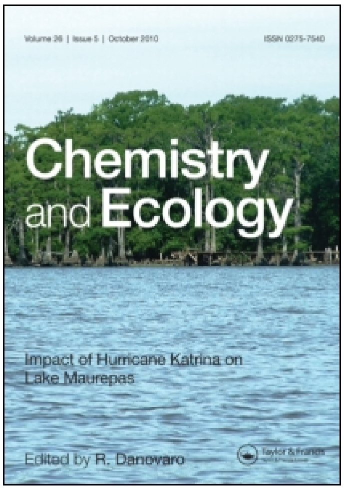

Chemistry and Ecology
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713455114

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To cite this Article Sabetta, Letizia , Fiocca, Annita , Margheriti, Lucia , Vignes, Fabio , Basset, Alberto , Mangoni, Olga , Carrada, Gian Carlo , Ruggieri, Nicoletta and Ianni, Carmela(2004) 'Phytoplankton size structure and environmental forcing within the euphotic zone in the Southern Adriatic-Ionian Coastal Area', Chemistry and Ecology, 20: 3, 303 — 317

To link to this Article: DOI: 10.1080/02757540410001664567

URL: http://dx.doi.org/10.1080/02757540410001664567

Chemistry and Ecology
June 2004, Vol. 20 (Supplement 1), pp. S303–S317

PHYTOPLANKTON SIZE STRUCTURE AND ENVIRONMENTAL FORCING WITHIN THE EUPHOTIC ZONE IN THE SOUTHERN ADRIATIC–IONIAN COASTAL AREA

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Here, we analysed the variation of size–abundance distributions of marine nano- and micro-phytoplankton guilds in relation to main environmental forcing factors and taxonomic composition. The study was carried out in the Southern Adriatic–Ionian Region and was based on physical, chemical and biological data collected during four cruises at 21 stations on seven transects. Biological data included density, individual cell size and species composition of nano- and micro-phytoplankton guilds and total and size-fractionated biomass of the entire phytoplankton community. We used canonical correspondence analysis to relate variation in nano- and micro-phytoplankton size–abundance distributions to variation of spatial, abiotic and biotic environmental forcing factors. Results showed that environmental forcing factors explained up to 75% of the size–abundance distribution variation in the study area. Variations in size–abundance distributions of the nano- and micro-phytoplankton guilds were relatively independent of taxonomic composition. Therefore, the obtained results suggested a relevant role of individual body size as an organizing factor of phytoplankton guilds.

Keywords: Phytoplankton size structure; Partitioning of variance; Spatial constraints; Biotic and abiotic forcing; Southern Adriatic and Ionian Seas

1 INTRODUCTION

The Adriatic basin is subjected to strong forcing factors, mainly related to seasonal changes in freshwater inputs from the northern basin, which introduce large amounts of nutrients and determine seasonal variability in water circulation (Artegiani *et al.*, 1997) and ecosystem structure and functioning (Zavatarelli *et al.*, 1998). In the northern basin, cool and freshwaters, mostly deriving from the Po river runoff, flow along the western coast of the Adriatic Sea, also reaching the middle and Southern Adriatic basins. In the Southern basin, runoff influence on water column dynamics is generally evident only in the autumn (Zavatarelli *et al.*, 1998),

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ISSN 0275-7540 print; ISSN 1029-0370 online © 2004 Taylor & Francis Ltd
DOI: 10.1080/02757540410001664567

and Levantine Intermediate Water (LIW) flowing through the Otranto Channel represents a possible additional carrier of allochthonous nutrients (Klein *et al.*, 1999).

In the present work, we report the results of a multidisciplinary study on the size structure of nano- and micro phytoplankton guilds, which was conducted in the Southern Adriatic–Ionian coastal marine area around the Salento peninsula in the frame of an INTERREG II Italy–Greece project.

The analysis of size structure, or body size–abundance distribution of organisms, is a common tool for studying the community and ecosystem structure of aquatic environments. Relevance of body size–abundance distributions is related to a strong underlying conceptual basis and to methodological convenience. The body size–abundance spectrum of a community is the result of evolutionary processes at the community level (Basset, 1995; Schmid *et al.*, 2000; Basset *et al.*, 2002) and of size-dependent thermodynamic processes at the individual level (Peters, 1983; Calder, 1984), which allow community energy fluxes to be estimated through allometric relationships (Sheldon *et al.*, 1972; Strayer, 1986; Morin and Dumont, 1994). Moreover, community analyses based on size as the organizing criterion have advantages over other methods based on taxonomic- or trophic-level aggregation, because of its comparability among different species assemblages and also because it does not require extensive taxonomic expertise (Hanson *et al.*, 1989; Rodríguez, 1994).

In planktonic communities, during the last decades, body size–abundance distributions were widely studied with a thermodynamic approach (Platt, 1985; Quinones, 1994), using an automated particle counter, which kept track of both living and non-living particles (Sheldon *et al.*, 1972), fractionated filtrations, which distinguished living organisms (Rodríguez and Mullin, 1986a, b) and microscopic counting, which permitted individual organism size to be evaluated (Sprules and Munawar, 1986; Rodríguez *et al.*, 1987; Sprules, 1988; Echevarría *et al.*, 1990), associated with automated flow cytometer assessments (Rodríguez *et al.*, 1998, 2002). These studies emphasized the roughly uniform distribution of planktonic biomass over logarithmic size classes, which were commonly peaked and unimodal when the analysis was limited only to body size–abundance distributions of the phytoplankton component (Rojo and Rodríguez, 1994; Rodríguez *et al.*, 2002).

The size structure of pelagic communities has received less attention from a point of view of a community approach (see Rodríguez and Mullin, 1986; Sprules, 1988; Sprules *et al.*, 1991), which was emphasized in other guilds and ecosystem components, such as benthic communities and detritus-based food chains, revealing remarkably constant and predictable features in both freshwater (Strayer, 1986) and marine (Warwick, 1984) ecosystems. Size-abundance distributions are commonly peaked (Mittelbach, 1981; Morin and Nadon, 1991; Morin, 1997) and exhibit limited temporal (Morin *et al.*, 1995) and spatial (Solimini *et al.*, 2001) changes, especially compared with taxonomic composition (Basset, 1994; Bourassa and Morin, 1995; Rodríguez and Magnan, 1995).

Here, we analysed the spatial and temporal patterns of the variation of body size–abundance distributions of marine nano- and micro-phytoplankton in relation to spatial, abiotic and biotic environmental forcing factors, on the one hand, and taxonomic composition, on the other hand.

In this work, we investigated the relevance of body size–abundance distribution as a phytoplankton community feature; to this aim, we tested the following hypotheses:

(1) spatial and temporal body size–abundance distribution patterns of marine phytoplankton were affected by environmental forcing factors; and
(2) spatial-temporal variation of body size–abundance distribution was independent of the taxonomic composition of marine phytoplankton guilds, i.e. variations in size–abundance distribution are not determined by selection processes at the species level.

The latter hypothesis also represents a test of one of the corollaries of body-size-related coexistence theory (Basset, 1995), also called body-size-related optimal foraging theory (Tokeshi, 1999), which proposed that invasion processes are affected by the degree of saturation of body size structure (Basset, 1995), before any influence of taxonomic composition and niche apportionment (*sensu* Tokeshi, 1993) among taxa.

2 MATERIALS AND METHODS

2.1 Field and Laboratory Methods

The present study has been conducted through four oceanographic cruises carried out in March, June, September and December 2000 along the Southern Apulian coast (Adriatic and Ionian Seas, south–east Italy) in the frame of the INTERREG II Italy–Greece Program.

Water samples were collected at seven transects of three stations each (at 3, 9, 15 NM from the coastline) and perpendicular to the coastline (Fig. 1).

At each station, vertical profiles of temperature, salinity, dissolved oxygen and fluorescence were obtained with an SBE 9/11 Plus CTD. Water samples for phytoplankton and nutrient analysis were collected using a Carousel sampler equipped with 12 Niskin bottles (12 l). Water samples for phytoplankton analysis were collected at three depths, selected according to the fluorescence signal and in order to collect always samples from the chlorophyll maximum layer.

Water samples for nutrients analysis were collected with a narrow sampling grid to obtain a clear definition of spatial patterns, if any. Sub-samples for nutrient analysis (silicate, phosphate, nitrate, nitrite, ammonia) were collected directly from the Niskin bottles, filtered

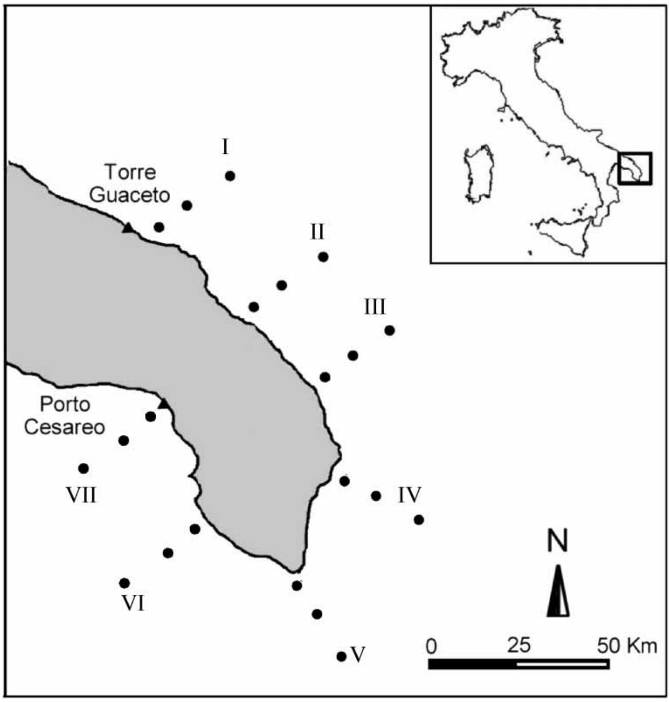

FIGURE 1 Localization of sampling transects in the Adriatic–Ionian coastal study area.

through a 0.7-μm GFF filter and stored at −20 °C in 100-ml low-density polyethylene bottles until analysis. In the laboratory, nutrient concentrations were determined using a Technicon II auto-analyzer, according to Hansen and Grasshoff (1983). Dissolved inorganic nitrogen (DIN) was calculated as the sum of nitrate, nitrite and ammonia, and phosphate was referred to as dissolved inorganic phosphorus (DIP).

Sub-samples for chlorophyll *a* (Chl*a*) determination were treated for phytoplankton biomass fractionation according to a protocol of serial filtration. For each sampling, an aliquot was filtered directly onto 25-mm GF/F 0.45-μm Whatman filters (total Chl*a* concentration); another aliquot was passed through 20-μm plankton nets and then onto 0.45-μm GF/F (microplanktonic fraction); a third aliquot was passed through 2-μm filters (Nuclepore) and collected afterwards onto 0.45 μm GF/F for the picoplanktonic fraction. The nanoplanktonic fraction (2–20 μm) was calculated by subtracting the <2-μm fraction from the <20-μm fraction. Filters were stored in a freezer at −20 °C until determination, and spectro-fluorimetric analyses of size-fractionated Chl*a* and phaeopigments were carried out according to Holm-Hansen *et al.* (1965). Filters were put into neutralized 90% (v/v) acetone, left to extract for 2 h and then the extract read, before and after acidification, using a Shimazu RF1501 spectro-fluorimeter. The instrument was daily checked against a solution of Chl*a* from *Anacystis nidulans* by Sigma.

Sub-samples for phytoplankton taxonomic determination and body size–abundance analysis were preserved with Lugol (15 ml per litre of sample). Taxonomic composition and body size–abundance distributions were determined under an inverted microscope (Nikon T300E) at 400× magnification following Utermöhl's method (Zingone *et al.*, 1990); consequently, they are referred only to the nano- and micro-phytoplankton guilds, covering the size range of 5–1000 μm. Phytoplankton nomenclature followed Tomas (1997). Taxonomic composition and body size–abundance distributions were determined on 200 cells per sub-sample, which were counted, identified and measured under 400 × magnifications under inverted microscope connected to a video-interactive image analysis system (L.U.C.I.A, Version 4.8, Laboratory Imaging s.r.o.). Colonial organisms, mainly from the genus *Chaetoceros*, were considered and measured as single individual cells. The individual cell volume (V, μm^3) of each measured cell was derived through the approximation of the cell shape to the most similar regular solid calculated directly by software. Cell bio-volume data were converted to weights (W, ng) using the relation $W = (V \times 1.03)/1000$, according to Hutchinson (1967). Body weight (calculated using the above equation) was used in this paper as individual body size.

Two major potential sources of bias on size–abundance distributions shape should be taken into account using the image-analysis technique used in this study, i.e. sample size and cell volume detection. As regards sample size, the number of cells counted per sample in this study guaranteed 10–20% accuracy on estimation of phytoplankton assemblage abundance, according to Lund *et al.* (1958); moreover, the sample size was in the range utilized in other studies of plankton body size–abundance distributions (Rodríguez *et al.*, 1987; Rojo and Rodríguez, 1994). As regards detection of cell volume, the image analysis L.U.C.I.A. had internal software options to minimize the potential bias arising from ascription of very different cell shapes to volumes according to simple parameters; moreover, it was already suggested that this bias does not significantly affect the size–abundance distribution shape (Rodríguez *et al.*, 1987; Echevarría *et al.*, 1990).

2.2 Data Analysis

From the individual cell weight, expressed in nanograms, we obtained phytoplankton body size–abundance distributions by grouping individuals into 0.5 logarithmic size classes.

Spatial and temporal similarity comparisons among phytoplankton communities and a canonical correspondence analysis between phytoplankton size structure and environmental variables were carried out. Size structure and taxonomic similarities among nano- and micro-phytoplankton communities were computed using the percentage similarity index (Renkonen, 1938).

A non-linear eigenvector ordination method, canonical correspondence analysis, was used to directly relate body size–abundance distribution of phytoplankton communities to environmental variables. The size–abundance data were transformed by square roots, environmental data were log-transformed, and the range of each environmental variable was divided into 10 equal-sized classes (Ter Braak, 1986).

Specifically, CCA was used to relate the variation in size–abundance distributions of communities to (1) abiotic environmental variables, (2) biotic environmental variables and (3) spatial variables. Partial canonical ordination (Bocard *et al.*, 1992; Rodríguez and Magnan, 1995) was used to partition the total variation in size structure of phytoplankton communities into different components, four of which can each be assigned to an independent source of variation: (1) variation related to abiotic environmental characteristics, (2) variation related to biotic environmental characteristics, (3) variation related to spatial structure and (4) unexplained variations. The residual explained variation is the portion shared by more than one component.

Because of the rough sea conditions during the March cruise, some samples were lost, and three out of the seven transects were not sampled at all. Some samples were also lost in September and December. Whenever required, statistical analyses were performed only on the common set sites, which were sampled at all times.

3 RESULTS

3.1 Physical, Chemical and Biological Characteristics

The Southern Adriatic–Ionian coastal marine area was characterized by a low concentration of dissolved nutrients (Tab. I). The average dissolved inorganic nitrogen (DIN) concentrations ranged from 0.97 to 5.38 μM, being higher in the cold period (winter and spring cruises) than in the warm period (summer and autumn cruises; Student's *t*-test, $t = 6.66$, d.f. $= 201$, $P < 0.001$; Tab. I). The average DIP concentrations varied within a much narrower range, from 0.10 to 0.17 μM. On a spatial bidimensional scale, with depth and distance from the coast as spatial dimensions, DIN concentration increased with depth and generally increased with distance from the coast. However, these two patterns, which are shown by DIN and DIP vertical profiles drawn on a seasonal scale (Fig. 2), were not statistically significant.

In this study, biological characteristics are expressed by the biomass (Chl*a* concentration) of the entire phytoplankton guild, and by the taxonomic and size-structure composition of the nano- and micro-phytoplankton fractions, which represented 36–50% of the entire community in the sampling period.

The Southern Adriatic–Ionian coastal marine area was characterized by a low phytoplankton biomass density, which ranged on average from 0.17 to 0.34 mg (Chl*a*) m^{-3} in the sampling period (Tab. I). Phytoplankton biomass covaried with DIN concentration, being significantly higher in winter and spring than in summer and autumn (Student's *t*-test, $t = 8.06$, d.f. $= 201$, $P < 0.001$, Tab. I).

Globally, we counted, measured and classified more than 40,000 cells of nano- and micro-phytoplankton, belonging to 320 nano- and micro-phytoplankton taxa, 76% of which were identified at the species level. In terms of the number of taxa, dominant taxonomic groups

TABLE I Seasonal variation of major physical, chemical environmental parameters and of biological characteristics of the phytoplankton communities in the study area.

Cruise	*Variate*	*Mean*	*Range*		*S.D.*
			Min	*Max*	
March	DIN (mM)	5.38	1.18	16.71	3.94
	DIP (mM)	0.13	4.50E-03	0.35	0.11
	DO (ml/l)	5.80	5.27	6.43	0.30
	Temperature	13.97	12.98	14.94	0.57
	Taxa (number)	15	6	29	6
	Biomass	0.34	0.14	0.67	0.13
	Micro-phytoplankton biomass (%)	13	2	40	10
	Pico-phytoplankton biomass (%)	61	23	82	12
June	DIN (mM)	0.98	0.06	11.07	1.48
	DIP (mM)	0.10	0.02	0.27	0.06
	DO (ml l^{-1})	6.54	5.38	7.79	0.65
	Temperature	18.55	14.36	24.12	3.65
	Taxa (number)	24	6	40	8
	Biomass	0.18	0.03	0.51	0.11
	Micro-phytoplankton biomass (%)	14	1	57	11
	Pico-phytoplankton biomass (%)	55	26	86	10
September	DIN (mM)	0.97	0.01	3.78	0.73
	DIP (mM)	0.17	0.01	0.45	0.11
	DO (ml l^{-1})	5.97	5.03	7.54	0.71
	Temperature	19.72	14.98	22.89	3.11
	Taxa (number)	17	9	32	5
	Biomass	0.17	0.04	0.34	0.07
	Micro-phytoplankton biomass (%)	15	1	33	8
	Pico-phytoplankton biomass (%)	64	29	96	14
December	DIN (mM)	1.89	0.01	6.82	1.57
	DIP (mM)	0.17	0.04	0.32	0.07
	DO (ml l^{-1})	5.90	5.28	6.59	0.37
	Temperature	16.91	14.89	18.78	0.80
	Taxa (number)	21	13	36	5
	Biomass	0.30	0.02	0.66	0.15
	Micro-phytoplankton biomass (%)	29	2	61	15
	Pico-phytoplankton biomass (%)	50	11	96	18

were Bacillariophyceae (127 taxa) and Dinophyceae (156 taxa). Coccolithophorids were represented by 16 taxa, and other groups were represented by fewer than five taxa. Taxonomic richness varied among seasons, from a maximum of 221 taxa recognized in the June cruise samples, to a minimum of 98 taxa recognized in the March cruise samples. The average number of taxa per sampling site and sampling time also varied among seasons in a range between 24.0 ± 0.97, during the June cruise, and 14.8 ± 0.93, during the March cruise (Student’s t-test, d.f. $= P < 0.001$).

A list of the most widespread nano- and micro-phytoplankton taxa, such as those occurring at more than 25% of sampling stations and sampling depths, is reported for each seasonal cruise (Fig. 3). These taxa accounted for 15.4–24.5% of overall taxonomic richness and as much as 84–88% of numerical abundance in the nano- and micro-phytoplankton guilds. The taxonomic composition of nano- and micro-phytoplankton guilds varied greatly among sampling cruises; 52% of these widespread nano- and micro-phytoplankton taxa were found exclusively in one sampling cruise, 23% occurred in two consecutive cruises, with the exception of *Ceritium fusus*, and only 16 and 9% of these widespread taxa were found in three or in all cruises, respectively. The relative importance of taxa also varied among sampling cruises (Fig. 3). The spatial and temporal variability of the

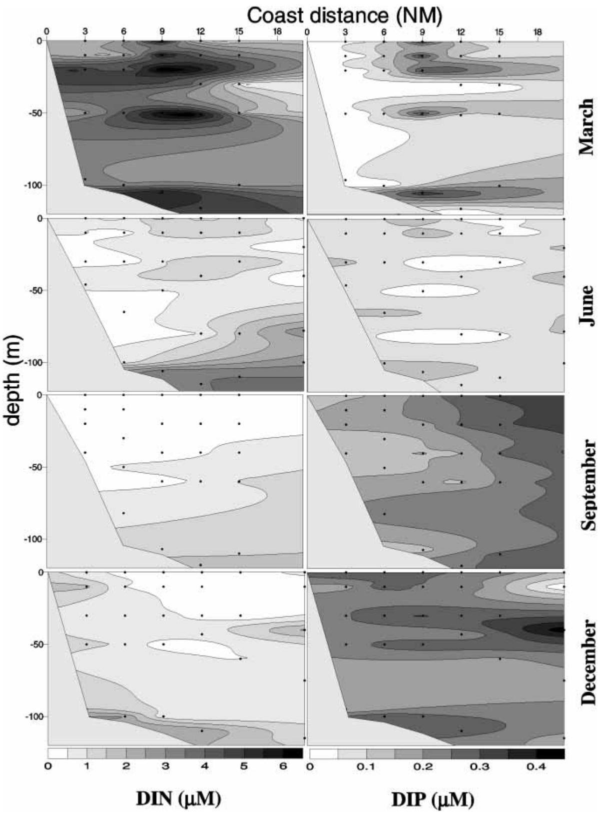

FIGURE 2 Vertical profiles of dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP) concentrations (μM) at the IV transect (see Fig. 1) for the four sampling cruises.

taxonomic composition and diversity of nano- and micro-phytoplankton guilds was quantified using the Renkonen similarity index (PS; Renkonen, 1938). The average taxonomic similarity among guilds was 32 ± 16% across sampling periods and ranged from 25 ± 16%, in the March cruise, to 38 ± 16%, in the September cruise (Tab. II).

With regard to the phytoplankton size structure, the phytoplankton individual cell size ranged from 0.07 ng (i.e. cells of the taxon *Nitzshia turgidula* (Hustedt)) to 1292.06 ng (diatoms of the genus *Rhizosolenia*). Body size and numerical abundance of nano- and micro-phytoplankton taxa were generally inversely related. Significant inverse allometric relationships between body size and numerical abundance of the widespread taxa were observed for each sampling cruise, with the exception of the March cruise (see Fig. 3; regression analysis, June: $R^2 = 0.28$, d.f. = 32, $P < 0.05$; September: $R^2 = 0.37$, d.f. = 27, $P < 0.05$; December: $R^2 = 0.42$, d.f. = 31, $P < 0.05$). The spatial and temporal variability of the size–abundance distributions of nano- and micro-phytoplankton guilds, which are described in Fig. 4, was also quantified by the Renkonen similarity index (PS; Renkonen, 1938). The average size structure similarity among guilds was 65 ± 15% across sampling periods and ranged from 46 ± 18%, in the March cruise, to 69 ± 12%, in the December cruise (Tab. II). The similarity of size–abundance distributions was significantly higher than the taxonomic similarity, both across sampling periods (65 ± 15% *vs.* 32 ± 16%; Student's *t*-test, $t = 12.23$, d.f. = 3, $P < 0.01$) and within each sampling cruise (Student's *t*-test, Tab. II).

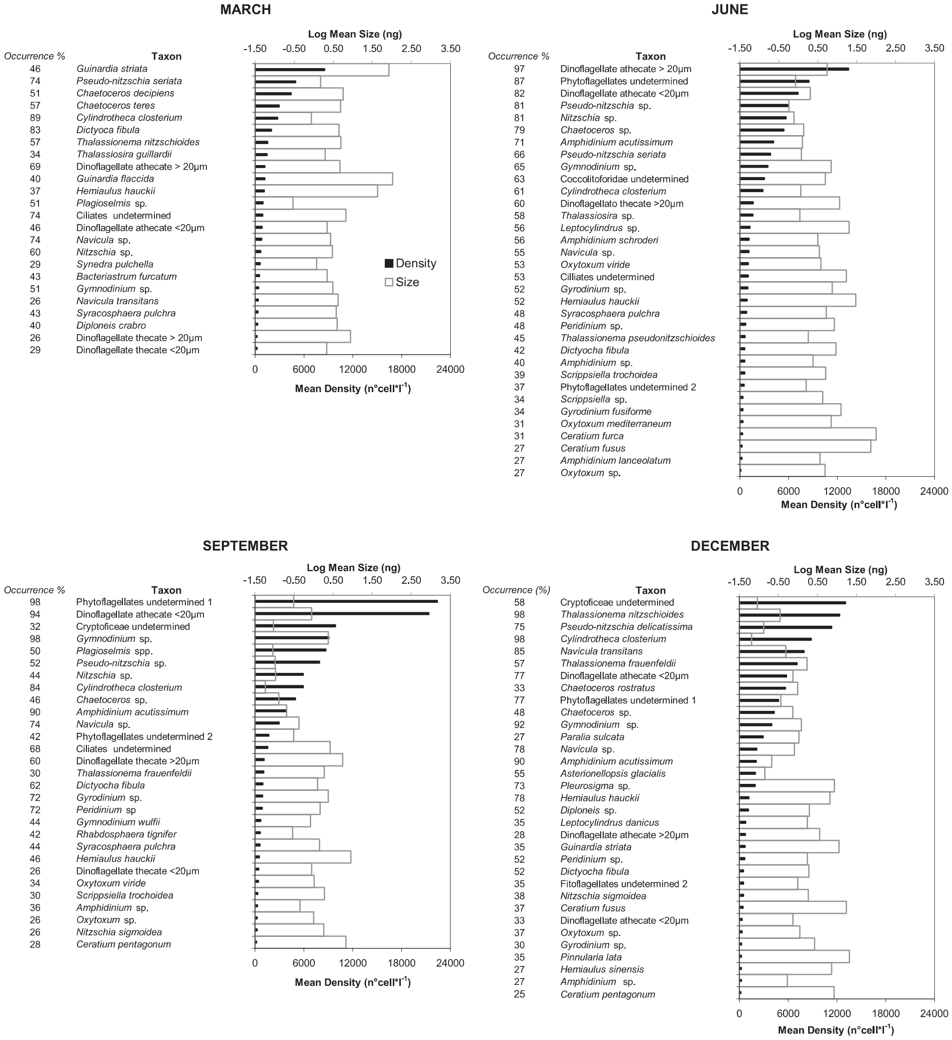

FIGURE 3 Mean size (weight, nanograms) and density (number of cells per litre) of the most widespread nano- and micro-phytoplankton taxa, i.e. those occurring at more than 25% of sampling stations and sampling depths for each sampling cruise.

3.2 Size-Abundance Distributions and Environmental Forcing

A non-linear correspondence analysis was performed to relate phytoplankton size structure to environmental forcing factors after a detrended correspondence analysis of data (Canoco; Ter Braak and Prentice, 1988). Moreover, a correspondence analysis using the forward selection procedure based on 1000 Monte Carlo permutations selected, at a 10% confidence level, of four abiotic environmental variables (DIN, DIP, oxygen concentration and water temperature), four biotic environmental variables (number of species, phytoplankton biomass, micro-phytoplankton and pico-phytoplankton biomass fraction) and four spatial variables (latitude, longitude, depth and distance from the coast).

Two parallel sets of analysis of variation partitioning are described, considering abiotic environmental variables and spatial components, hereafter called the abiotic-space set

TABLE II Average similarities (percentage similarity (PS); Renkonen, 1938) of taxonomic composition and size–abundance distributions of nano- and micro-phytoplankton guilds, among sampling stations and sampling depths, (within each sampling cruise with standard errors in parentheses) and student *t*-test results for taxonomic composition and size–abundance distributions.

	Similarity				
	Taxa	*Size*	*t*	*d.f.*	*P*
March	24.98 (16.37)	46.06 (17.92)	−30.73	594	<0.001
June	27.76 (14.55)	65.11 (13.14)	−99.25	1890	<0.001
September	38.61 (15.72)	67.78 (11.78)	−77.36	1225	<0.001
December	34.00 (13.59)	68.77 (11.96)	−88.65	1769	<0.001

(Fig. 5A), or biotic environmental variables and spatial component, hereafter called the biotic-space set (Fig. 5B), as sources of size–abundance distribution variation. Globally, explained size–abundance distribution variation was 54.0 ± 7.7% in the abiotic-space set and 46.3 ± 5.10% in the biotic-space set. In both sets, the spatial component alone accounted for a larger fraction of explained variance than the environmental abiotic or biotic variables, explaining 26.0 ± 2.6 and 26.9 ± 3.7% of size–abundance distribution variance in the abiotic and biotic sets, respectively. The abiotic variables alone explained on average a larger

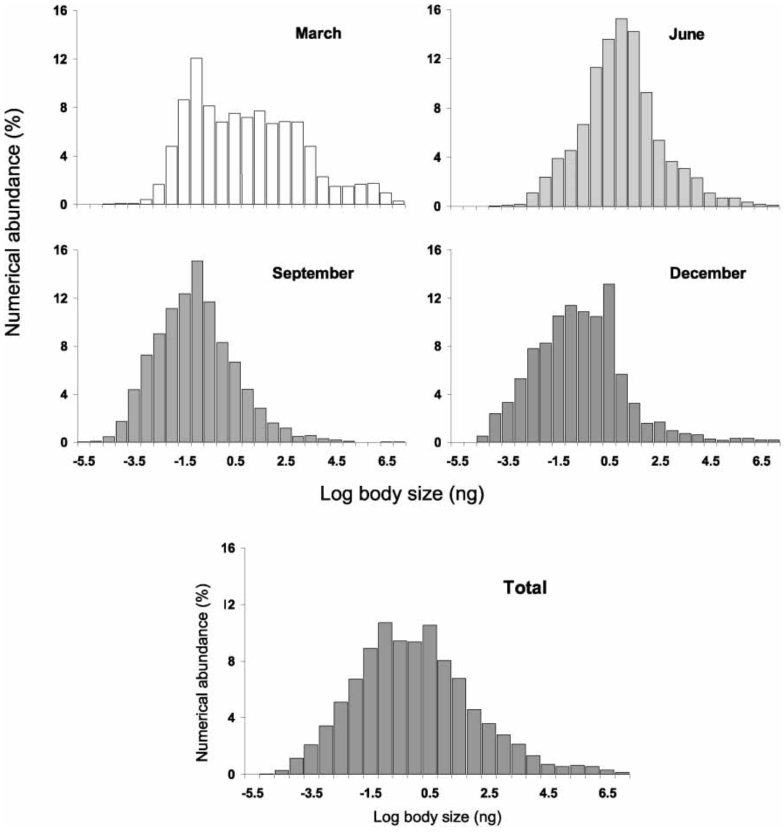

FIGURE 4 Seasonal and annual (total) size–abundance distributions of nano- and micro-phytoplankton guilds.

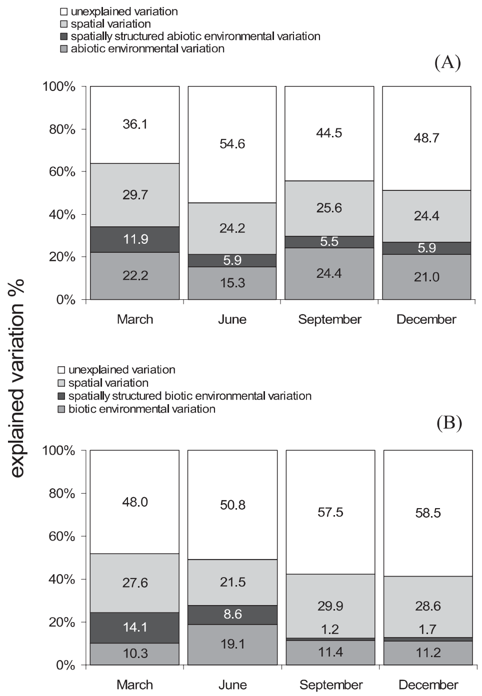

FIGURE 5 Percentages of total variation of plankton size–abundance distributions explained by (A) abiotic environmental variables and space and (B) biotic environmental variables and space. The whole variation is partitioned as a non-spatial environmental variation, a spatial size distribution variation that is not shared by the environmental variables and an unexplained variation.

variance component than the biotic variables alone (20.7 ± 3.9 *vs.* $13.0 \pm 4.0\%$; Student's t-test, $t = 2.74$, d.f. $= 6$, $P < 0.05$).

To determine whether the two sets of environmental variables extracted different components of the spatial variation of the size–abundance distribution, an analysis simultaneously incorporating the three sets of explanatory variables was performed (hereafter called the 3-set; Fig. 5). Explained size–abundance distribution variation was significantly higher when the three groups of variables were considered together (3-set) than when pairwise comparisons (abiotic-space and biotic-space sets) were made, (3-set *vs.* abiotic-space set: Student's t-test, $t = 7.49$, d.f. $= 3$, $P < 0.01$; 3-set *vs.* biotic-space set: Student's t-test, $t = 7.87$, d.f. $= 3$, $P < 0.01$). On average, $65.9 \pm 6.3\%$ of the size–abundance distribution variation was explained by the 3-set (Fig. 6). The contribution of each of the three groups of variables did not vary significantly between 3-set and abiotic-space and biotic-space sets, apart from a 3% significant reduction in variance explained by the spatial component in the 3-set with respect to the biotic-space set (Student's t-test, $t = -4.98$, d.f. $= 3$, $P < 0.05$). The 'pure' spatial component still accounted for the largest portion of explained variation. This fraction ranged from 18.5 to 25.4% among sampling periods. At the same time, the portion of variation uniquely due to the abiotic variables, which ranged from 12.9 to 24.4%, was larger than the portion uniquely due to biotic variables (9.2–16.7%) in each sampling period, but not in June.

The shared variation was higher in the 3-set than in abiotic-space and biotic-space sets, but the differences were statistically significant only with respect to biotic-space sets (Student's t-test, $t = 3.45$, d.f. $= 3$, $P < 0.05$) and were not statistically different from the sum of shared variation in biotic and abiotic sets (shared variation: 3-V $11.3 \pm 4.4\%$; 2-V biotic + abiotic sets $13.7 \pm 8.9\%$, Student's t-test, $t = 0.89$, d.f. $= 3$, n.s.).

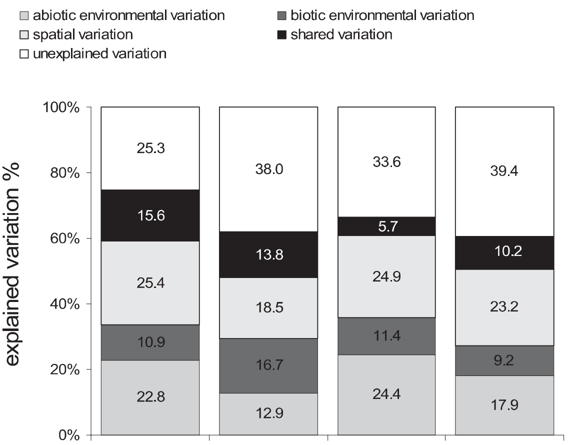

FIGURE 6 Partitioning of the total variation in plankton size–abundance distributions among the three sets of explanatory variables (abiotic environmental, biotic environmental, spatial component).

4 DISCUSSION

Our results suggested the relevance of size structure as a structural feature of coastal marine phytoplankton guilds in the Southern Adriatic–Ionian coastal marine area.

In fact, the results obtained supported both the hypotheses tested here: *i.e.* most of the observed nano- and micro-phytoplankton size structure heterogeneity was explained by environmental constraints and occurred independently of niche apportionment of phytoplankton taxa along the environmental gradients.

As regards the first hypothesis, it is widely recognized that body size is a relevant phenotypic feature of individuals strictly related to individual fitness (see Peters, 1983); consequently, environmental factors such as nutrient content, water turbulence and predation can be relevant to determine coexistence conditions for phytoplankton at the local scale. Body-size spectra and size-fraction distributions of pelagic plankton guilds were already observed to respond to selective forces or variation sources. Trophic conditions were found to affect size-fractionated chlorophyll distribution, with pico-phytoplankton being dominant in oligotrophic conditions (Glover *et al.*, 1985; Hewes *et al.*, 1990), and micro-phytoplankton was more represented at eutrophic and coastal sites (Kitchen *et al.*, 1975; Tamigneaux *et al.*, 1999; Yew-Hoong Gin *et al.*, 2000). Trophic state and biotope size (Sprules and Munawar, 1986; Gaedke, 1992) were also found to affect plankton size spectra, too. Diatoms and generally large cells were also observed to dominate upwelling areas (Margalef, 1978), suggesting a positive influence of water turbulence, even though turbulence was also found to be a source of perturbation for the phytoplankton size structure (Sabetta, pers. obs.). Therefore, our results are in agreement with existing evidence and expand the previous findings on the local scale effects of specific environmental parameters on the body size–abundance distribution of marine phytoplankton guilds to mesoscale effects of main groups of environmental forcing factors.

It was beyond the aim of this study to analyse local scale effects of specific environmental parameters on body size–abundance distributions of marine phytoplankton guilds; the spatial and temporal variation of phytoplankton size structure observed in this study at a spatial mesoscale seemed more likely to be an integrated response to local scale effects of many factors, including nutrient content and turbulence as well as of the other potential factors, than to be the result of single or few factors. This is supported by the lack of a major role of abiotic factors on the observed patterns of body size–abundance distributions and of a relevant covariance of biotic and spatial factors with the abiotic factors. In fact, nutrient concentrations were expected to be major forcing factors, among the investigated environmental sources of variation, also with a spatial component according to the distance from the coastline; nutrients were also expected to control the temporal and spatial variability of biotic components, such as phytoplankton biomass, taxonomic composition (see Haeky and Kilman, 1988, for a review) and size-fraction distribution (Watson and Kalff, 1980; Duarte *et al.*, 1992). Therefore, our results suggested that in the study area, other factors prevailed locally on nutrient inputs from both a terrestrial and freshwater origin as structuring factors determining an integrated response from the phytoplankton community. The size–abundance distribution variations accounted for by space components alone, which suggests that the spatial matrix acted as a synthetic descriptor of unmeasured spatially structured variables (Bocard *et al.*, 1992; Legendre, 1993), supported this view. Moreover, the oligotrophic nature of the Southern Adriatic–Ionian coastal marine area (Zavatarelli *et al.*, 1998, 2000; Socal *et al.*, 1999), the occurrence of a localized influence of Levantine water during the summer season (Zavatarelli *et al.*, 1998) and an inflow of northern Adriatic waters to the most northern transects in the studied area (Zavatarelli *et al.*, 1998) also supported this point. In fact, the addition of these sources of nutrients to the expected nutrient input from terrestrial ecosystems through the coast, which was very low due to the precipitation regimes and the lack of major freshwater basins, emphasized the weakness of the environmental spatial gradients in the study area (see also Vadrucci *et al.*, in press).

As regards the second hypothesis, the relevance of size structure as a structural feature of nano- and micro-phytoplankton guilds is supported by the comparison between taxonomic and size-structure similarity. Size-structure variation with environmental forcing in the study area was more than just a result of niche partitioning among phytoplankton species on environmental gradients; in fact, size structures were relatively invariant with respect to the taxonomic composition of nano- and micro-phytoplankton guilds both in time and in space.

The relationships between size structure and taxonomic composition of guilds and communities represent a key aspect to evaluate the ecological relevance of body size on community organization. In fact, size structure can be simply considered to reflect species composition, but it was also suggested that colonization of potential invaders can be conditioned by the occurrence of empty body size space in body size–abundance distribution (Basset, 1994).

The observed species composition of phytoplankton guilds, which generally agreed with literature evidence for the study area (Socal *et al.*, 1999), exhibited a high degree of temporal and spatial heterogeneity. Therefore, the similarity of size structures of phytoplankton communities among seasons and sites suggested that size structures can set constraints to taxonomic composition, thus supporting a deterministic basis of phytoplankton size structure in the study area.

A relative invariance of size structures was already observed in both pelagic (Warwick, 1984; Strayer, 1986) and benthic (Morin and Nadon, 1991; Bourassa and Morin, 1995; Morin *et al.*, 1995; Solimini *et al.*, 2001) communities. A significantly higher similarity of body size–abundance distributions with respect to taxonomic composition was also observed (Basset, 1994). Therefore, the results of this study agreed with the available literature evidence and extended the findings to nano- and micro-phytoplankton pelagic marine guilds.

These findings also supported the fact that directional environmental sources of variation were more important in phytoplankton size structures in the study area than random invasion processes. In fact, these latter would have implied comparable values of taxonomic and size structure similarity and little influence of environmental constraints on size distributions.

The body-size structure of marine phytoplankton, whose variation could be explained to a large extent by the quantified variables, seemed to be very sensitive even to weak and local gradients of environmental pressures characteristic of the Southern Adriatic–Ionian coastal area. Therefore, quantifiable and standardized parameters of size structures could be synthetic descriptors of marine phytoplankton ecological status and marine ecosystem health.

The results of this study strongly supported the hypothesis that the body size–abundance distribution of marine nano- and micro-phytoplankton guilds was affected by environmental forcing factors independently of the niche requirements of phytoplankton taxa, thus emphasizing the relevance of phytoplankton size structures as an intrinsic property of pelagic communities, functionally depending on ecological constraints related to trophic factors and intra-guild coexistence relationships.

Acknowledgements

This research was supported by an Italian Ministry of University and Research (MIUR) 60% grant and by an ECC and Regione Puglia grant to the INTERREG II Italy–Greece project 'Structure and processes in the water column'.

References

Artegiani, A., Bregant, D., Paschini, E., Pinardi, N., Raicich, F. and Russo, A. (1997). The Adriatic Sea general circulation. Air–sea interactions and water mass structure. *Journal of Physical Oceanography*, **27**, 1492–1514.

Basset, A. (1994). Role of body size on detritus-based guild organization at the land–freshwater ecotone. *S.IT.E Atti*, **16**, 155–160.

Basset, A. (1995). Body size-related coexistence: an approach through allometric constraints on home range use. *Ecology*, **76** (4), 1027–1035.

Basset, A., Fedele, M. L. and DeAngelis, D. L. (2002). Optimal exploitation of spatially distributed trophic resource and population stability. *Ecological Modelling*, **151**, 245–260.

Bocard, D., Legendre, P. and Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, **73** (3), 1045–1055.

Bourassa, N. and Morin, A. (1995). Relationships between size structure of invertebrate assemblages and trophy and substrate composition in streams. *Journal of the North American Benthological Society*, **14** (3), 393–403.

Calder, W. A. III (1984). *Size, function and life history.* Harvard University Press, Cambridge, MA.

Duarte, C. M., Augusti, S. and Canfield, D. E. J. (1992). Size plasticity of freshwater phytoplankton: Implications for community structure. *Limnology Oceanography*, **35**, 1846–1851.

Echevarría, F., Carrillo, P., Jimenez, F., Sanchez-Castillo, P., Cruz-Pizarro, L. and Rodríguez, J. (1990). The size-abundance distribution and taxonomic composition of plankton in an oligotrophic, high mountain lake (La Caldera, Sierra Nevada, Spain). *Journal of Plankton Research*, **12**, 415–422.

Gaedke, U. (1992). The size distribution of plankton biomass in a large lake and its seasonal variability. *Limnology Oceanography*, **37**, 1202–1220.

Glover, H. E., Smith, A. E. and Shapiro, L. (1985). Diurnal variations in photosynthetic rates: comparisons of ultra-phytoplankton size fraction. *Journal of Plankton Research*, **7**, 519–535.

Haeky, R. E. and Kilman, P. (1988). Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. *Limnology Oceanography*, **33**, 796–822.

Hansen, H. P. and Grasshoff, H. (1983). Automated chemical analysis. In: Grasshoff, K., Ehrardt, M. and Kremling, K. (eds.), *Methods of Sea Water Analysis.* Verlag Chemie, Weinheim, pp. 347–379.

Hanson, J. M., Prepas, E. E. and MacKay, W. C. (1989). Size distribution of the macroinvertebrate community in a freshwater lake. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1510–1519.

Hewes, C. D., Sakshaug, E., Reid, F. M. H. and Holm-Hansen, O. (1990). Microbial autotrophic and heterotrophic eukaryotes in Antarctic waters: relationships between biomass and chlorophyll, adenosine triphosphate and particulate organic carbon. *Marine Ecology Progress Series*, **63**, 27–35.

Holm-Hansen, O., Lorenzen, C. J., Holmes, R. W. and Strickland, J. D. H. (1965). Fluorimetric determination of chlorophyll. *Conseil permanent international pour l'Exploration de la Mer* **30** (1), 3–15.

Hutchinson, G. E. (1967). *A Treatise on Limnology*, Vol. 2. *Introduction to Lake Biology and the Limnoplankton*, Wiley, New York.

Kitchen, J. C., Menzies, D., Pak, H. and Zaneyeld, J. R. V. (1975). Particle size distributions in a region of coastal up welling analysed by characteristic vectors. *Limnology Oceanography*, **20**, 775–783.

Klein, B., Roether, W., Beniamino, M. B., Bregant, D., Volker, B. and Vedrana, K. (1999). The large deep water transient in the Eastern Mediterranean. *Deep Sea Research I*, **46**, 371–414.

Legendre, P. (1993). Spatial autocorrelation: trouble or new paradigm? *Ecology*, **74**, 1654–1673.

Lund, J. W. G., Kipling, C. and LeCren, E. D. (1958). The inverted microscope method of estimating algae numbers and the statistical basis of estimations by counting. *Hydrobiologia*, **11**, 143–170.

Margalef, R. (1978). Phytoplankton communities in upwelling areas. The example of NW Africa. *Oecologia Aquatica*, **3**, 97–132.

Mittelbach, G. G. (1981). Patterns of invertebrate size and abundance in aquatic habitats. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 896–904.

Morin, A. (1997). Empirical models predicting population abundance and productivity in lotic systems. *Journal of the North American Benthological Society*, **16**, 319–337.

Morin, A. and Dumont, P. (1994). A simple model to estimate growth rate of lotic insect larvae and its value for estimating population and community production. *Journal of the North American Benthological Society*, **13**, 357–367.

Morin, A. and Nadon, D. (1991). Size distribution of epilithic lotic invertebrates and implications for community metabolism. *Journal of the North American Benthological Society*, **10**, 300–308.

Morin, A., Rodríguez, M. A. and Nadon, D. (1995). Temporal and environmental variation in the biomass spectrum of benthic invertebrates in streams: an application of thin-plate splines and relative warp analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1789–1794.

Peters, R. H. (1983). *The ecological implication of body size.* Cambridge University Press, Cambridge.

Platt, T. (1985). Structure of the marine ecosystem: Its allometric basis. In *Ecosystem theory for biological oceanography. Canadian Bulletin of Fisheries and Aquatic Sciences*, **213**, 55–64.

Quinones, R. A. (1994). A comments on the use of allometry in the study of pelagic ecosystem. In: Rodríguez, J. and Li, W. K. W. (eds.), *The Size Structure and Metabolism of the Pelagic Ecosystem. Scientia Marina*, **58** (1–2), 11–16.

Renkonen, O. (1938). Statich-okologische. Untersuchungen uber die terrestiche kaferwelt der finnischen bruchmoore. *Archivum Societatis Zoologicae Botanicae Fennicae 'Vanamo'* **6**, 1–231.

Rodríguez, J. (1994). Some comments on the size-based structural analysis of the pelagic ecosystem. In: Rodríguez, J. and Li, W. K. W. (eds.), *The Size Structure and Metabolism of the Pelagic Ecosystem. Scientia Marina*, **58** (1–2), 1–10.

Rodríguez, M. A. and Magnan, P. (1995). Application of multivariate analyses in studies of the organization and structure of fish and invertebrate communities. *Aquatic Science*, **57** (3), 199–216.

Rodríguez, J. and Mullin, M. M. (1986a). Relation between biomass and body weight of plankton in a steady state oceanic ecosystem. *Limnology Oceanography*, **31** (2), 361–370.

Rodríguez, J. and Mullin, M. M. (1986b). Diel and interannual variation of size distribution of oceanic zooplanktonic biomass. *Ecology*, **67** (1), 215–222.

Rodríguez, J., Jiménez, F., Bautista, B. and Rodríguez, V. (1987). Planktonic biomass spectra dynamics during a winter production pulse in Mediterranean coastal waters. *Journal of Plankton Research*, **9** (6), 1183–1194.

Rodríguez, J., Blanco, J. M., Jiménez-Gomez, F., Echevarría, F., Gil, J., Rodríguez, V., Ruiz, J., Bautista, B. and Guerrero, F. (1998). Patterns in the Size structure of the phytoplankton community in the deep fluorescence maximum of the Alboran Sea (Southwestern Mediterranean). *Deep-Sea Research I*, **45**, 1577–1593.

Rodríguez, J., Jimenez-Gomez, F., Blanco, J. M. and Figueroa, F. L. (2002). Physical gradients and spatial variability of the size structure and composition of phytoplankton in the Gerlache Strait (Antarctica). *Deep-Sea Research II*, **49**, 693–706.

Rojo, C. and Rodríguez, J. (1994). Seasonal variability of phytoplankton size structure in a hypertrophic lake. *Journal of Plankton Research*, **16** (4), 317–335.

Schmid, P. E., Tokeshi, M. and Schmid-Araya, J. M. (2000). Relation between population density and body size in stream community. *Science*, **289**, 1557–1559.

Schwinghamer, P. (1981). Characteristic size distributions of integral benthic communities. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 1255–1263.

Sheldon, R. W., Prakash, A. and Sutcliffe, W. H. J. (1972). The size distribution of particles in the ocean. *Limnology Oceanography*, **17**, 327–340.

Sieburth, J. McN. (1979). *Sea Microbes.* Oxford University Press, New York.

Socal, G., Boldrin, A., Bianchi, F., Civitarese, G., De Lazzari, A., Rabbitti, A., Totti, C. and Turchetto, M. M. (1999). Nutrient, particulate matter and phytoplankton variabilità in the photic layer of the Otranto Strait. *Journal of Marine System*, **20**, 391–398.

Solimini, A. G., Benvenuti, A, D'Olimpio, R., De Cicco, M. and Carchini, G. (2001). Size structure of benthic invertebrate assemblages in a Mediterranean river. *Journal of the North American Benthological Society*, **20** (3), 421–431.

Sprules, W. G. (1988). Effects of trophic interactions on the shape of pelagic size spectra. *Internationale Vereinigung für Theoretische und Angewandte Limnologie*, **23**, 234–240.

Sprules, W. G. and Munawar, M. (1986). Plankton size spectra in relation to ecosystem productivity, size, and perturbation. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1789–1794.

Sprules, W. G., Brandt, S. B., Stewart, D. J., Munawar, M., Jin, E. and Love, J. (1991). Biomass size spectrum of the Lake Michigan pelagic food web. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 105–115.

Strayer, D. (1986). The size structure of a lacustrine zoobenthic community. *Oecologia*, **69**, 513–516.

Tamigneaux, E., Legendre, L., Klein, B. and Mingelbeir, M. (1999). Seasonal dynamics and potential fate of size-frationated phytoplankton in a temperate near shore environment (western Gulf of St. Lawrence, Canada). *Estuarine Coastal and Shelf Science*, **48**, 253–269.

Ter Braak, C. J. F. (1986). Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **65** (5), 1167–1179.

Ter Braak, C. J. F. and Prentice, I. C. (1988). A theory of gradient analysis. *Advances in Ecological Research*, **18**, 271–317.

Tokeshi, M. (1993). Species abundance patterns and community structure. *Advances in Ecological Research*, **24**, 111–186.

Tokeshi, M. (1999). *Species Coexistence—Ecological and Evolotionary Perspective.* Blackwell Science, Oxford.

Tomas, C. R. (1997). *Identifying Marine Phytoplankton.* Academic Press, New York.

Vadrucci, M. R., Vignes, F., Fiocca, A., Basset, A., Santarpia, I., Carrada, G. C., Cabrini, M. and Fonda Umani, S. (2003). Space-time patterns of co-variation of biodiversity and primary production in phytoplankton guilds of coastal marine environments. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **13**, 489–506.

Warwick, R. M. (1984). Species size distributions in marine benthic communities. *Oecologia*, **61**, 32–41.

Warwick, R. M. (1988). The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. *Marine Pollution Bulletin*, **19**, 259–268.

Watson, S. and Kalff, J. (1980). Relationships between nanoplankton and lake trophic status. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 960–967.

Yew-Hoong Gin, K., Lin, X. and Zhang, S. (2000). Dynamics and size structure of phytoplankton in the coastal waters of Singapore. *Journal of Plankton Research*, **22**, 1465–1484.

Zavatarelli, M., Raicich, F., Bregant, D., Russo, A. and Artegiani, A. (1998). Climatological biogeochemical characteristics of the Adriatic Sea. *Journal of Marine Systems*, **18**, 227–263.

Zavatarelli, M., Beretta, J. W., Beker, J. G. and Pinardi, N. (2000). The dynamics of the Adriatic Sea ecosystem: An idealized model study. *Deep Sea Research I*, **47**, 937–970.

Zingone, A., Honsell, G., Marino, D., Montresor, M. and Socal, G. (1990). Fitoplancton. In Metodi nell'ecologia del plancton marino. *Nova Thalassia*, **11**, 183–198.