilize variance and attain homoscedasticity. We used the linear regression module of Systat (Wilkinson 1987) to estimate the relationships between variables and to conduct analyses of covariance to test for differences between coastal and open-ocean systems. We scaled heterotrophic biomass to autotrophic biomass (computing the ratio H:A) to represent the amount of heterotrophic biomass supported per unit autotrophic biomass. This provides a dimensionless variable that we correlated to autotrophic biomass, chlorophyll, or primary production as indices of trophic status. Regressions between the ratio H:A and autotrophic biomass may be potentially spurious (Prairie and Bird 1989) if the slope of the log-log relationship between heterotrophic biomass and autotrophic biomass does not differ significantly from 1 (Jackson et al. 1990). Accordingly, the hypothesis that the ratio H:A declines with increasing algal biomass was not rejected only when the slope of the log-log relationship between total heterotrophic biomass and autotrophic biomass differed significantly from 1 (*t*-tests).

Results

Total water-column-integrated planktonic biomass tended to be lower and more variable in coastal compared to open-ocean sites (Fig. 1). Such biomass ranged from 0.2 to 40 g C m^{-2} in coastal samples and from 0.4 to 84 g C m^{-2} in open-ocean communities. The tendency of open-ocean sites to support greater total biomass than coastal areas probably results from the deeper mixing layer and the greater depth of integration in the open sea, because the concentration of plankton (g C m^{-3}) was not significantly different between the coastal and open-ocean sites (*t*-tests, all $P > 0.05$). Autotrophic biomass showed a similar range of variation in coastal and open-sea sites (Table 1). The integrated biomass of heterotrophs, however, tended to be higher in the open ocean, with this pattern applying especially to bacteria (Fig. 1, Table 1).

Bacterial and zooplankton biomass were positively, albeit nonlinearly, correlated to autotrophic biomass (Fig. 2). For both bacteria and zooplankton, the slopes of the log-log relationships with autotrophic biomass ranged from 0.20 to 0.65 and were in all cases significantly lower than 1 ($P < 0.001$, Table 2). That the biomass of heterotrophs was approximately scaled to the one-third power of autotrophic biomass indicates that their relative contribution to community biomass declines as phytoplankton standing stocks increase. Moreover, the biomasses of both bacteria and zooplankton were much less variable across ocean sites than was the biomass of phytoplankton (*see* also Verity et al. 1996b). The latter ranged three orders of magnitude in the systems studied, whereas the former varied only by two orders of magnitude (Fig. 1). These patterns were evident both in open-ocean and coastal sites, but open-ocean systems supported about 10-fold more bacterial biomass (Fig. 2A) and zooplankton biomass (Fig. 2B) than did coastal systems (ANCOVA H_0 : equal intercepts for the different systems, all $P < 0.00005$) at similar autotrophic biomasses.

The total biomass of planktonic heterotrophs (bacteria, protozoans, and zooplankton) varied with autotrophic bio-

Fig. 1. Frequency distribution of samples with a given total planktonic biomass, autotrophic, heterotrophic, bacterial, or zooplankton biomass for surface-integrated samples in coastal (left) or open-ocean (right) communities.

mass in a manner similar to that described above for the biomasses of the individual planktonic components. Total heterotrophic biomass was positively correlated to autotrophic biomass (Fig. 3A), but it increased approximately as the one-third power of the latter (Table 2). Again, there is comparatively little variation in total heterotrophic biomass relative to the variation found in phytoplankton standing stocks. As a consequence of the nonlinear increase in heterotrophic biomass with increasing autotrophic biomass, the ratio of heterotrophic biomass to autotrophic biomass (H:A) varied consistently with autotrophic biomass (Fig. 3B). The H:A ratio decreased as the -0.55 power of autotrophic biomass, this tendency accounting for up to 70% of the variation in the H:A ratio (Table 3). This implies that heterotrophic biomass exceeds autotrophic biomass when this is low, whereas autotrophs far exceed the biomass of heterotrophs in systems with high autotrophic biomass. Open-ocean systems, however, supported about 10-fold higher H:A ratios

Fig. 2. Relationship of bacterial biomass (A) and zooplankton biomass (B) with autotrophic biomass for surface-integrated samples in open-ocean (○) or coastal (●) communities. The regression lines are shown to make the patterns more clear. The line of equal autotrophic and heterotrophic biomass is also shown. The patterns are similar for volumetric samples (see Table 2).

for the same autotrophic biomass than did coastal systems (ANCOVA H_0 : equal intercepts for the different systems, all $P < 0.00005$), so that a balance between heterotrophic and autotrophic biomass was achieved at a higher autotrophic biomass ($\sim 3 \text{ g C m}^{-2}$) in the open ocean than in coastal communities ($\sim 0.6 \text{ g C m}^{-2}$, Fig. 3B).

These results suggest a systematic shift from completely inverted biomass pyramids in extremely oligotrophic areas with low autotrophic biomass, to normal biomass pyramids, with a broad autotrophic base, in areas with larger phytoplankton standing stocks. Because coastal areas tended to have higher autotrophic biomass (in g C m^{-3}) than open-ocean areas, normal pyramids predominated in coastal areas, whereas open-ocean sites were usually characterized by inverted pyramids (Fig. 4). These results also indicate that marine plankton communities may exhibit a broad range of biomass distributions, often departing from the traditional inverted pyramid that has usually been assumed for such communities (Fig. 4).

Construction of an average biomass pyramid, standardized to autotrophic biomass, shows differences in the biomass distribution among the different planktonic components from open-ocean and coastal sites (Fig. 4). In open-ocean com-

Table 2. Relationship of the heterotrophic components of the plankton with the autotrophic components and among them. All values are base-10 logarithms of biomass in mg C m^{-3} or m^{-2} . P is the probability of the H_0 : slope = 0 to which the F -ratio corresponds. P ($b = 1$) is the probability of the H_0 : slope = 1 tested with a t -test. HB, total heterotrophic biomass; AutoB, autotrophic biomass; BB, bacterial biomass; ProB, protozooplankton biomass; and ZooB, zooplankton biomass. Volumetric data were not split into coastal or open ocean because almost all were from coastal sites.

Data	Y	X	N	$b \pm \text{SE}$	P ($b = 1$)	F -ratio	P
Areal data	HB	AutoB	192	0.37 ± 0.06	<0.0005	43.8	<0.00005
Coastal	HB	AutoB	70	0.54 ± 0.10	<0.0005	30.4	<0.00005
Open ocean	HB	AutoB	122	0.20 ± 0.05	<0.0005	16.7	0.00008
Volumetric	HB	AutoB	165	0.45 ± 0.05	<0.0005	82.8	<0.00005
Areal data	BB	AutoB	271	0.30 ± 0.06	<0.0005	29.3	<0.00005
Coastal	BB	AutoB	81	0.43 ± 0.09	<0.0005	23.4	<0.00005
Open ocean	BB	AutoB	190	0.20 ± 0.05	<0.0005	13.7	0.0003
Volumetric	BB	AutoB	170	0.55 ± 0.06	<0.0005	91.9	<0.00005
Areal data	ZooB	AutoB	340	0.61 ± 0.06	<0.0005	94.3	<0.00005
Coastal	ZooB	AutoB	148	0.65 ± 0.10	0.0066	38.0	<0.00005
Open ocean	ZooB	AutoB	192	0.57 ± 0.08	<0.0005	57.9	<0.00005
Volumetric	ZooB	AutoB	182	0.37 ± 0.08	<0.0005	22.8	<0.00005
Areal data	ProB	AutoB	188	0.62 ± 0.06	<0.0005	92.2	<0.00005
Coastal	ProB	AutoB	85	0.51 ± 0.11	<0.0005	20.4	<0.00005
Open ocean	ProB	AutoB	103	0.75 ± 0.08	0.002	84.8	<0.00005
Volumetric	ProB	AutoB	165	0.67 ± 0.05	<0.0005	185.8	<0.00005

munities, planktonic biomass is about evenly distributed between zooplankton + protozoans, bacteria, and autotrophs (Fig. 4). In contrast, zooplankton represented a disproportionately larger and more variable fraction of the biomass relative to autotrophic biomass in coastal communities, whereas protozoans represented a much smaller percentage. Most of the data reflected a striking similarity between the biomass of bacteria and that of zooplankton (Fig. 1). Bacteria and zooplankton biomass were significantly and positively correlated (Pearson correlation coefficients for volumetric and areal data are 0.42 and 0.52, all $P < 0.0005$), with log-log slopes significantly smaller than 1 (slopes: 0.4 and 0.6; t -tests, $P < 0.0005$), indicating a tendency for zooplankton biomass to be slightly higher than bacterial biomass at low autotrophic biomasses.

We further explored the hypothesis that variations in the shape of the biomass pyramid may be linked to changes in phytoplankton turnover rate. Systems with fast turnover of the autotrophic biomass may, in the absence of covariation with that of heterotrophs, support higher heterotrophic biomass than do systems with low turnover, leading to inverted biomass pyramids. Hence, the decline in H:A ratio with increasing autotrophic biomass can be accounted for by a parallel decline in the rate of phytoplankton turnover. In a subset of our dataset we analyzed the relationship between the biomass distribution and the turnover rate or specific production rate of the phytoplankton (P_B : primary production divided by autotrophic biomass). Primary production changed as the two-thirds power of autotrophic biomass (log-log slope = 0.60 ± 0.10 , significantly smaller than 1, t -test, $P < 0.0005$), indicating that the turnover rate of autotrophs declines with increasing biomass (Pearson $r = -0.4$, $P < 0.0005$). In our dataset, the turnover rate of the

autotrophs varied about 100-fold over the range of autotrophic biomass studied (Table 1).

The data we gathered seem to support the hypothesis that the H:A ratio covaries with phytoplankton P_B . There was a significant positive relationship between P_B and the H:A biomass ratio (Fig. 5), and the H:A ratio increased as the one-third power of P_B (Table 3). Plankton communities with high phytoplankton turnover rates ($>1 \text{ d}^{-1}$) are in general dominated by heterotrophic biomass, whereas communities with lower phytoplankton turnover rates seem to be dominated by autotrophic biomass. This tendency, however, fails to account for the order-of-magnitude difference in H:A biomass ratio between open-ocean and coastal systems with similar autotrophic biomasses.

Discussion

Our results indicate that plankton communities in extensive areas of the coastal and open oceans are characterized by inverted biomass pyramids and an important dominance of heterotrophic biomass (Holligan et al. 1984; Cho and Azam 1990; Roman et al. 1995). Our results also indicate that the shape of the biomass pyramid is not constant but rather varies considerably among marine plankton communities, and that often includes "straight" biomass pyramids. This variation in biomass distribution is not random, however, and it follows gradients of phytoplankton biomass and productivity. The biomass of heterotrophs (bacteria, protozoans, and metazoan mesozooplankton) increases as the one-third power of the biomass of autotrophs, leading to an increased dominance of heterotrophic biomass in oligotrophic systems with low phytoplankton biomass. The average dis-

Fig. 3. (A) Relationship of total heterotrophic biomass with autotrophic biomass for surface-integrated samples in open-ocean (○) or coastal (●) communities. The 1:1 line is also shown. (B) Relationship of the biomass ratio to autotrophic biomass for surface-integrated samples in open-ocean (○) or coastal (●) communities. The regression lines are shown to make the pattern more clear. The line of equal autotrophic and heterotrophic biomass is also shown. The patterns are similar for volumetric samples (see Tables 2 and 3).

tribution of biomass in marine plankton (Figs. 1, 4) shows a tendency toward a regular partitioning between groups, with quite similar biomasses of bacteria, phytoplankton, protozoans (in open-ocean communities), and zooplankton. Such a uniform biomass distribution resembles the uniformity of biomass distribution among logarithmic size classes in planktonic communities (Sheldon et al. 1972).

The results obtained have great variability that may partially derive from imprecision in the estimate of the different biomass compartments. In fact, and even though we relied on the autotrophic biomass estimates performed by the different authors, some did estimate biomass from chlorophyll and used conversion factors that could be too low for present-day standards. The C:Chl factor for open-ocean oligotrophic communities is now thought to be 100 or even more (Welschmeyer and Lorenzen 1984; Hewes et al. 1990; Verity et al. 1996a; Buck et al. 1996). However, the patterns that we show in this paper are so strong that even errors in those parameters do not affect them. This affirmation is supported

by the data presented by Buck et al. (1996) from a north-south transect in the North Atlantic and the subequatorial and equatorial regions of the Atlantic. These authors used flow cytometry to evaluate the biomass contribution of pico- and nanoalgae to autotrophic biomass, finding C:Chl ratios as large as 200. However, they encountered patterns very consistent with those that we present: the ratio of (pico- and nano-) heterotrophic biomass to (pico- and nano-) autotrophic biomass was above unity (1.4) in the very oligotrophic subequatorial Atlantic, whereas it was below unity (0.9) in the more eutrophic North Atlantic. This confirms that our results are strong enough to stand method imprecisions.

The more important group that has been consistently overlooked in the open ocean is that of the smallest autotrophs: the prochlorophytes. Monger and Landry (1993) showed that the bacterial epifluorescence counts as usually performed in most laboratories were close to the addition of the counts of prochlorophytes and heterotrophic bacteria as estimated with dual-laser flow cytometry. That would suggest that some of the biomass previously considered to be heterotrophic bacteria in the ocean is in fact phototrophic. Varying dominance of prochlorophytes in different parts of the ocean could explain why at some sites bacterial biomass greatly exceeded algal biomass (Fuhrman et al. 1989; Cho and Azam 1990), whereas in other sites algal and bacterial biomass were of similar magnitude (Li et al. 1992; Buck et al. 1996) and in some other sites bacterial biomass was much less than algal biomass (Ducklow et al. 1993). Campbell et al. (1994) calculated that in the central North Pacific prochlorophytes counted as bacteria could overestimate heterotrophic biomass by 31%. Li et al. (1995) arrived at a value of 11% in the central North Atlantic, whereas Binder et al. (1996) found a value of 17% for the equatorial Pacific. A much more detailed study with sophisticated image cytometry allowed Sieracki et al. (1995) to compare size and biomass distributions of prochlorophytes and heterotrophic bacteria at several sites in the Sargasso Sea. Overestimation of bacterial biomass ranged from 18 to 22% of integrated biomass.

If 20% of the biomass assigned to the heterotrophic bacteria compartment was instead added to that of autotrophs, the H:A ratio of open-ocean communities would change from 1.85 to 1.23, leading to a less inverted and more "squared" biomass pyramid there where bacteria would contribute less to the heterotrophic compartment (but still more than protozoans and zooplankton). The resulting ratio would still be higher than that for coastal communities (0.98) but less significantly so. The relationship between autotrophic biomass and the H:A ratio would still be significant and significantly different from that of coastal sites. However, this last calculation should be taken as a maximum for various reasons. Algal biomass is estimated in most of the open-ocean data from chlorophyll, which already contains prochlorophyte biomass. Correcting the biomass values should therefore be done by subtracting 20% of the bacterial biomass without adding any biomass to the autotrophic compartment. In fact, when the calculations are done in this way, bacteria average 80% of algal biomass and the average H:A ratio for open-ocean samples is 1.6 (as compared to a value of 0.98 for coastal sites). Moreover, prochlorophytes are not universally dominating autotrophic biomass in open-

Table 3. Relationships between the ratio of heterotrophic to autotrophic biomass and the different autotrophic parameters. All values are base-10 logarithms. Chlorophyll *a* (Chl) in mg m^{-3} or m^{-2} , Autotrophic biomass (AutoB) in mg C m^{-3} or m^{-2} , primary production (PP) in $\text{mg C d}^{-1} \text{m}^{-3}$ or m^{-2} , biomass-specific primary production, P_B , in $\text{mg C (mg C}^{-1}) \text{d}^{-1}$.

Data	Y	X	N	Intercept $\pm$ SE	$b\pm$ SE	r^2	F-ratio	P
Areal data	Ratio	AutoB	191	1.82 ± 0.29	-0.55 ± 0.09	0.16	37.3	<0.00005
Coastal	Ratio	AutoB	69	1.19 ± 0.30	-0.43 ± 0.09	0.23	20.1	<0.00005
Open ocean	Ratio	AutoB	122	2.67 ± 0.16	-0.80 ± 0.05	0.69	261.0	<0.00005
Volumetric	Ratio	AutoB	165	1.06 ± 0.11	-0.55 ± 0.05	0.43	124.6	<0.00005
Areal data	Ratio	Chl	76	1.67 ± 0.13	-0.91 ± 0.07	0.67	149.3	<0.00005
Coastal	Ratio	Chl	15	2.30 ± 0.14	-1.19 ± 0.09	0.93	185.1	<0.00005
Open ocean	Ratio	Chl	61	0.64 ± 0.15	-0.36 ± 0.08	0.24	18.1	<0.00005
Volumetric	Ratio	Chl	127	0.03 ± 0.05	-0.43 ± 0.06	0.32	58.5	<0.00005
Areal data	Ratio	PP	140	0.64 ± 0.29	-0.20 ± 0.09	0.03	4.3	0.0397
Coastal	Ratio	PP	50	1.52 ± 0.54	-0.60 ± 0.20	0.16	8.9	0.0043
Open ocean	Ratio	PP	90	0.45 ± 0.34	-0.12 ± 0.11	0.01	1.3	0.3109
Volumetric	Ratio	PP	91	0.30 ± 0.20	-0.24 ± 0.09	0.08	7.4	0.0077
Areal data	Ratio	P_B	138	0.11 ± 0.03	0.43 ± 0.06	0.25	46.1	<0.00005
Coastal	Ratio	P_B	48	0.10 ± 0.06	0.10 ± 0.15	0.01	0.5	0.5031
Open ocean	Ratio	P_B	90	0.17 ± 0.15	0.49 ± 0.07	0.37	52.3	<0.00005
Volumetric	Ratio	P_B	91	-0.21 ± 0.03	0.25 ± 0.09	0.08	7.5	0.0074
All data	Ratio	P_B	229	-0.04 ± 0.03	0.29 ± 0.06	0.11	27.1	<0.00005

ocean environments. They seem to dominate nutrient-depleted, well-stratified warm waters with deep nitraclines (Campbell and Vault 1993; Veldhuis et al. 1993; Lindell and Post 1995) although they have been found also in some mixed water bodies (Vault et al. 1990), albeit in low abundances. They seem to develop in a pattern opposite to that of *Synechococcus* (Campbell and Vault 1993; Veldhuis and

Kraay 1993; Buck et al. 1996). Our open-ocean dataset included data from sites that would be expected to have a large percentage of prochlorophytes, such as the Sargasso Sea, the Equator, and the central Pacific. However, it also included data from sites that would not be expected to have many prochlorophytes, such as the Weddell Sea or the subarctic Atlantic and Pacific Oceans or the North Atlantic Bloom

Fig. 4. Left: Frequency distribution of samples with a given biomass ratio (heterotrophic:autotrophic) for open-ocean communities (upper panel) or coastal communities (lower panel). Right: Mean (plus standard deviation) biomasses of zooplankton, protozoans (heterotrophic protists), and bacteria, relative to that of autotrophic biomass for open ocean communities (upper panel) and coastal communities (lower panel). The mean values $\pm$ standard error are provided for each of the boxes.

Fig. 5. Relationship between the biomass ratio (heterotrophic biomass divided by autotrophic biomass) and the turnover time of the autotrophic pool (biomass-specific primary production) for open-ocean (○) and coastal (●) communities. The line of equal autotrophic and heterotrophic biomass is also shown.

Experiment area. The dataset is split almost evenly between both groups of sites. Some of the papers used as sources of data did take into account prochlorophyte biomass as separated from bacterial biomass (i.e. Li et al. 1992). Hence, the results described remained virtually unchanged even if 20% of the previously considered heterotrophic biomass is to be reclassified as autotrophic prochlorophytes.

Another issue that is worth mentioning because it could confound some of the patterns presented in this paper is that of mixotrophy, which includes both autotrophs that behave partially or totally as heterotrophs and heterotrophs that partially behave as autotrophs (Jones 1994). Mixotrophic nanoflagellates seem to dominate in nutrient-poor waters (Estep et al. 1986; Arenovski et al. 1995), although they may at times be abundant in richer waters (Sanders 1991; Havskum and Riemann 1996) together with heterotrophic dinoflagellates (Hansen 1991). Their abundance will not alter any of the patterns shown above. If anything, the heterotrophic dominance of biomass partitioning in oligotrophy and the probable heterotrophic control of primary production will be even more important than is shown by the data we have collected. A different case would be that of heterotrophic ciliates that retain chloroplasts and may act as phototrophs (i.e. Dolan 1992). There is some evidence that they may dominate in oligotrophic situations (Stoecker et al. 1989), and a reasonable estimate would be that 40% of all ciliates are mixotrophic (Stoecker et al. 1987, 1989, 1996; Bernard and Rassoulzadegan 1994). If 40% of the biomass assigned to the protozoan compartment was instead added to that of autotrophs, the H:A ratio of open-ocean communities would change from $1.85 (\pm 0.16)$ to $1.71 (\pm 0.16)$, still leading to an inverted biomass pyramid where protozoans would contribute less to the heterotrophic compartment (ratio protozoans:autotrophs would change from 0.53 to 0.21). The resulting biomass ratio would still be much higher than that for coastal communities (0.98). However, and because mixo-

trophic ciliates still need to feed on algae as the endosymbiotic chloroplasts do not divide inside the ciliate (Dolan 1992), it is not clear whether it can be said that they function as true autotrophic producers. In any case, and at the scale analyzed here, whether they are considered autotrophic or heterotrophic does not make any significant difference.

The patterns in the structure of planktonic food webs that we have presented offer considerable insight into the functioning of these communities. The inverted pyramid or squared biomass distributions of marine plankton contrast greatly with the broad-base pyramids that characterize communities dominated by higher plants (Odum 1971; Hairston and Hairston 1993). The observation of pyramidal biomass distribution has been typically explained by the expectation of a 10% reduction in biomass between consecutive trophic levels due to considerations of respiratory losses and assimilatory efficiencies. Strayer (1988), however, pointed out that these considerations should only apply to the relative production of different trophic levels. Because production is the product of biomass and turnover rate, the observed biomass distribution implies a high turnover or growth rate of the autotrophs. The average turnover rate of the autotrophs in the dataset ($1.41 \pm 0.21 \text{ d}^{-1}$) is extremely high compared to that of higher plants (see data compilation in Cebrián and Duarte 1994). Hence, the very fast turnover of marine planktonic autotrophs allows them to support exceedingly high relative biomasses of planktonic heterotrophs. The high biomass of heterotrophs depicted by the squared or inverse pyramid biomass distribution in the sea suggests much greater consumer pressure on marine planktonic autotrophs than that on land plants. This is consistent with the observation that >40% of phytoplankton production, on average, is channeled to herbivores (Cebrián and Duarte 1994). Moreover, the greater H:A biomass ratio in oligotrophic systems suggests these to be the systems where heterotrophs exert the greatest control over primary production (see also Banse 1995). In fact, the modelling exercise presented by Fasham (1995) suggests that squared pyramids ($H:A = 1$) would be a necessary condition to prevent frequent blooms and confer stability to the plankton structure. One could also consider that heterotrophic bacteria, because they are efficient nutrient accumulators, could also exert control over the primary producers (Banse 1995) even in those ocean areas limited by iron (Tortell et al. 1996).

The high heterotrophic biomass in the most oligotrophic regions of the ocean is probably the result of several factors: changes in the turnover rate of autotrophs, high detritus mass that feeds the heterotrophs, or high losses of autotrophs in the most eutrophic regions. Our results show that the trend toward a dominance of autotrophs in eutrophic systems seemed to be supported by a parallel reduction of turnover rate in marine phytoplankton in these systems. The higher turnover rate of autotrophs in oligotrophy is one of the often cited but seldom demonstrated paradigms of aquatic ecology (Odum 1971; Goldman et al. 1979; Harris 1984), and unanimity as to whether it holds for marine plankton communities has not been reached [see Baines et al. (1994) and Banse (1995) for contradictory results]. Our data showed the paradigm to apply to marine plankton, but it failed to be confirmed in lakes (del Giorgio and Gasol 1995). It is certain

that the pattern that we describe could have arisen from overestimated values of P_b in oligotrophic samples due to underestimation of autotrophic carbon derived from too low C:Chl factors, but without access to the original data we cannot test whether this is the case in the dataset analyzed here.

An additional factor that could account for the tendency of the H:A biomass ratio to decrease with autotrophic biomass is the tendency toward increased carbon export at high-production sites (Wassmann 1990; Bienfang and Ziemann 1992; Baines et al. 1994). This process would reduce the amount of phytoplankton production available for conversion to heterotrophic biomass as autotrophic biomass increases. A compatible explanation for the maintenance of a high H:A ratio without higher levels of phytoplankton turnover would be the presence of higher detritus biomasses at the sites where the H:A ratio is higher. Heterotrophs could be maintained by this extra carbon as long as there would exist a permanent source of detritus. Roman et al. (1995), in their detailed examination of the carbon allocation in the Sargasso Sea, found higher detritus biomasses when the H:A ratio was 3.2 than when it was 1.7. The development of new techniques for the simple estimation of detritus mass could provide a test for the hypothesis of detritus mass sustaining heterotrophic biomass in the most oligotrophic regions of the ocean. In fact, Verity et al. (1996a) recently provided a new method and an estimation of detritus by which this was much more abundant than living biomass, especially in the most oligotrophic regions of the ocean (up to 60% of total particulate organic carbon). However, the origin of this detritus in a region where phytoplankton is assumed to be the main source of primary production is still an enigma that certainly requires more data before a coherent picture of the role of detritus in plankton structure and functioning can be drawn.

The 10-fold higher biomass of heterotrophs for a given autotrophic biomass in the open sea implies a greater heterotrophic pressure there. Examination of biomass partitioning shows important differences in food-web structure between open-sea and coastal systems (Fig. 4). Zooplankton dominate heterotrophic biomass in coastal systems, whereas this is equally partitioned, on the average, between bacteria and protozoa + mesozooplankton in the open ocean. This outlines a direct carbon flow from phytoplankton to zooplankton, which would also efficiently maintain low protozoan biomass in the coastal zone and a greater importance of flow through microbial food webs in the open ocean, as suggested in the past (Kiorbøe et al. 1990; Longhurst 1991). The lower H:A ratio of coastal plankton communities could be altered if benthic heterotrophs were included. Then, the balance between heterotrophs and autotrophs would be similar in open-ocean and coastal sites if benthic heterotrophs used a substantial fraction of planktonic production there.

The production of open ocean plankton and that of coastal plankton in summer when nitrate is depleted is dominated by recycled production (Cushing 1989) and regulated by the quasi-steady-state internal regeneration of nutrients. Microbial food webs play an important role in nutrient recycling there (Azam et al. 1983) and bacteria use a higher portion of primary production (Andersen 1988). Primary production is dominated by picoplanktonic phototrophs (Søndergaard et

Fig. 6. Schematic change of the biomass ratio (heterotrophic biomass divided by the autotrophic biomass) with changing autotrophic biomass levels as presented in the present study and in del Giorgio and Gasol (1995).

al. 1991) and zooplankton by copepods, which seem to be the zooplankters better adapted to low food conditions (Paffenhöfer and Stearns 1988). In such systems, however, the turnover time of the heterotrophs is probably low. The specific production of bacteria increases with increasing chlorophyll (White et al. 1991), indicating that bacterial growth rates are slowest at low levels of algal biomass (Fuhrman et al. 1989). High turnover rate of autotrophs and a low turnover rate of heterotrophs should be conducive to the high H:A biomass ratios observed in open-ocean systems. In contrast, there may be a higher export rate of primary production in coastal systems (Baines et al. 1994), thus being less available to planktonic heterotrophs.

Our results demonstrate a parallel reduction in the H:A biomass ratio with increasing autotrophic planktonic biomass in the open-ocean and coastal systems, similar to that previously reported for lake plankton (del Giorgio and Gasol 1995). However, open-ocean plankton support for a given autotrophic biomass an order of magnitude higher heterotrophic biomass than do coastal systems, and this, in turn, supports an order of magnitude more heterotrophic biomass than lakes with similar autotrophic biomass (Fig. 6). Simon et al. (1992) also found bacterial biomass to be 2.5 times more abundant in lakes than in the ocean at a given autotrophic biomass, and Baines et al. (1994) showed the turnover rate of marine autotrophs to be higher than that of freshwater autotrophs at low algal biomasses. Overall, these patterns probably reflect consistent differences in the relative turnover rates of autotrophs and heterotrophs, the efficiency of autotrophic carbon flow, the different importance of allochthonous carbon sources, and the relative importance of exportation in these systems that need to be investigated further.

The patterns described confirm previous suggestions of a dominant role of heterotrophs in the structure of oligotrophic planktonic systems (Campbell et al. 1979; Dortch and Packard 1989; Fuhrman et al. 1989; Cho and Azam 1990; Agustí 1994). This dominant role should be reflected in a major functional role, with heterotrophs being able to dominate

carbon and nutrient pools and flows (Cho and Azam 1988; Fuhrman et al. 1989) and light capture (Agustí 1994) in oligotrophic systems. Most importantly, heterotrophs should also control autotrophic populations in oligotrophic systems (Cullen 1991; Agustí et al. 1992; Banse 1995), maintaining sparse, but fast-growing (Goldman et al. 1979; Murray et al. 1994) phytoplankton populations, switching to resource, rather than consumer control in more productive systems.

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