

Variation in the transfer of energy in marine plankton along a productivity gradient in the Atlantic Ocean

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Abstract

Plankton play a key role in oceanic carbon flux as the primary biological mechanism for the sequestration of carbon out of the atmosphere into surface waters. The transfer of energy between phytoplankton and zooplankton can be inferred from regular patterns in population size structure, where plots of abundance within size classes typically show a power-law dependence on size. Here we analyze such picoplankton to mesozooplankton size spectra along a 50°N to 50°S transect in the Atlantic. Contrary to common perception, the transfer efficiency in the oceans is not related to ecosystem productivity. Our results challenge the view that biomass transfer efficiency is lower in oligotrophic oceanic ecosystems. This suggests that global carbon flux models should reconsider the trophic transfer efficiency of productive and oligotrophic areas.

The power decay of abundance with increasing body size in marine and freshwater plankton ecosystems is an indicator of the efficiency of biomass transfer between trophic levels (Gaedke 1993; Jennings and Mackinson 2003). Double log plots of normalized biomass versus body size can be interpreted as a continuous flow of biomass up the food web (Platt and Denman 1978). Although aquatic

trophic chains can be complex, predators are larger than their prey and trophic position tends to increase with increasing size, i.e., the large eats the small (Jennings and Warr 2003). There may be some exceptions to this rule, such as parasites, some dinoflagellates, etc., but the majority of organic matter in pelagic ecosystems is transferred from small to large organisms, regardless of whether the individuals are autotrophic or heterotrophic. Hence, the steeper the slope of the log–log plot the larger the trophic step and the more energy lost in the transfer from the small and abundant primary producers to the larger and less dominant secondary consumers (Brown and Gillooly 2003). However, given that pelagic food webs are a non-steady state system, the slope cannot be considered an instantaneous measure of trophic transfer efficiency. The slope of the normalized biomass-size (NB-S) spectrum is, thus, an integration of the efficiency of biomass transfer to larger organisms in recent times and indicates the number of large individuals that are maintained by small ones (Jennings and Mackinson 2003; Jennings and Warr 2003).

Primary production in oceanic oligotrophic areas is dominated by picoplankton (Agawin et al. 2000), which are not efficiently captured by most mesozooplankton. Therefore, the conventional wisdom is that in oligotrophic areas the “microbial loop” dominates the trophic web and that the energy transfer efficiency to mesozooplankton is lower

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than in productive areas (Ryther 1969; Jackson 1980), where large phytoplanktonic cells are directly consumed by copepods. Such an increase in the energy transfer efficiency with eutrophy has been shown in comparative analyses of lakes using NB-S slopes (Sprules and Munawar 1986; Ahrens and Peters 1991; Tittel et al. 1998). For marine systems it has been proposed that more stable systems should have longer food chains and therefore steeper size spectra slopes (Jennings and Mackinson 2003).

However, recent work has challenged this view for oceanic ecosystems, suggesting that mesozooplankton grazing impact on primary production in oligotrophic areas is higher than in eutrophic areas (Calbet 2001). Furthermore, in marine ecosystems most size spectra analysis studies have been conducted at local scales or for only a small size range of planktonic organisms. A large-scale comparative analysis including complete plankton community size spectra, spanning several trophic levels, has not been carried out. In this study we analyzed plankton size spectra (from picoplankton to mesozooplankton) on three latitudinal transect cruises along the Atlantic (50°N to 50°S, Fig. 1), with total plankton biomass ranging from 647 to 11,877 mg C m⁻², in order to investigate the relations between productivity and the energy transfer efficiency in oceanic ecosystems.

Methods

Three latitudinal transects (50°N–50°S) of the Atlantic Ocean (Atlantic Meridional Transect, AMT 12–14, Fig. 1) were carried out on board RRS *James Clark Ross*. All samples were taken during night stations between 02:00 and 05:00 h local time. Water was collected on each cast from five depths (55%, 33%, 14%, 1%, and 0.1% light levels) for the determination of chemical and biological variables. Water samples were fixed with paraformaldehyde for picoplankton and 1% Lugol's iodine for nanoplankton to microplankton size structure analyses. Water samples from the same depths were also collected for ¹⁴C-fixation determination. Inorganic nitrate was measured colorimetrically on fresh unfiltered seawater samples collected at each depth with a five-channel Bran and Luebbe A4111 segmented flow autoanalyzer and a liquid waveguide capillary cell (LWCC) using standard techniques. Vertical WP-2 200- μ m mesh nets were hauled at 30 m min⁻¹ from 50 m to the surface at each station and fixed in borax-buffered formaldehyde to a final concentration of 4%.

Primary production rates were measured with the radioisotope ¹⁴C by means of simulated in situ incubations cooled with either sea-surface water or chilled freshwater to in situ temperatures $\pm 3^\circ\text{C}$ and under neutral density, with blue plastic filters to simulate the varying light levels with depth. Seawater samples (three light and three dark) collected from each depth were inoculated with 7.4×10^5 Bq ¹⁴C-labeled NaH¹⁴CO₃ and incubated over a daylight period from dawn to dusk of typically 10–12 h. Samples were then filtered onto 0.2- μ m pore 47-mm diameter polycarbonate filters under gentle vacuum (<20 kPa) and fumed for 30 min over concentrated hydrochloric acid in a desiccator. After fuming, samples were placed in 6-mL

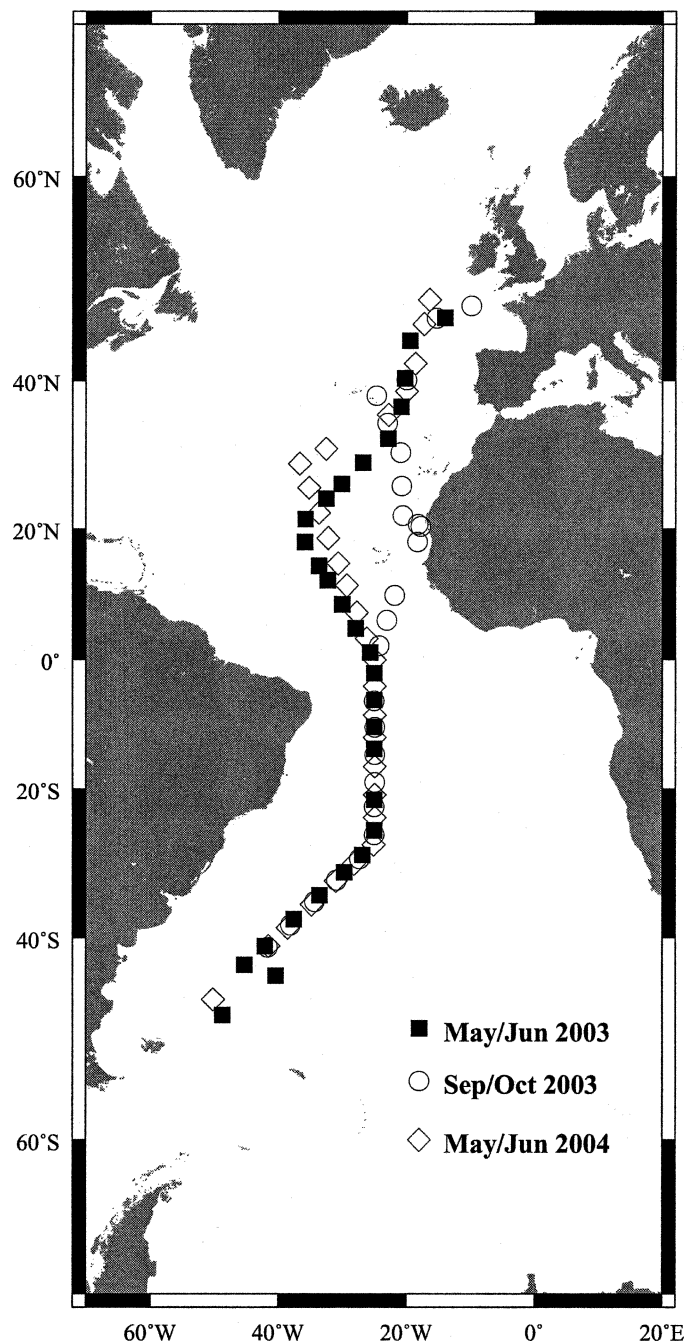


Fig. 1. Location of stations sampled along the Atlantic Ocean between 50°N and 50°S. The different cruise tracks for AMT 12 (May/June 2003), AMT 13 (September/October 2003), and AMT 14 (May/June 2004) are shown.

pony vials with 5 mL of Optiphase HiSafe 3 and radioactivity counted in a TriCarb 2100TR low activity liquid scintillation counter (LSC) onboard. Dark bottle values were subtracted from the counts obtained in the light samples.

Picoplankton samples were analyzed by flow cytometry. The size structure of the nanoplankton (10–20 μ m) and microplankton community (20–130 μ m) was determined using the FlowCAM. Image analysis software (Plankton

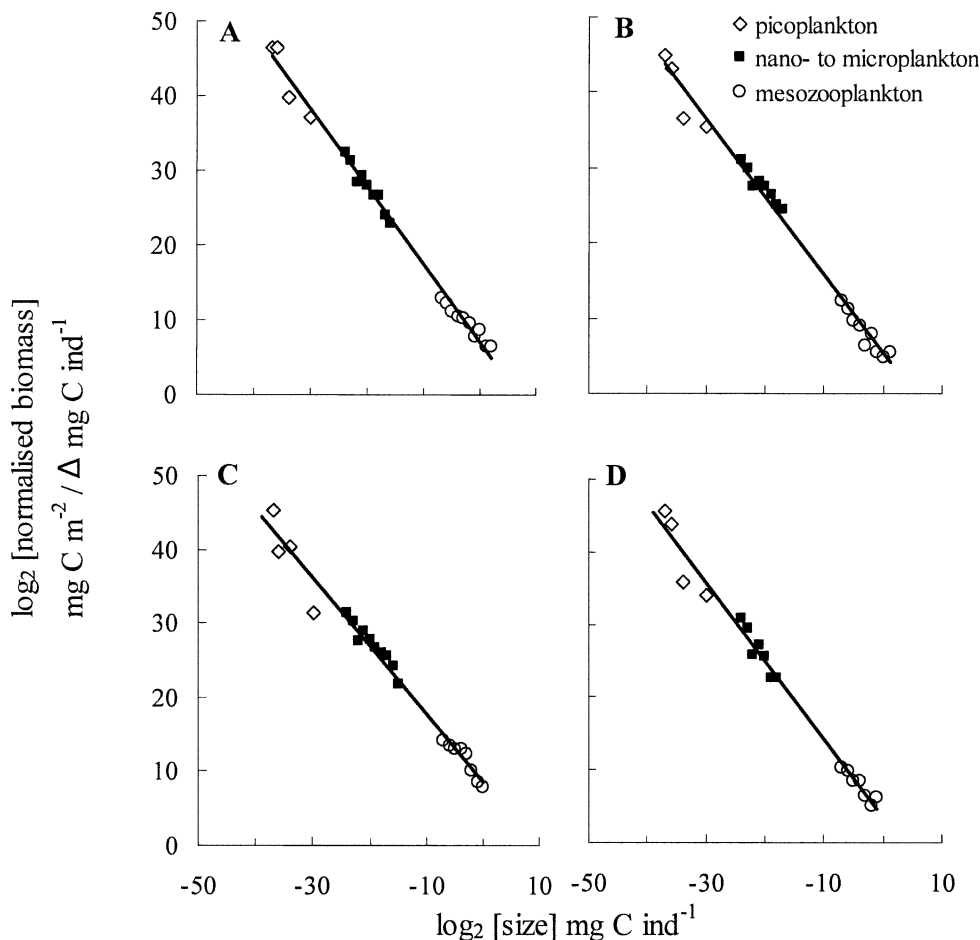


Fig. 2. 50–0 meters depth-integrated NB-S spectra of the picoplankton, nanoplankton to microplankton, and mesozooplankton community at (a) 1°N on AMT 12 (slope = -1.03 ± 0.02 (SE), $r^2 = 0.99$, $F_{21} = 2,848$, $p < 0.001$), (b) 35°N on AMT 13 (slope = -1.04 ± 0.03 (SE), $r^2 = 0.99$, $p < 0.001$), (c) 41°S on AMT 13 (slope = -0.92 ± 0.03 (SE), $r^2 = 0.98$, $p < 0.001$), and (d) 24°S on AMT 14 (slope = -1.07 ± 0.03 (SE), $r^2 = 0.99$, $p < 0.001$). The straight lines are the least-squares (model 1) regressions fitted to these data.

Visual Analyzer [PVA], <http://www.azti.es/ingles/PVA.htm>) was used to measure the size structure of the preserved net samples. Mesozooplankton net samples were stained for 24 h with 4 mL 1% eosin. An image of a subsample was scanned in 256 (eight-bit) colors at a resolution of 600 dpi. The JPEG images were imported and the equivalent spherical diameter (ESD) of each particle $>200 \mu\text{m}$ was measured. Cell and individual organism carbon biomass was estimated by conversion from volume or ESD measurements using published relations (Menden-Deuer and Lessard 2000; Zubkov et al. 2000; Alcaraz et al. 2003) after corrections for shrinkage due to fixation (Montagnes et al. 1994).

Data were fitted using NB-S spectra ($B_m/\Delta m = am^b$) where B_m is the total biomass in carbon per size class m , a and b are constants, and Δm is the size class interval (Platt and Denman 1978). The slope (b), y -intercept (a), and coefficient of determination (r^2) of the least-squares linear (model 1) regression fitted to the \log_2 -transformed data are considered the parameters that summarize the size structure of the community. These were calculated over the range

from 0.45 to 4,300 μm ESD or 1.15×10^{-11} to 4.30 mg C individual $^{-1}$. The organisms measured covered a size range over 10 orders of magnitude ranging from picoplankton to mesozooplankton (Fig. 2).

The extreme size ranges of each sampling technique can be subject to error resulting in curvature, and referred to as “inflection points,” at either end of the linear relationship on a double log plot. Net sampling, for example, does not always quantitatively retain organisms in the smaller size ranges and can only sample representatively within a limited size range because of the impact of mesh size and net avoidance (Harris et al. 2000). Furthermore, the small volumes analyzed by the FlowCAM limit the detection of larger microplankton. The inflection points at the extreme size ranges of the spectrum for each method were not included, since they could cause potential error in the calculation of the parameters of the spectrum. Any size class with zero biomass was also excluded from the analysis, leaving an average of 20 size classes for each AMT sampling station (Fig. 2). Although the application of Platt and Denman’s model has the limitation that it is

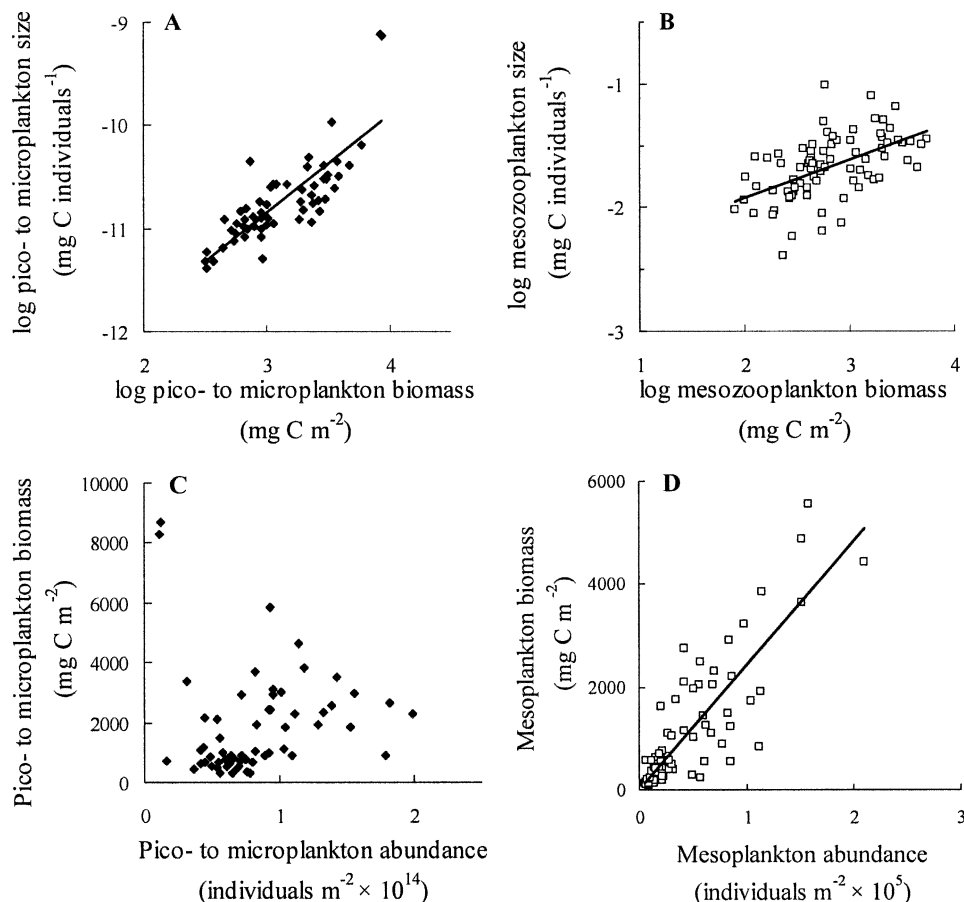


Fig. 3. Log mean size versus log biomass of (A) picoplankton to microplankton ($\log y = 0.94 \log x - 13.66$, $r^2 = 0.64$, $p < 0.001$, $n = 60$) and (B) mesozooplankton ($\log y = 0.30 \log x - 2.53$, $r^2 = 0.28$, $p < 0.001$, $n = 78$), and the relationship between abundance and biomass of (C) picoplankton to microplankton ($y = 2 \times 10^{-12}x + 1,664.95$, $r^2 = 0.003$, $p > 0.68$, $n = 59$) and (D) mesozooplankton ($y = 0.02x + 10.96$, $r^2 = 0.71$, $p < 0.001$, $n = 78$) on a vertically integrated basis. Values were calculated by integration of values from 0 to 50 m. The straight lines are the least-squares (model 1) regressions fitted to these data.

very sensitive to the existence of missing size ranges in the size spectrum, the mean r^2 of community spectra was 0.99 and ranged between 0.96 and 1.00. All spectra had a significant regression ($p < 0.001$).

For the data interpretation we considered the NB-S slopes in three classes: picoplankton to microplankton (mainly phytoplankton, although also including microzooplankton), mesoplankton (mainly mesozooplankton), and the whole community (combining picoplankton to mesoplankton).

Results

As previously found (Irigoiien et al. 2004), picoplankton to microplankton average cell size increased with picoplankton to microplankton biomass (Fig. 3A). In contrast, for mesoplankton the relationship between individual size and mesoplankton biomass was weaker (Fig. 3B). This indicates that increases in picoplankton to microplankton biomass are mainly due to large cells, whereas increases in mesoplankton biomass are not strongly related to changes

in size. Consequently, abundance and biomass are proxies of each other in the case of mesoplankton but not for phytoplankton, where there is no relationship between cell abundance and total biomass in the picoplankton to microplankton size range (Fig. 3C,D). When calculating the NB-S slopes, another interesting consequence of the relationship between cell size and biomass in the picoplankton to microplankton size range arises: The NB-S slopes in the picoplankton to microplankton size range are positively related to biomass and negatively to abundance (Fig. 4).

Although only explaining a small percentage of the variance ($r^2 = 0.14$), the picoplankton to mesozooplankton NB-S slopes show some relationship with maximum nitrate concentrations, where areas with higher nitrate levels had slightly less negative slopes ($y = 0.001x - 1.06$, $F_{58} = 9.12$, $p < 0.01$, Fig. 5A).

^{14}C -fixed primary production was normalized by dividing by total chlorophyll *a* (Chl *a*) concentration. This Chl *a*-normalized rate of photosynthesis (PP/B_{tot}) characterizes the turnover rate of phytoplankton (mg C mg

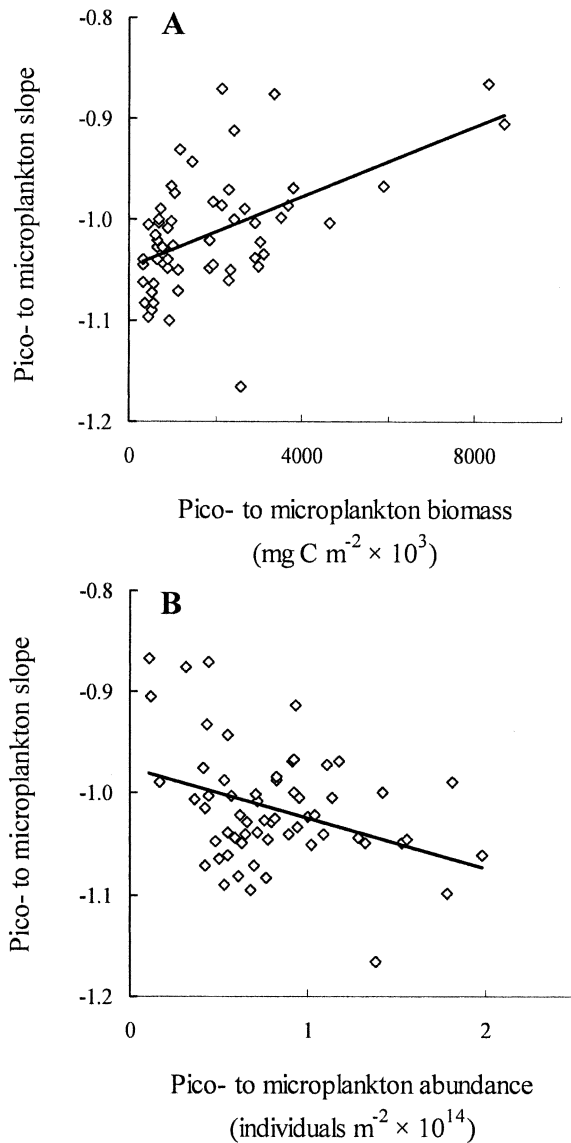


Fig. 4. Picoplankton to microplankton cell size distribution, represented as the slope of the NB-S, versus (A) biomass ($y = 2 \times 10^{-5}x - 1.05$, $r^2 = 0.28$, $p < 0.001$, $n = 60$) and (B) abundance ($y = -5 \times 10^{-16}x - 0.93$, $r^2 = 0.13$, $p < 0.01$, $n = 78$). The straight lines are the least-squares (model 1) regressions fitted to these data.

$\text{Chl}^{-1} \text{d}^{-1}$) and indicates the intensity of energy flow per biomass unit. There was no significant relationship ($r^2 = 0.04$, $F_{39} = 1.59$, $p > 0.22$) between the community slope and $\text{PP}/\text{B}_{\text{tot}}$ (Fig. 5B).

Community slopes showed a nonsignificant negative relationship with picoplankton to microplankton biomass, a significant positive relation with mesoplankton biomass, and no relation with total biomass (Fig. 5C–E). These results indicate that the transfer efficiency between trophic levels is not higher in more productive areas and that variations in mesoplankton biomass determine the community slope. The coefficient of variation (CV) of the normalized biomass in each size class plotted against the corresponding \log_2 size class shows that normalized biomass in larger size classes was more variable than in

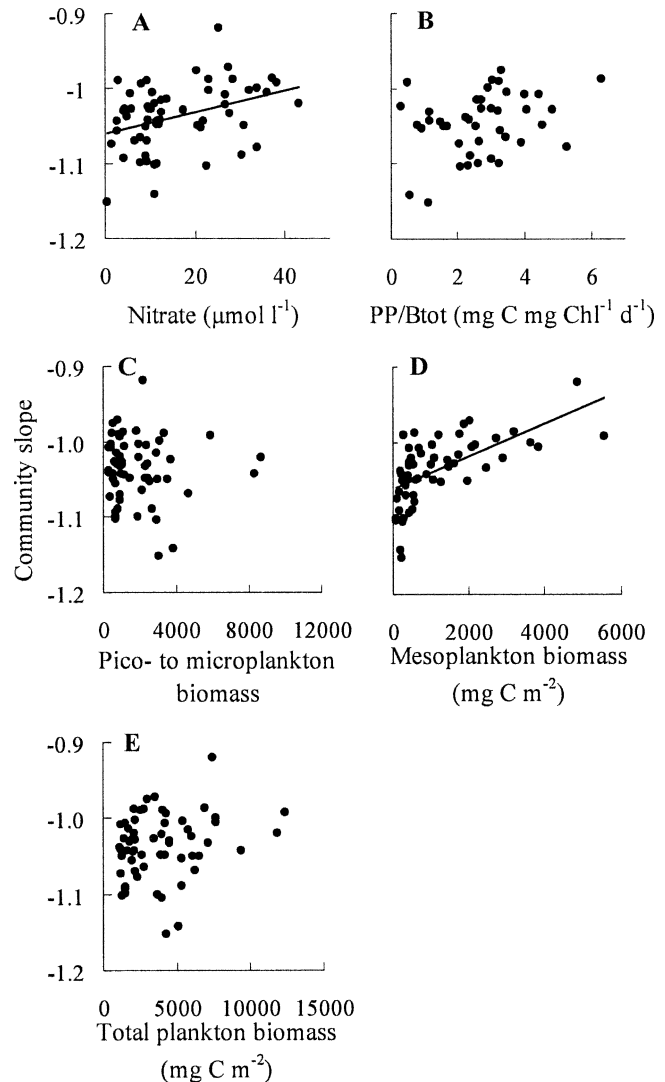


Fig. 5. Relationship between NB-S slopes of the picoplankton to mesozooplankton community and (A) maximum nitrate concentrations in 300–0 m ($y = 0.001x - 1.06$, $r^2 = 0.14$, $p < 0.01$, $n = 58$), (B) 50–0 m depth-integrated normalized primary production ($y = 0.008x - 1.07$, $r^2 = 0.07$, $p > 0.10$, $n = 41$), (C) picoplankton to microplankton biomass ($y = -1.20 \times 10^{-6}x - 1.03$, $r^2 = 0.02$, $p > 0.71$, $n = 60$), (D) mesozooplankton biomass ($y = 2.17 \times 10^{-5}x - 1.06$, $r^2 = 0.39$, $p < 0.001$, $n = 60$), and (E) total plankton biomass ($y = 3.60 \times 10^{-6}x - 1.05$, $r^2 = 0.05$, $p > 0.09$, $n = 60$). The straight lines are the least-squares (model 1) regressions fitted to these data.

smaller size classes (Fig. 6). The CV statistic is scale independent, i.e., the relation is not a result of the disproportionate effect that the extreme size range of the size spectrum has on the community spectrum. Hence, the biomass of small phytoplankton, i.e., the top left corner of the spectrum, remains stable and the changes in the larger size classes cause the variations in the community slope.

Discussion

Depth-integrated NB-S slopes of the planktonic community showed a weak relationship with nitrate concen-

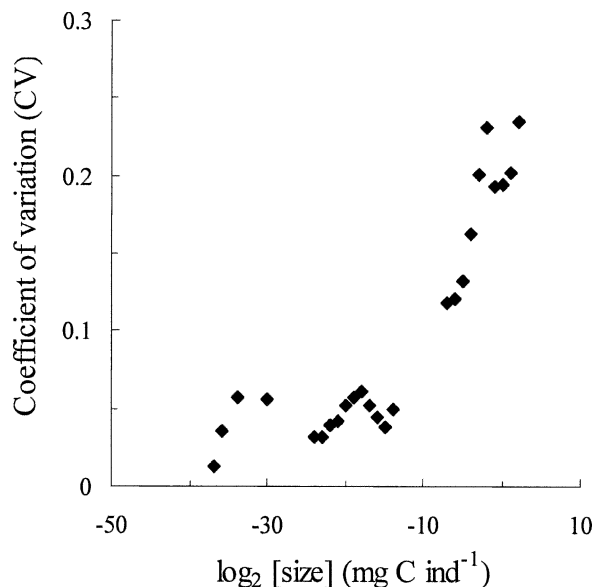


Fig. 6. The coefficient of variation (CV) of normalized biomass (ca. abundance) in each size class plotted against the corresponding \log_2 size class from picoplankton to mesozooplankton NB-S spectra.

tration, which suggests that the nutrient environment has only a very limited effect on the trophic food web efficiency. This contrasts with studies in freshwater lakes that found a significant positive relationship between phosphorus concentration and the slopes of plankton size spectra (Fig. 5A; Ahrens and Peters 1991; Cottingham 1999).

Nor was there a significant relation between primary productivity (phytoplankton $P:B$ ratio, Fig. 5B) or biomass (picoplankton to microplankton or total plankton biomass, Fig. 5C) and the community slope. This differs from Gaedke's (1993) analysis of plankton size spectra in a large oligotrophic lake, where higher $P:B$ ratios were related to steeper slopes and a decrease in the biomass flux up the spectrum. These results suggest that although oligotrophic regions are characterized by high turnover rates of phytoplankton (Marañón et al. 2001), low phytoplankton abundance and biomass (Marañón et al. 2000), and a low export ratio (Legendre and Le Fèvre 1991), this does not necessarily mean a lower transfer of photosynthetically fixed organic C to higher trophic levels. On the contrary, our results suggest a tight coupling between phytoplankton and mesozooplankton (Fig. 5D), supporting recent evidence of consumer control in oligotrophic regions (Gasol et al. 1997). The relationship between mesozooplankton biomass and trophic transfer efficiency is unsurprising (Fig. 5D), given that the slope of a community spectrum represents the proportion of organisms in increasing size classes. However, there were not proportionally more mesozooplankton in eutrophic areas than in oligotrophic areas.

Our results challenge the common perception that the energy transfer efficiency between planktonic trophic levels is lower in oligotrophic oceanic ecosystems and confirm recent results suggesting a higher grazing effect by

mesozooplankton on phytoplankton in oligotrophic regions (Calbet 2001). Our field data also contradict recent theoretical studies that predict steeper abundance–body mass relationships and lower efficiency in more stable environments (Jennings and Mackinson 2003; Makarieva et al. 2004). Although stability has not been defined here, it is generally true to say that oligotrophic gyres are more stable than higher latitudes. Nevertheless, slopes were not found to be significantly steeper in oligotrophic systems than in upwelling systems or higher latitudes. Hence, this study found that eutrophic systems do not seem to be more efficient than oligotrophic ones in the transfer of organic matter and that the trophic transfer efficiency is invariant with increasing productivity. These findings further suggest that, contrary to original theory (Gaedke 1993; Jennings and Mackinson 2003), stable oligotrophic areas do not necessarily favor small predator-to-prey size ratios and long food chains. In other words, the “efficient classical linear” and “inefficient microbial loop” pathways may be less characteristic of upwelling and oligotrophic areas, respectively, than previously thought.

Further, the results presented contrast with plankton size spectra studies conducted in freshwater lake ecosystems, which have shown a more efficient transfer of material between lower and higher trophic levels with increasing productivity (Sprules and Munawar 1986; Ahrens and Peters 1991; Tittel et al. 1998). Our data, thus, suggest basic differences between marine and freshwater (lake) plankton. These differences could be caused by (1) differences in the phytoplankton size structure between freshwater and marine systems or (2) differences in spatiotemporal variability of production between marine and freshwater systems or both.

In contrast to freshwater ecosystems, where small cells often dominate blooms, phytoplankton blooms in marine systems are characterized by large cells (Irigoien et al. 2004). Larger sizes of phytoplankton in productive areas may contribute to a flatter slope through sinking losses of larger cells (Rodríguez et al. 2001; Li 2002). Phytoplankton sinking is now considered to be a substantial component of the global sink of carbon (Turner 2002). Field studies (Billet et al. 1983; Scharek et al. 1999) have questioned the traditionally accepted low sinking rates measured in the laboratory (Smayda 1970) and shown that ungrazed phytoplankton, particularly from blooms, can sink out of the upper ocean at very high rates. Mesozooplankton are unable to exploit this resource pulse because of the slow response times of copepod life cycles, contributing therefore to a lower transfer efficiency of productive marine areas. Furthermore, the differences in phytoplankton size structure between freshwater lakes and the ocean contribute to the different relationship between sinking flux and planktonic primary production, whereby the export ratio increases with productivity in the ocean and decreases in lakes (Baines et al. 1994).

In addition, high production in oceanic systems is also subject to high spatial and temporal variability (formation of thermoclines, upwelling events, etc.), as well as to high advective dispersion of plankton, resulting in a weak coupling between planktonic producers and consumers.

In contrast, oligotrophic areas of the ocean show a higher stability, which could result in a stronger coupling between phytoplankton and zooplankton via grazing (Calbet 2001) and zooplankton-mediated processes, such as nutrient regeneration by excretion and liberation of dissolved organic matter by sloppy feeding, both of which affect the rate of phytoplankton and bacterial production (Banse 1995). This is further suggested by the high turnover rates and low densities of phytoplankton (Marañón et al. 2001), as well as the lower proportion of primary production exported from the upper mixed layer in these regions (Legendre and Le Fèvre 1991). In this way, the tight trophic linkage would compensate for the potential efficiency losses due to the small size of the producers.

Although there may be many processes (sedimentation, respiration, sloppy feeding) that can affect the biomass–size spectrum slope, there can be no disagreement that the size spectrum represents the proportion of organisms in different size classes. In other words, the measured biomass, and hence slope, is what remains after adding (e.g., growth) and subtracting (e.g., mortality) rates in the different size ranges. The slope of a biomass spectrum integrates the whole plankton community and therefore can be considered an effective approach that integrates all these effects. There are limitations, however, to the slope–energy transfer efficiency correlation theory. The slope is not an instantaneous measure of trophic transfer efficiency but an integration of variations over recent times. We have to consider that larger sized organisms may have a time lag to respond to changes in the system, and therefore a slope-to-slope comparison is not very useful to determine the efficiency of the system. Also, this slope–transfer efficiency theory may not be applicable to the oceanic ecosystem because of large-scale variability. Individual slopes of size spectra may not be sensitive enough to measure the differences in transfer efficiency between different systems, particularly in large spatial areas and seasonal systems that are not in steady state. The noise caused by different factors affecting the slope (e.g., temperature, light) may be higher than the variations caused by different transfer efficiencies. As such, the comparison of two slopes is not a reliable indication of one measure being more efficient than the other. However, if some types of systems (e.g., eutrophic) are systematically more efficient than others (e.g., oligotrophic) then this should be reflected in the average size spectra slope of the system. That is, an analysis of a large number of slopes in different areas as we report here should show a pattern in relation to productivity and remove any potential bias by sampling different non–steady state areas. Nevertheless, we found no pattern in the relation between size spectra slopes and different measures of system productivity (nutrients, primary production, and biomass), so there cannot be much variability due to these different factors. Furthermore, if slopes of size spectra are not sensitive enough to show the differences in transfer efficiency between systems, it suggests that such differences are not very large, or at least smaller than in freshwater systems where the same approach was able to detect differences (Sprules and Munawar 1986; Ahrens and Peters 1991; Tittel et al. 1998).

In any case, our results indicate that carbon flux models should reconsider the carbon transfer efficiency differences between productive and oligotrophic areas of the world ocean. This is fundamental in evaluating the future potential effect of climatic change on the nature of interactions between plankton (Edwards and Richardson 2004) and the resource flow to upper trophic levels (Winder and Schindler 2004).

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