Vol. 250: 125–144, 2003 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published March 26

Variability of phytoplankton and mesozooplankton biomass in the subtropical and tropical Atlantic Ocean

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ABSTRACT: Data from over 40 yr (1950–1992) of expeditions to the Atlantic Ocean are summarised in the form of macroscale contour maps between 40° N and 40° S. The chl *a* concentrations from the surface and mesozooplankton in the upper layer (0 to 100 m) were analysed from 3992 casts and 1124 hauls respectively. General agreement between chlorophyll concentrations and mesozooplankton biomass distributions was noted on an ocean basin scale. There were non-linear relationships between mean chlorophyll concentration within the 0 to 10 m layer and mesozooplankton biomass within the 0 to 100 m layer for summed data between December to May and June to November. A comparison of the total biomass of mesozooplankton und phytoplankton, in carbon units, indicated that this ratio varied from 0.15 to 1 in the 0 to 100 m layer and, on average, the phytoplankton biomass exceeded twice that of mesozooplankton. The seasonal cycles of phyto- and zooplankton biomass for 6 provinces of the tropical zone were qualitatively comparable. Quantitative differences were found in the seasonal amplitudes, which were greater for the regions with nutrient enrichment of the upper layer. Relationships were established between phytoplankton and mesozooplankton biomass for 8 provinces.

KEY WORDS: Phytoplankton · Zooplankton · Spatial variability · Atlantic Ocean

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INTRODUCTION

Interactions between physical and biological processes affect the biogeochemical cycling of carbon in the oceans. The basin scale circulation in the Atlantic Ocean incorporates a system of gyres located in the northern and southern hemispheres. North and south of the equator, from 20 to 45° latitude, anticyclonic gyres occur, which are dominated by downwelling processes. In this scheme, most extended upwelling areas in the Atlantic Ocean occur in zones of subtropical divergences. The Northern Tropical Divergence stretches from 50° W to the African coast along 8° N latitude in the west and 8 to 15° N latitude in the east (Voituriez 1981, Bezrukov 1989). It is weakly developed from the winter to the spring period, but achieves its maximum in the autumn. The Southern Tropical Divergence takes place along latitudes 4 to 5° S and turns eastward at 23° W and reaches 15° S latitude (Bezrukov 1989, Longhurst 1998).

The northern and southwestern coasts of Africa are believed to have permanent upwelling with high concentrations of nutrients reaching the subsurface layer. These nutrients are not fully utilised by phytoplankton and, with waters of the Canary and Benguela Currents, they are carried south and northwestwards. The regions with high chlorophyll concentration away from the upwelling regions have been remotely sensed by satellites (McClain et al. 1990, Falkowski et al. 1998, Hoepffner et al. 1999). The structural changes in the water masses also influence the major structural-functional characteristics of the plankton communities, which in turn causes differences in biological processes.

Much of our understanding of the biological processes and distribution of the plankton biomass within the tropical Atlantic Ocean has been obtained from

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shipboard observation collected within the framework of international and national projects: METEOR (1925–1927), Equalant I and II (1963–1965), CIPREA (1978–1979), SEQUAL-FOCAL (1983–1985), JGOFS (1989–1990), and World Ocean (national project Former Soviet Union, FSU 1970–1990). On the basis of these numerous measurements, maps were constructed of the plankton distribution (Bogorov et al. 1968, Corcoran & Manken 1969, Bé et al. 1971, Zernova 1974, Semina 1977, Chromov 1986, Piontkovski & Ignatyev 1992, Piontkovski et al. 1997, Tseitlin et al. 1997a,b) and also for phytoplankton production (Koblentz-Mishke et al. 1970, Finenko 1978, 1994, Berger 1989). Similarities in the distributions of phytoplankton, primary production and mesozooplankton with the circulation of surface water masses were noted in these studies. Observations of ocean colour from the Coastal Zone Color Scanner (CZCS) satellite showed the macroscale variability (hundreds of km) of the near surface chlorophyll-like pigment concentration (NASA 1989). These observations confirmed the role of physics operating in the ocean creating these large-scale geographic and temporal patterns of chlorophyll concentration (McClain et al. 1990, Falkowski et al. 1998).

The relationship between chlorophyll and primary production in the integrated upper layer (Eppley et al. 1985, 1987, Berger 1989, Monger et al. 1997), in the euphotic layer (Lorenzen 1970, Smith 1981, Platt & Herman 1983) and chlorophyll vertical distribution and primary production (Morel & Berthon 1989, Hoepffner et al. 1999) was shown for a number of regions. It has been shown from these data that the chlorophyll concentration in the upper layer might be used as an index of changes in water productivity i.e. primary production on a scale of hundreds of km. Changes of primary production on this scale are accompanied by changes of species, plankton community size structure, and biomass ratio between phytoplankton, bacteria, protists, and mesozooplankton. In contrast to upwelling regions, high species diversity and a complex trophic web, which is affected by the size of the phytoplankton cells, can characterize the pelagic communities of oligotrophic waters in the tropical and subtropical regions. Picoplankton (<1 µm) and nanophytoplankton (1 to 5 µm) comprises the major part of phytoplankton biomass (Olson et al. 1990, Li 1995, Buck et al. 1996) and serves as a major food resource for heterotrophic microplankton (Burkill et al. 1993, Harrison et al. 1993, Verity et al. 1993).

Microheterotrophs make up over 50% of the total metabolism of the heterotrophic part of the community and carbon flux from primary production to zooplankton (Williams 1981, Bender et al. 1992, Fasham et al. 1999, Bode et al. 2001). Mesozooplankton consumes a minor part of phytoplankton primary production (Moralis et al. 1991, Dam et al. 1993, Harrison et al. 1993). However, due to the balance of production processes in the plankton community, mesozooplankton biomass increases with the rise of phytoplankton production and chlorophyll concentration.

The results of continuous measurements of zooplankton abundance and biomass by optical plankton counters in a range from 0.25 to 8.0 mm have indicated that minimal values are typical for the oligotrophic South Atlantic Subtropical Gyre and oligotrophic Canary Basin along a transect from 49° N to 46° S (Gallienne & Robins 1998). Values were 20 times higher in the equatorial region and 10 times higher in the waters near the West African upwelling. Sampling along a transect from 30° N to 50° S (Galbert & Agusti 1999) resulted in similar correlated changes of copepod abundance and chlorophyll concentration. This reinforces the known fact that autotrophic and heterotrophic production is more balanced in tropical waters than in higher latitudes.

Vinogradov & Shushkina (1987), working with the plankton communities of the coastal upwelling regions of Peru, reported the imbalance between primary production and its utilization by heterotrophs. This imbalance results in a weak correlation between phyto- and zooplankton biomass (Gibbons & Hutchings 1996). Overall, despite the spatial heterogeneity of distributions of the plankton, the observed general tendency is that the biomass of mesozooplankton and other heterotrophs declines with the decline of primary production and phytoplankton biomass.

Micro- and mesozooplankton consume phytoplankton and its production, therefore their distributions in space and time should be linked. However, these links are extremely difficult to verify statistically due to their multiscale spatial-temporal origins (Piontkovski & Williams 1995). From the point of view of ocean-monitoring of variables by satellite, zooplankton can be considered as a 'filter' impacting, through trophic interactions, on the oceanic phytoplankton and primary production fields (Banse 1994). It is also known that zooplankton plays a significant role in vertical transport of carbon within marine ecosystems, forming the so-called 'biological pump' (Longhurst & Harrison 1989).

We confined our work to the upper 100 m layer because in the subtropical and tropical regions, the major part of phyto- and mesozooplankton biomass is concentrated here. Our objectives were to compare the distribution of the chlorophyll concentration with that of the mesozooplankton biomass for the open ocean system and coastal zone, and to examine the relationship between primary production, phytoplankton, and mesozooplankton stocks. In particular, we applied correlation analysis to ascertain whether there are defined co-variation patterns between chl *a* and mesozooplankton biomass.

MATERIAL AND METHODS

Chlorophyll data. ***Methods:*** Water samples for chl *a* and phaeopigments were filtered through membrane filters (effective pore size 0.45 to 0.6 µm) and Whatman GF/F glass-fiber filters (effective pore size 0.7 µm) and pigments were extracted in 90% acetone. After extraction, chl *a* and its degradation products were measured using standard fluorometric (Jeffrey et al. 1997) and spectro-photometric (Jeffrey & Humphrey 1975) methods. Phaeopigment concentration was not used in this work because the fluorometric method often over estimates the concentration of phaeopigments due to the abundant prokaryotes in the tropical waters and presence of chlorophyll *b* (Neveux & Lantoine 1993).

Field data: The database contains data from sampling carried out from 1968 to 1992 by national and international programs of the Former Soviet Union (FSU), United Kingdom, France, Canada, Spain, and Germany. The chl *a* data was obtained from the National Oceanographic Data Center (NODC) (USA) and Banque National de Données Oceanographiques Brest (BNDO) (France) data banks. Chlorophyll measurements from 1435 stations, which were collected during expeditions of the National Ukrainian Academy of Sciences (NUAS), extended these data. Ukrainian data comprised 35% of NODC and BNDO data sets (Table 1). The total database has 4178 stations with measurements of chl *a*, of which 3992 were selected to extract the 0–10 m data in the coastal and open ocean regions. The spatial pattern of sampling was irregular (Fig. 1). Station sampling was partially carried out in a form of grids, with a spatial resolution of 20 km between stations. The winter-spring period was not as well represented as the summer-autumn period, in spite of its importance in the seasonal cycle of the phytoplankton activity. Prior to data analysis, the following editing and data compilation techniques were applied: (1) repeated stations were excluded; (2) stations with obvious mistakes in values of chl *a* were deleted; (3) stations with measurements carried out by a submersible profiling fluorometer were excluded; (4) data for the stations with diel time series were averaged (i.e. one average value for the whole diel time series was used). In general, our analysis and synthesis of data provides a new data base, which is valuable for the analysis of the meso- and macroscale variability of chl *a* in the tropical and subtropical regions of the Atlantic Ocean.

Data processing: The edited data were sorted and distributed over the 8 biogeochemical provinces (see Table 3 for names and abbreviations) of the subtropical and tropical Atlantic Ocean (Fig. 1) proposed by Longhurst (1995, 1998). Data partitioning was necessary to allow us to estimate chlorophyll concentration and compare the mesozooplankton/chlorophyll relationships over biogeochemical provinces. Two seasonal periods were used in the data analysis: from December to May and from June to November. These periods agree with a flat U-shaped seasonal variation of CZCS surface chlorophyll recently reviewed by Yoder et al. (1993), Banse & English (1994), and Longhurst (1998) in subtropical and tropical regimes. The distribution of the stations within the geographical provinces for the summer-autumn and winter-spring periods is shown in Fig. 1.

The data set from 1968 to 1992 (4178 stations) was also used to select data to obtain the relationship between the water column chlorophyll concentration (0 to 100 m) and the near-surface chlorophyll (0 to 10 m). Analyses were conducted for 1614 vertical profiles, of which approximately 70% were located in the eastern part of the ocean. This total was made up of 1339 profiles from the deep-sea regions and 275 profiles off the continental shelves. Sampling was carried out to depths of 100 or 150 m, with a vertical resolution of 5 to 25 m. Using the trapezoid rule, chlorophyll concentration in discrete depth intervals was integrated throughout the water column. To approach a normal distribution, logarithmic values of data were used. The following equation was derived:

$$\log \mathrm{chl}_{(\mathrm{tot})} = 1.75 \pm 0.16 + 0.527 \pm 0.01 \log \mathrm{chl}_{(0)}$$

or:

$$\mathrm{chl}_{(\mathrm{tot})} = 56.2\ \mathrm{chl}_{(0)}{}^{0.527} \quad (1)$$

for $0.01 \le \mathrm{chl}_{(0)} \le 10$ mg m^{-3}; $5 \le \mathrm{chl}_{(\mathrm{tot})} \le 100$ mg m^{-2}; n = 1614; $r^2 = 0.62$; $p < 0.001$; SE (standard error of regression line) = 0.157, where $\mathrm{chl}_{(0)}$ is concentration of chl *a* (mg m^{-3}) in the upper layer (0 to 10 m) and $\mathrm{chl}_{(\mathrm{tot})}$ is concentration (mg m^{-2}) in the 0 to 100 m layer. According to Eq. (1), the measured $\mathrm{chl}_{(\mathrm{tot})}$ values might differ 2 times from the calculated ones, following $E_r = 10^{2\mathrm{SE}}$, where E_r is a relative error (Vinogradov et al. 1999).

To estimate phytoplankton biomass in carbon units, the following equation was applied:

$$B = \mathrm{chl}_{(\mathrm{tot})}\,\theta \quad (2)$$

where B is phytoplankton biomass (mg C m^{-2}) and θ is the average weighted ratio between organic carbon of phytoplankton and the chlorophyll concentration in the 100 m layer. Values of θ were calculated from measurements (Li et al. 1992, 1993, Buck et al. 1996) and modeling of seasonal and vertical changes of θ over different regions of the Atlantic Ocean (Taylor et al. 1997). In the provinces of the North subtropical gyre (NAST), South Atlantic gyre (SATL), Tropical gyre (NATR), and Western tropical Atlantic (WTRA), θ was taken as 60 g C g chl a^{-1}, but was 50 g C g chl a^{-1} for the provinces ETRA (eastern tropical Atlantic), GUIN (Guinea coastal boundary), and CNRY (eastern coastal boundary) for all seasons.

Table 1. Sources of data for chlorophyll data base. IBSS = Institute of Biology of the Southern Seas, NASU, Sevastopol, Ukraine (see www.ibss.iuf.net); MHI = Marine Hydrophysical Institute, NASU, Sevastopol, Ukraine (see www.mhi.iuf.net); BNDO = Banque National de Données Oceanographiques, Brest, France (see www.ifremer.fr:582/sismer/sismer/banque_nat_ag. htql); NODC = National Oceanographic Data Center, Silver Spring, Maryland, USA (see www.nodc.noaa.gov/OC5/indwod98. html); BODC/BOFS = British Oceanographic Data Centre/BOFS CD-ROM (see www.bodc.ac.uk/); FOCAL = Programme Francais Ocean et Climat Atlantique Equatorial

Time period	Ship and cruise no./ data set name	Region of Atlantic	Source	Number of stations/ data used
1968: May	U7EX	North subtropical	NODC	6/6
1971: Jan–Feb	X6	Morocco upwelling	NODC	12/12
1972: Oct–Nov	PLA	Bay of Biscay	NODC	7/7
1973: Apr–May	PH32	Northeast	NODC	27/27
1974: Mar	CR	Cape Blanc region	NODC	39/39
1974: Mar–Apr	CH	Cape Blanc region	NODC	78/78
1974: Mar–May	AD14	Cape Blanc region	NODC	56/56
1974: Mar–May	AD18	Cape Blanc region	NODC	126/126
1976: Sep–Oct	GM	Canary Islands region	NODC	75/75
1978: Jul–Aug	NZ	Gulf of Guinea	NODC	51/51
1978: Aug–Sep	Capricorne, 1	East equatorial	BNDO	63/62
1978: Aug–Sep	SU	East equatorial	NODC	59/58
1979: Feb	SOP1	East equatorial	NODC	13/13
1979: Apr	Capricorne, 2	East equatorial	BNDO	29/29
1979: May	K110	Central equatorial	NODC	159/158
1979: Jun–Jul	Capricorne, 3	Gulf of Guinea	BNDO	49/48
1979: Oct–Nov	Capricorne, 4	East equatorial	BNDO	79/73
1979: Dec–1980: Jan	Vodyanitsky, 7	Cape Blanc region	IBSS Archives (1980)	49/49
1980: Jan	Capricorne, 5	East equatorial	BNDO, FOCAL 1	17/16
1980: Jan	Lomonosov, 38	Conakri region	MHI Archives (1980a)	33/25
1980: Nov	Lomonosov, 40	Conakri region	MHI Archives (1980b)	5/5
1981: Aug–Sep	X25	Portugal coast	NODC	8/8
1981: May	Z	Central subtropical	NODC	9/8
1981: Dec–1982: Jan	Vodyanitsky, 11	South subtropical	IBSS Archives (1982a)	80/80
1982: Jul	Capricorne, 6	Equatorial	BNDO (FOCAL 2)	45/42
1982: Jul–Oct	Vodyanitsky, 13	Tropical and central	IBSS Archives (1982b)	126/117
1983: Jan–Feb	Capricorne, 7	Tropical and equatorial	BNDO (FOCAL 3)	50/48
1983: Mar–Apr	IF	Cape Blanc region	NODC	52/52
1983: Mar–Apr	Meteor, 1	Cape Blanc region	NODC	83/73
1983: Apr	V302	West subtropical	NODC	25/25
1983: Jul–Aug	Capricorne, 8	Tropical and equatorial	BNDO (FOCAL 4)	88/86
1984: Jan–Feb	Capricorne, 9	Tropical and equatorial	BNDO (FOCAL 5)	92/92
1984: Mar	Meteor, 2	Cape Blanc region	NODC	17/17
1984: Apr	Meteor, 3	Cape Blanc region	NODC	20/20
1984: Jul–Aug	Capricorne, 10	Tropical and equatorial	BNDO	96/91
1984: Dec	V449	West Sargasso Sea	NODC	7/6
1985: Jun–Aug	Vernadsky, 32	West tropical	MHI Archives (1985)	164/164
1985: Aug	V520	West Sargasso Sea	NODC	4/2
1985: Nov–Dec	Vodyanitsky, 20	Tropical	IBSS Archives (1985b)	29/29
1986: Jun–Aug	Capricorne, 11	East tropical	BNDO	154/152
1986: Jul	U7DI	East subtropical	NODC	1/1
1986: Sep–Oct	Vernadsky, 34	West tropical	MHI Archives (1986a)	238/238
1986: Oct–Dec	Vodyanitsky, 21	Tropical	IBSS Archives (1986)	48/48
1986: Nov	Lomonosov, 47	East tropical	MHI Archives (1986b)	281/277
1987: Jun–Jul	Vernadsky, 36	West tropical	MHI Archives (1987)	234/234
1987: Jun–Jul	Hudson, 1	Northwest subtropical	BNDO	16/12
1987: Jun–Jul	V722	West Sargasso Sea	NODC	105/102
1987: Jul–Oct	Vodyanitsky, 24	Tropical	IBSS Archives (1987)	91/58
1988: Sep	Hudson, 2	Northwest subtropical	BNDO	16/16
1988: Sep	V826	West Sargasso Sea	NODC	15/15
1989: Mar	SE1	Central subtropical	NODC	7/0
1989: Mar–Apr	DR1	Central subtropical	NODC	20/20
1989: Apr	DR2	East subtropical	NODC	21/12
1989: Apr	SE	Central subtropical	NODC	23/23
1989: Apr–May	A2	North sutropical	NODC	34/30
1989: Apr–May	V903	West tropical	NODC	29/29

Table 1 (continued)

Time period	Ship and cruise no./ data set name	Region of Atlantic	Source	Number of stations/ data used
1989: May	A3	North tropical	NODC	23/23
1989: May	DR3	East subtropical	NODC	30/30
1989: May–Jun	DR4	Northeast tropical	NODC	20/16
1989: Aug–Sep	N8	Northeast tropical	NODC	9/8
1989: Sep–Dec	Vodyanitsky, 29	Morocco upwelling and Gulf of Guinea	IBSS Archives (1989)	57/41
1989: Oct–1990: Sep	Sg	West subtropical	NODC	52/52
1989: Nov–1990: Sep	Sb	West subtropical	NODC	15/15
1990: Apr	D001	West subtropical	NODC	30/25
1990: Apr–May	N9	East tropical	NODC	14/14
1990: Apr–Jun	BOFS	NE and Morocco	BODC/BOFS	334/320
1991: Apr	D101	West	NODC	12/12
1991: Apr–May	D17	Northwest tropical	NODC	81/81
1992: Sep–Oct	D237	NW and Morocco	NODC	62/62
1992: Sep–Oct	Hudson, 3	NW and Morocco	BNDO	63/53
1992: Dec	Jean Charcot	Cape Blanc	J. Neveux pers. comm.	16/13
Total				4178/3992

Zooplankton data. ***Methods:*** The plankton samples were collected by Bogorov-Rass nets and the oceanic model of the Juday nets (80 cm mouth diameter) with mesh sizes of 178 and 200 µm. All tows were taken in a vertical or oblique manner in the upper 100 to 0 m and hauled at a speed of approximately 0.5 m s^{-1}. Typically, 50 m^3 of water was filtered by the net during the collection of each sample. The filtered volume was estimated from the length of the wire out, mouth diameter of the net and duration of tow. The wet weight of samples was obtained either by displacement volume (precision ± 0.1 ml), assuming the specific gravity of

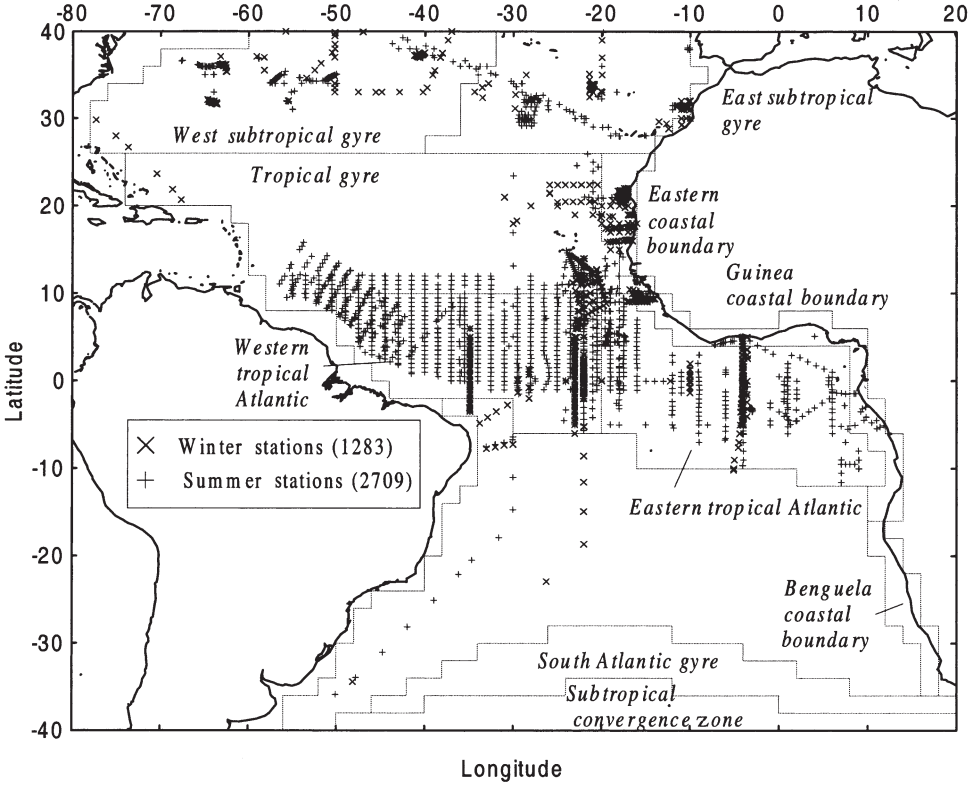

Fig. 1. Chl *a* measurements in the upper 10 m layer. Stations from expeditions conducted in summer-autumn (June to November) and winter-spring (December to May) periods (1968–1992)

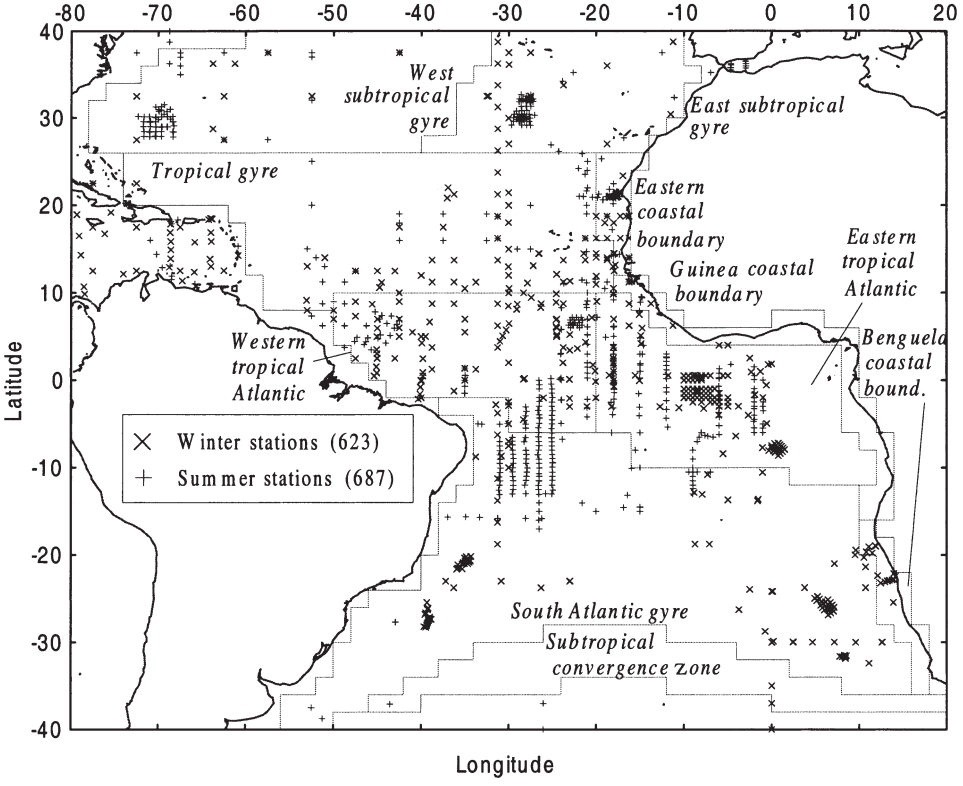

Fig. 2. Mesozooplankton measurements in the upper 100 m. Stations from expeditions of the Former Soviet Union for summer-autumn (June to November) and winter-spring (December to May) periods (1950–1989)

seston to be 1 g cm^{-3}, or by wet weighing, after blotting, using a balance (precision ± 0.1 mg). Organisms larger than 30 mm and all jelly fish (medusas, salps, and ctenophores) were removed from the samples before determining the weight or volume. Jelly fish were excluded when determining the weight of the mesozooplankton.

Field data: The data on mesozooplankton biomass at 1310 stations from 40 FSU expeditions to the Atlantic Ocean (1950–1989) were used (Fig. 2, Table 2). These stations were obtained from archives of Marine Hydrophysical Institute (MHI) and Institute of Biology of the Southern Seas (IBSS) and some of them (179) were taken from publications. The network of national programmes and the spatial resolution of sampling was irregular (Fig. 2). Certain stations had fine spatial resolution, ca. 10s of km, and were performed in station grids. The hauls were taken over many seasons and years and at different times of the day. Prior to data analysis, the following editing and data compilation were applied: (1) stations with obvious mistakes in the values of mesozooplankton biomass were excluded; (2) data for the stations with diel time series were averaged and one average value was used; (3) data were not used when an excessive amount of phytoplankton or detritus was noted in the seston samples.

The number of stations with mesozooplankton following the above analysis was 1124. The maximum number of stations (745) was in the following 3 provinces: WTRA (230), ETRA (231), and SATL (284). The minimal number of stations was in CNRY (67) and the GUIN (11). The total number of stations for the winter-spring and summer-autumn seasons were almost equal (537 and 587 respectively).

Carbon biomass conversions: Mesozooplankton biovolume was converted to carbon using a factor of 0.05 g C cm^{-3}. To convert wet weight (W_w) into dry weight (W_d), the formula $W_w = 6.25 W_d$ (Vinogradov & Shushkina 1987) was used. The relationship $W_c = 0.31 W_d$ (Wiebe 1988) converted dry mesozooplankton biomass into carbon (W_c).

Basin-wide maps. Data on chlorophyll concentration (0 to 10 m) and mesozooplankton biomass of the upper 0 to 100 m layer enabled us to reconstruct the spatial distribution on a scale of the whole tropical and subtropical Atlantic Ocean (Figs. 3 & 4). The Surfer Golden Software (USA) package was applied to design the macroscale field of chlorophyll and mesozooplankton. The Kriging gridding method (Cressie 1991) and smoothing of the grid matrix, with the weight of matrix center = 2, and the distance- weighting power = 2, were applied to create the map.

The mean of all measurements at stations over provinces were calculated to estimate chlorophyll in the upper 10 m and mesozooplankton in the upper 100 m (Table 3).

Table 2. Sources of data for mesozooplankton data base

Time period	Ship and cruise no.	Region of Atlantic	Source	Stn
1950: Jan	Grot, 1	Guinea coast	Semenova (1961), Chromov (1962)	5
1958: Mar–May	Lomonosov, 2	Central subtropical	Vladimirskaya (1972)	5
1958: Nov	Chukovsky, 1	Guinea coast	Chromov (1965)	2
1959: May	Lomonosov, 5	Meridional section	Kanaeva (1962, 1973)	48
1959: Aug–Dec	Lomonosov, 6	Central subtropical	Yashnov (1962)	46
1960: Jan–Apr	Lomonosov, 7	Central subtropical and Cape Blanc	Kanaeva (1962, 1973)	18
1960: Jul–1961: Jan	Lomonosov, 8	Central subtropical and Cape Blanc	Kanaeva (1962), Yashnov (1962)	11
1961: Mar	Lomonosov, 10	Guinea coast	Chromov (1965)	9
1962: Oct	Lomonosov, 12	Guinea coast	Chromov (1965)	4
1963: Mar–May	Lomonosov, 13	Central equatorial and Guinea coast	Greze (1971)	21
1963: Sep–Oct	Lomonosov, 14	Central equatorial	Greze (1971), MHI Archives (1963)	49
1964: Aug	Ak. Kovalevsky	Cuba coast	Kolesnikov & Kovaleva (1973)	2
1964: Dec–1965: Feb	Lomonosov, 17	Carribean Sea and Northwest	MHI Archives (1965)	21
1964: May	Lomonosov, 15	West tropical	MHI Archives (1964), Greze (1971)	27
1967: Jan–Mar	Kurchatov, 1	Carribean Sea, Guinea coast	Lubni-Gercik (1972, 1975), Kovalevskaya et al. 1968)	12
1969: Mar	Kurchatov, 3	West tropical	Lubni-Gercik (1972, 1975)	4
1969: Dec–1970: Mar	Lomonosov, 24	Central and Morocco	Kolesnikov & Kovaleva (1973)	13
1970: Nov–Dec	Vernadsky, 3	Carribean Sea	MHI Archives (1970)	30
1971: Nov	Kurchatov, 11	South Central	Voronina (1975)	2
1972: Apr–May	Lomonosov, 26	Central equatorial and Benguela	MHI Archives (1972)	42
1973: Jan–Mar	Kurchatov, 14	Carribean Sea	Lubni-Gercik (1975)	11
1973: Jan–Mar	Lomonosov, 27	South subtropical	Greze et al. (1984)	8
1974: JanApr	Vernadsky, 8	Central tropical	MHI Archives74a	53
1974: Feb–Apr	Lomonosov, 28	Central equatorial and Guinea coast	MHI Archives (1974b)	36
1974: Nov	Vernadsky, 9	W Mediterranean	MHI Archives (1974c)	8
1976: Jun–Jul	Lomonosov, 30	South subtropical	Greze et al. (1984)	9
1976: Jul	Vernadsky, 13	Mediterranean	MHI Archives (1976)	1
1977: Jun–Aug	Lomonosov, 32	Central equatorial	Greze et al. (1984)	112
1977: Jul–Aug	Vernadsky, 16	Sargasso Sea	MHI Archives (1977)	50
1977: Oct–Nov	Vodyanitsky, 3	East subtropical	IBSS Archives (1977)	23
1978: Feb–Apr	Est.Oktaybr	Easr equatorial	ATLANTNIRO archives (1978)	48
1978: Dec–1979: Feb	Vodyanitsky, 5	Southeast subtropical	IBSS Archives (1979)	72
1981: Dec–1982: Jan	Vodyanitsky, 11	South subtropical	IBSS Archives (1982a)	98
1982: Jul–Oct	Vodyanitsky, 13	Meridional grids	IBSS Archives (1982b)	142
1984: Aug	Vernadsky, 28	West tropical	MHI Archives (1984a)	17
1984: Aug–Oct	Vernadsky, 29	West tropical	MHI Archives (1984b)	30
1984: Dec–1985: Feb	Vodyanitsky, 18	East Equatorial	IBSS Archives (1985a)	42
1986: Oct–Nov	Vodyanitsky, 21	East Equatorial	IBSS Archives (1986)	46
1987: Jul–Sep	Vodyanitsky, 24	East Equatorial	IBSS Archives (1987)	78
1989: Oct–Dec	Vodyanitsky, 29	East Equatorial and Cape Blanc	IBSS Archives (1989)	55
Total:				1310

Data sets of chlorophyll—mesozooplankton relationship. To analyse relationships between chlorophyll concentration in the 0 to 10 m layer, and mesozooplankton biomass in the 100 m layer, the subtropical and tropical Atlantic was partitioned over 3° × 3° trapeziums and mean parameter values were estimated for each. Trapeziums containing data for only 1 parameter were excluded from the analysis. In the 3° trapeziums, the average number of measurements was 6 to 20 for chl *a* and 2 to 8 for mesozooplankton biomass.

RESULTS

In spite of the sampling carried out during different expeditions, seasons and years, the macroscale patterns of chl *a* and mesozooplankton biomass presented in Figs. 3 & 4 show similarities in their distributions.

The chl *a* and zooplankton biomass increased from oceanic to neritic waters. In the central regions of the NAST and SATL gyres, chl *a* and mesozooplankton biomass levels were low. In the winter-spring season, chl *a* and zooplankton biomass over the northern and eastern periphery of the subtropical gyre were higher than those observed in the summer-autumn period. Details of patterns of isolines of biomass and their geometry changed over the seasons: the zooplankton distributions through and around the equatorial region were more heterogeneous than those of chl *a*, especially in the summer-autumn season.

The average biomass for the 8 provinces covering the subtropical and tropical zones allowed a compari-

Table 3. Average chl *a* concentration and range for surface layer (0 to 10 m, mg m^{-3}) and mesozooplankton (MZ) biomass in wet weight in the upper 100 m layer (mg m^{-3}). In brackets: minimal and maximal values; n: number of measurements; Ave: mean; SD: Standard deviation

Province	Chl *a*			Mesozooplankton			Chl *a*/MZ
	n	Avg.	SD	n	Avg.	SD	$\times 10^{-3}$
Summer–autumn (June to November)							
East subtropical gyre (NAST, E)	168	0.37 (0.01–3.17)	0.62	75	24 (21–80)	13	15.0
West subtropical gyre (NAST, W)	182	0.10 (0.03–0.43)	0.05	68	70 (18–250)	44	1.4
Tropical gyre (NATR)	527	0.14 (0.01–0.73)	0.10	56	110 (3–1000)	154	1.2
Western tropical Atlantic (WTRA)	962	0.16 (0.01–3.93)	0.18	124	113 (8–800)	111	1.4
Eastern tropical Atlantic (ETRA)	757	0.29 (0.01–3.56)	0.24	115	132 (67–450)	66	2.2
South Atlantic gyre (SATL)	31	0.09 (0.02–0.19)	0.04	118	79 (15–411)	62	1.1
Eastern coastal boundary (CNRY)	17	0.87 (0.17–3.75)	0.86	27	162 (3–700)	178	5.3
Guinea coastal boundary (GUIN)	65	0.76 (0.10–4.57)	0.88	4	399 (27–1000)	419	1.9
Sub-total:	2709			587			
Winter–spring (December to May)							
East subtropical gyre (NAST, E)	111	0.44 (0.04–2.64)	0.37	25	81 (49–120)	24	5.4
West subtropical gyre (NAST, W)	154	0.35 (0.04–2.06)	0.34	15	88 (50–250)	48	3.9
Tropical gyre (NATR)	76	0.18 (0.03–0.885)	0.17	75	379 (20–3000)	461	0.5
Western tropical Atlantic (WTRA)	303	0.11 (0.01–0.33)	0.05	96	212 (27–1060)	202	0.5
Eastern tropical Atlantic (ETRA)	128	0.15 (0.06–0.67)	0.10	116	240 (40–1000)	177	0.6
South Atlantic gyre (SATL)	39	0.08 (0.02–0.50)	0.09	163	73 (3–1088)	121	1.1
Eastern coastal boundary (CNRY)	441	3.75 (0.03–21.75)	3.12	40	818 (6.5–3000)	820	4.6
Guinea coastal boundary (GUIN)	23	0.74 (0.10–3.58)	0.58	7	1247 (530–3000)	830	0.6
Sub-total:	1283			537			

son of the productivity and chlorophyll:mesozooplankton ratios over the regions (Table 3). The biogeochemical provinces differed in their average values of chl *a* and mesozooplankton biomass. At the same time, the coefficients of variation are fairly similar and high. On average, values of the chlorophyll and mesozooplankton in the oceanic provinces differ by 4 to 5 times, while this difference is 1 order of magnitude between oceanic and neritic provinces. High chl *a* values were observed in the NAST, especially in its eastern part (near upwelling off Morocco and Portugal) in the summer-autumn period (Fig. 2). There, chl *a* values were 0.5 to 1.0 mg m^{-3} but they did not exceed 0.1 mg m^{-3} in the central part of the gyre. In the NAST (E), zooplankton biomass was low with values of 24 to 82 mg m^{-3} against a background of high annual chl *a* biomass (Table 3). There was a similar zooplankton average biomass in the SATL and WTRA, but the chl *a* values were 3 times lower in the SATL gyre. In the provinces of the WTRA and NATR gyres, chl *a* was 0.14 to 0.18 mg m^{-3}, while the mesozooplankton biomass differed several times and was higher than in the NAST province.

The chlorophyll:zooplankton biomass ratio was not stable throughout the year (except in the SATL province). In the summer-autumn, this ratio was 2 times higher than in the winter-spring period. In the 5 provinces (NAST [E], NATR, WTRA, ETRA, and GUIN), a 2.5 to 4 times increase in the ratio was noted from the winter-spring to summer-autumn periods.

However, this ratio was higher in the summer-autumn period in NAST (W) and it was permanently high in the SATL throughout the year. The maximum ratio was observed in the NAST (E) and its adjacent neritic province (CNRY) for both periods. In the other oceanic provinces, ratios were 5 to 10 times lower; i.e. there was more mesozooplankton biomass per phytoplankton biomass in these provinces.

If data on chl *a* and zooplankton are averaged within the provinces and these averaged values are compared, no correlation is observed between chl *a* and zooplankton on a basin-wide scale.

To analyse mesozooplankton-chl *a* relationships in detail, average values of both parameters were calculated for 3° × 3° trapeziums. The positions of the graph points have an elliptical type trajectory for both periods (Fig. 5b,f). In a range of chl *a* from 0.2 to 1.0 mg m^{-3}, different zooplankton biomass values correspond to the same chl *a* concentration. Several reasons can be put forward to explain this pattern. First, the pattern obtained is a random one due to correspondence of data to various seasons and years. Second, mesozooplankton-chl *a* relationships can change over regions and depend upon a number of trophic levels. Third, the pattern observed is due to biotic interactions (like the 'predator-prey' system), where the increase of phyto- and mesozooplankton biomass takes place with a time lag (as is known for polar and temperate regions).

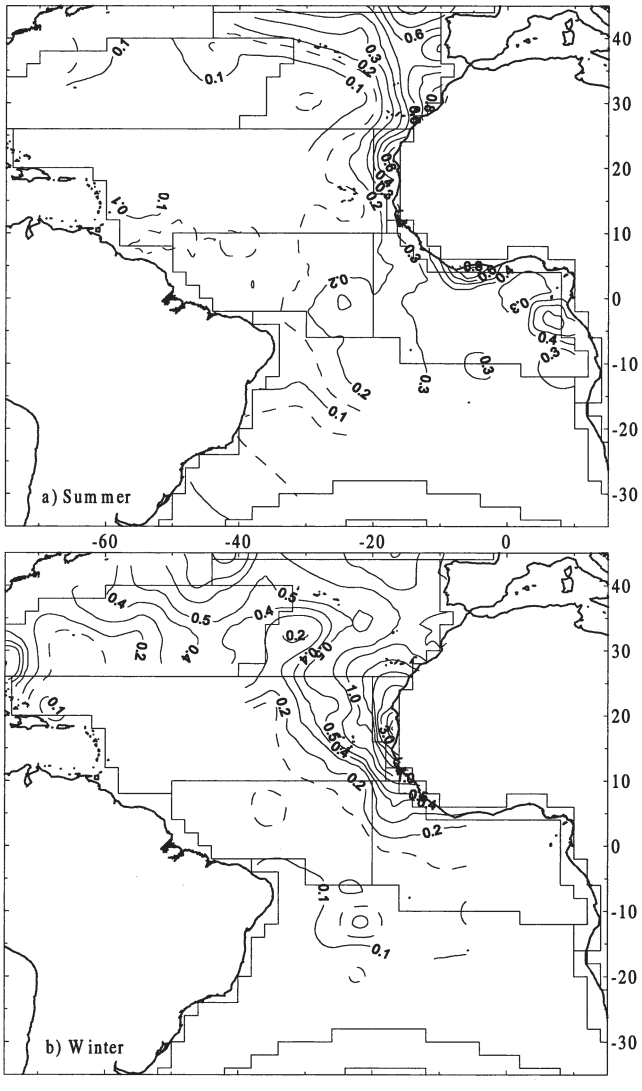

Fig. 3. Spatial distribution of chl *a* (mg m^{-3}, 0 to 10 m) for (a) summer–autumn (June to November) and (b) winter–spring (December to May)

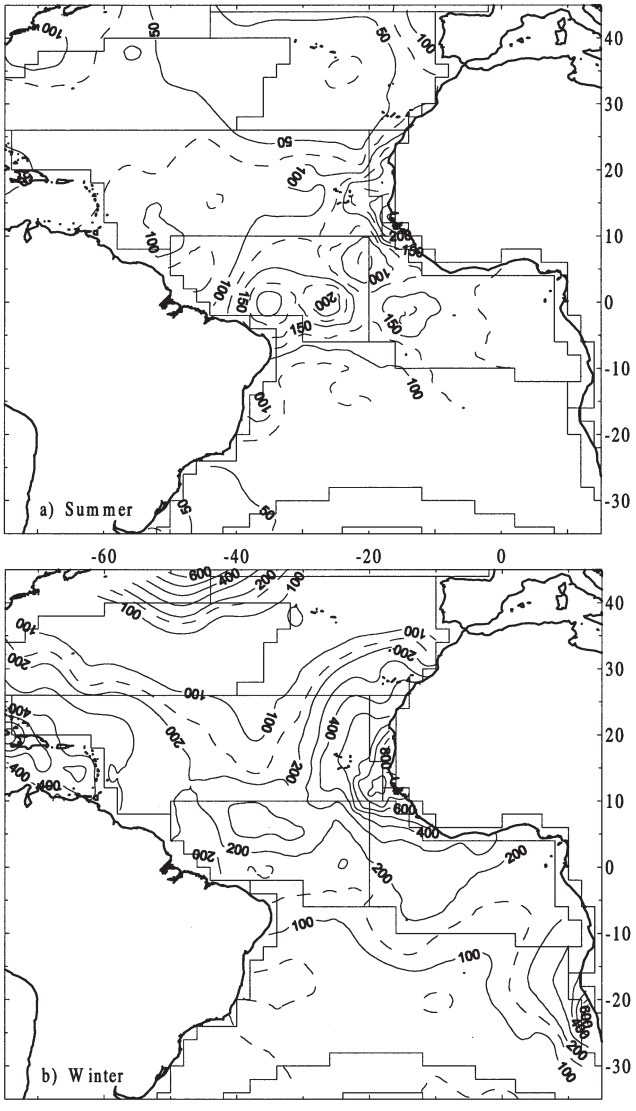

Fig. 4. Spatial distribution of mesozooplankton biomass (mg m^{-3}, 0 to 100 m, wet weight) for (a) summer–autumn (June to November) and (b) winter–spring (December to May) periods

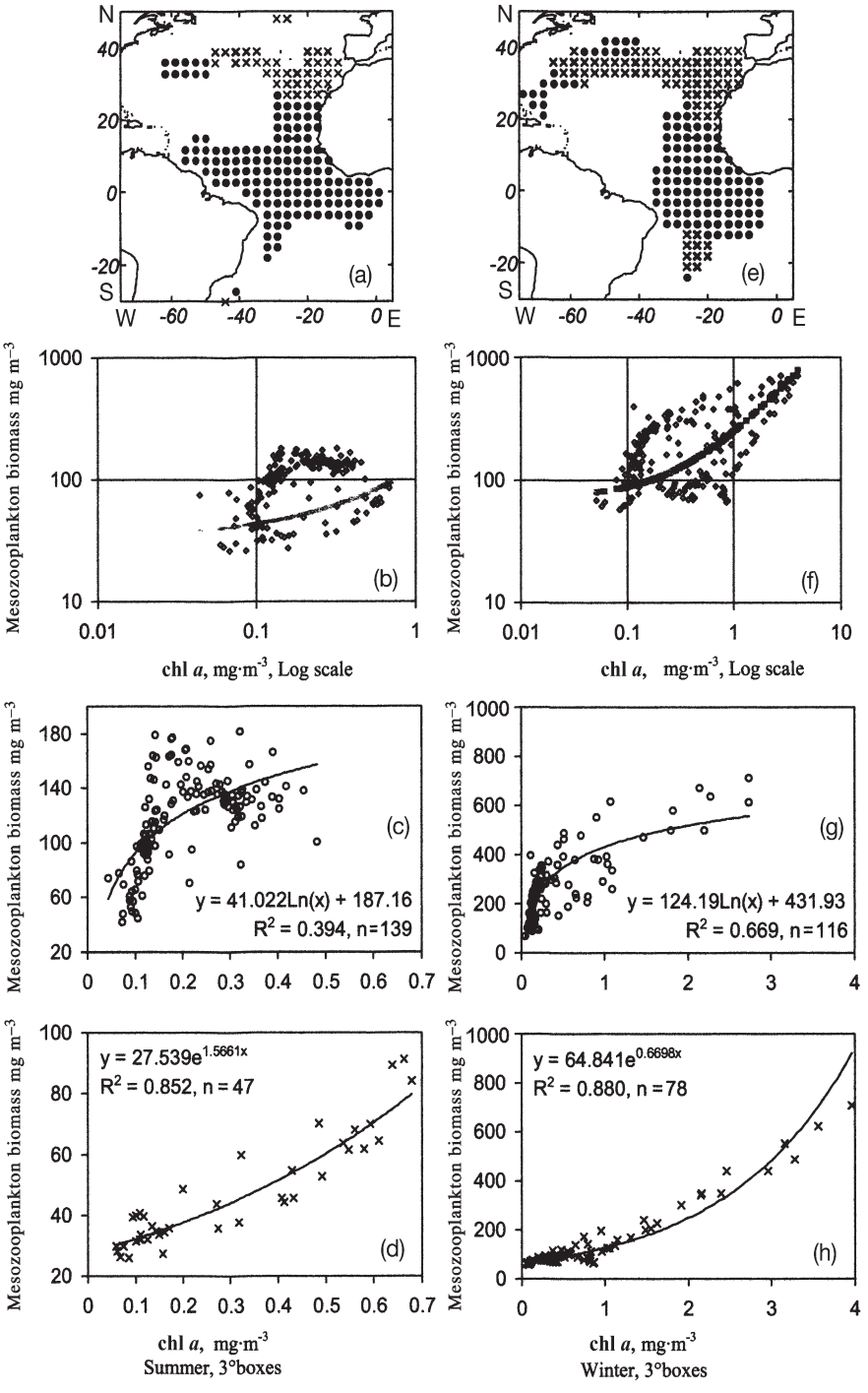

Fig. 5. Relationships between average mesozooplankton biomass (mg m^{-3}; 0–100 m) and chl *a* concentration (mg m^{-3}, 0 to 10 m) in the subtropical and tropical Atlantic Ocean for 3° × 3° grids, for June to November and December to May: (a) and (e): distribution of stations with low (**x**) and high (•) mesozooplankton:chl *a* ratios, for summer-autumn and winter-spring, respectively; (b) and (f): changes of mesozooplankton biomass in relation to chl *a* concentration for summer-autumn and winter-spring, respectively; (c) and (g): relations between mesozooplankton biomass and chl *a* concentration in provinces of the NATR, WTRA, ETRA, and GUIN for summer-autumn and winter-spring, respectively; (d) and (h): relationship between mesozooplankton and chl *a* concentration in provinces of the NAST, SATL, and CNRY for summer-autumn and winter-spring, respectively

To test these hypotheses, the whole data set (Fig. 5b) was partitioned into the upper and lower parts along the major axis of the ellipse. The lower part of the data set could be mostly attributed to the SATL, NAST and its adjacent neritic province (Fig. 5a,e). The upper part of the data came from the 5 other provinces covering the tropical zone. When the data were averaged in 1° × 1° trapeziums, the pattern observed in the mesozooplankton-chl *a* relationship was still the same as the 3° trapeziums and the data (from the upper and low parts of the ellipse in Fig. 6b) did not change their positions (Figs. 5a & 6a) and curved shape (Figs. 6c,d). Thus, we conclude that the observed pattern in the mesozooplankton-chl *a* relationships is not a random one. Mesozooplankton biomass was positively related to the chlorophyll concentration. The coefficient of determination was in the range from 0.39 to 0.88 with an average of 0.7 (Fig. 5c,d,g,h). Low coefficient values were obtained for the summer-autumn period (Fig. 5c). Possibly, the parabolic relationship we used is not an optimal way to parameterise this link. For instance, the third order polynomial ($y = 9085x^3 - 8388x^2 + 2457x - 91$) increased r^2 to 0.6 for data in Fig. 5c. Although r^2 increased 1.5 times, the results obtained using these 2 algorithms only differed by 13%. Therefore we decided to use the parabolic approximation.

In the SATL, NAST and its adjacent neritic province (CNRY), mesozooplankton biomass increased exponentially to chl *a* concentration. (Fig. 5c,g). This relationship held in the range of chl *a* to 0.7 mg m^{-3} in summer and to 4.0 mg m^{-3} in the winter period. The slope of the curve changes from 0.67 in the winter-spring period to 1.57 in the summer and autumn. The growth of zooplankton biomass with the increase of chlorophyll concentration was lower in the tropical provinces (NATR, WTRA, and ETRA), which had narrow and numerous zones of local upwelling and downwelling (Fig. 5c,g). The one order of magnitude increase of chl *a*, from 0.3 to 3.0 mg m^{-3}, was only

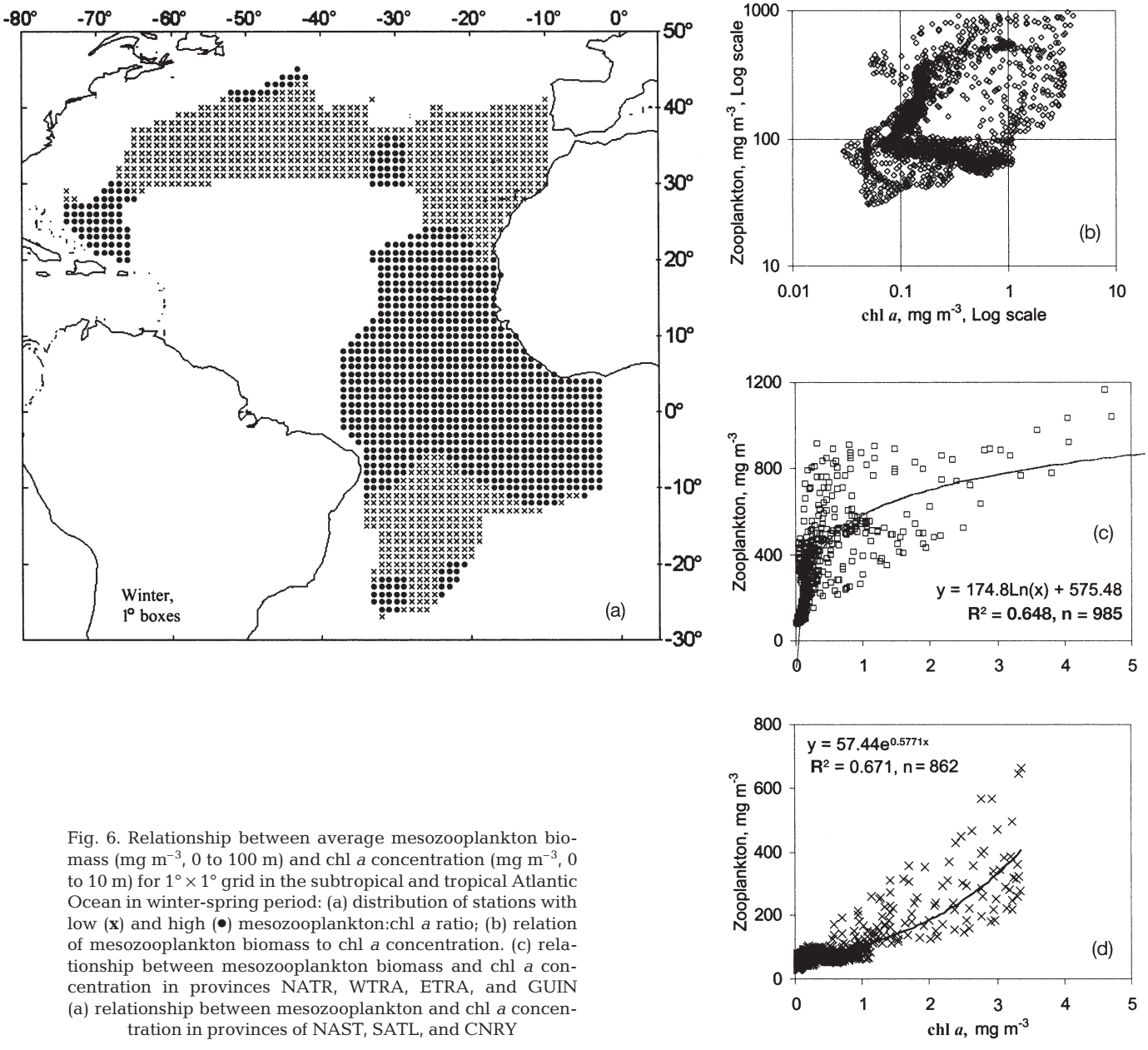

Fig. 6. Relationship between average mesozooplankton biomass (mg m^{-3}, 0 to 100 m) and chl *a* concentration (mg m^{-3}, 0 to 10 m) for 1° × 1° grid in the subtropical and tropical Atlantic Ocean in winter-spring period: (a) distribution of stations with low (**x**) and high (•) mesozooplankton:chl *a* ratio; (b) relation of mesozooplankton biomass to chl *a* concentration. (c) relationship between mesozooplankton biomass and chl *a* concentration in provinces NATR, WTRA, ETRA, and GUIN (a) relationship between mesozooplankton and chl *a* concentration in provinces of NAST, SATL, and CNRY

accompanied by a doubling of mesozooplankton-chlorophyll relationships (Fig. 5c–h) and the average chl *a* concentration in each province (Table 3) mesozooplankton biomass in these regions (Fig. 5g). The mesozooplankton-chlorophyll relationships (Fig. 5c–h) and the average chl *a* concentration in each province (Table 3) was used to calculate the mesozooplankton biomass. These calculated values were in fairly good agreement with the observed values in Table 3, with r^2 = 0.73. Distinct differences between calculated and observed values were observed for some of the coastal provinces, where the average mesozooplankton biomass was obtained from a low number of measurements (4 to 7 stations).

In order to compare the phyto- and zooplankton biomass for the 0 to 100 m layer in carbon units, we used average chl *a* in the 0 to 10 m layer (data for 3° × 3°), ratio (1) and coefficients transferring chl *a* and wet zooplankton biomass into organic carbon (see 'Materials and methods'). The shapes of the relationships of the mesozooplankton and phytoplankton for the 100 m layer in carbon units per m^{-2} are similar to

those in Fig. 5. The mesozooplankton carbon in the NAST and SATL provinces for data between June and November can be characterized by the following relationships:

$$\text{Ln } B_{MZ} = \text{Ln } 0.09 + 0.56\ B_P \quad (3)$$

for $0.5 \le B_P \le 5$; $r^2 = 0.82$, $p < 0.001$, $n = 40$

Between December and May:

$$\text{Ln } B_{MZ} = \text{Ln } 0.20 + 0.37\ B_P \quad (4)$$

for $0.5 \le B_P \le 5$; $r^2 = 0.84$, $p < 0.001$, $n = 77$

where B_{MZ} and B_P are mesozooplankton and phytoplankton carbon, g C m^{-2}, respectively.

For the other provinces between June and November:

$$B_{MZ} = 0.39\ \text{Ln}(B_P) + 0.46 \quad (5)$$

for $0.5 \le B_P \le 3$; $r^2 = 0.4$, $p < 0.01$, $n = 139$

Between December and May:

$$B_{MZ} = 1.17\ \text{Ln}(B_P) + 0.72 \quad (6)$$

for $0.5 \le B_P \le 3$; $r^2 = 0.67$, $p < 0.001$, $n = 116$

Eqs. (4) to (6) lead to the conclusion that the B_{MZ}:B_p ratio declines with an increasing phytoplankton biomass. This refers to the NAST and SALT provinces where the B_{MZ}:B_P ratio declines from 0.2 to 0.1 from June to November and from 0.5 to 0.2 from December to May. In the other provinces, in summer and autumn the B_{MZ}:B_P ratio equals 0.5 at a low level of phytoplankton biomass (1 g C m^{-2}), and 0.3 at a high level of phytoplankton biomass (3 g C m^{-2}). In the winter and spring seasons, this ratio increases 1.5 times and varies in the range of 0.4 to 0.8. Thus, in the subequatorial and tropical regions, mesozooplankton biomass is half that of phytoplankton. The lowest B_{MZ}:B_p ratios were in the NAST and SALT provinces, where values were the half those measured in the other provinces.

DISCUSSION

Chlorophyll *a*

Remote sensing of the ocean colour has enabled the estimation for the first time, on a global scale, of the spatial-temporal changes of chlorophyll concentrations in the upper layer of the ocean. The analysis of these data has shown that chlorophyll changes do correlate with oceanic circulation and physical processes favouring the nutrient flux into the photosynthesis zone (Falkowski et al. 1998). In the central oceanic gyres (spanning NAST and SALT), where nutrient flux is low and chlorophyll concentration is <0.2 mg m^{-3}, the oligotrophic area shrinks from summer to winter in both hemispheres, between 40° N and 40° S, according to CZCS images (Falkowski et al. 1998). The map of chlorophyll concentration derived herein from direct sampling is less detailed than the CZCS maps. However, contours of regions with a significant chlorophyll concentration corroborate qualitatively. In both maps (i.e. in the CZCS and Fig. 3), high values were observed in coastal upwelling regions, whereas the lowest ones were in the central oceanic gyres. From the map based on direct sampling (Fig. 3), the area with low chlorophyll is wider in the northern summer than in winter. From June to November, chlorophyll values in NAST (W), NATR, WTRA, ETRA and SALT were averaged from 1968 through 1992 (Table 3). The CZCS data averaged from 1978 through 1986 (Longhurst 1995) were different by only 0.01 mg m^{-3}. In the coastal provinces (CNRY and GUN), the CZCS data were 20% higher. In December through May, differences between satellite and direct field measurements were higher, but they were in a range of ±30%. This low variability enables us to assume that climatic variability of chlorophyll is relatively low.

Mesozooplankton

We have compared our sampled data on mesozooplankton biomass (Fig. 4) with the map of zooplankton biomass published by Tseitlin et al. (1997b), who used annually averaged values. Tseitlin et al. (1997b) used data from different mesh sizes and depths sampled in the 0 to 500 m layer and calculated the values for the 0 to 100 m layer; he only used 9 of the 40 cruises given in Table 2. We restricted ourselves to the data primarily collected at night using the same nets covering the 0 to 100 m layer. In both maps, elevated values were observed outside the coastal upwelling off Africa, where the upwelling zones tend to span 50 to 100 km coastal zones. Elevated biomass values can cover several hundred km in these coastal zones (Cushing 1975). The lowest values were in the NAST and SATL provinces. According to our map, annual biomass was in the range of 65 to 75 mg m^{-3}. Tseitlin et al. (1997b) reported values from 25 to 100 mg m^{-3} for the same regions. The most distinct differences noted were for the central SATL where Tseitlin et al. had values <25 mg m^{-3}. They emphasized, however, that due to the lack of measurement between 20° and 40° S, these values should be taken with caution.

Using concentrations of chlorophyll and mesozooplankton converted into carbon we determined that the mesozooplankton:phytoplankton ratio varied from 0.15 to 1.0 in subtropical and tropical regions. Low ratios are typical for NAST and SALT with the aver-

age values of 0.15 and 0.23 for summer and winter seasons respectively. These values were 2.5 to 3 times higher in the other provinces. In general, the amount of mesozooplankton carbon per unit of phytoplankton carbon is less in low-productive regions, in comparison with the moderate productive ones. One of the reasons is the difference in the phytoplankton consumption rate by mesozooplankton due to variance in its abundance and size structure. For instance, consumption of phytoplankton by copepods was studied by Huskin et al. (2001a,b) in spring and autumn along the latitudinal transect from 50° N to 50° S. The rate measured by the chlorophyll content in copepod stomachs reached 150 mg C m^{-2} d^{-1} in the upwelling region in the BENG province. At the equator (WTRA and ETRA), where zones of intensive or low upwelling were associated with the divergence, the rate was 44 to 77 mg C m^{-2} d^{-1}. In the regions with stable water mass structure (i.e. NAST and SATL) the rate was 9 to 12 and 17 to 34 mg C m^{-2} d^{-1} respectively, which, in terms of daily grazing, removes 3 to 29% of primary production. Quantitative assessments of mesozooplankton grazing in regard to primary production rates were reported for various coastal and oceanic ecosystems by Calbert (2001), who showed that in a wide range (from 28 to 4000 mg C m^{-2} d^{-1}), the ingestion rate and the intensity of feeding (i.e. grazing rate normalized by mesozooplankton biomass in carbon units per day) could be represented by a parabolic equation with a degree of 0.64 and 0.53 respectively. In low-productive communities, where primary production is in the region of 0.05 to 0.25 g C m^{-2} d^{-1}, algae contribute 3 to 7% of the daily biomass diet of mesozooplankton in carbon units. In the communities with moderate productivity (0.25 to 1.0 g C m^{-2} d^{-1}) this contribution was 7 to 15%, whereas in the productive communities it was 15 to 30% (Calbert 2001, Fig. 2). Estimates of phytoplankton consumption by copepods in oligotrophic subtropical waters near to the Azores indicated that, depending on season, phytoplankton contributes 4 to 12% (8% average) of copepod carbon biomass (Huskin et al. 2001b). For a metabolism of 60% as the level of food assimilation, the minimal food requirements of copepods with a wet weight of 5×10^{-4} to 5×10^{-5} g should be 20 to 40% of their body mass (Sushchenya 1975). Thus it seems obvious that copepods are unable to cover energy expenditures at the ingestion rates observed in the oligotrophic regions of the tropical and subtropical Atlantic. They can only supplement this energy requirement if they act as predators. On the other hand, when primary production changes from 0.05 to 1.0 g C m^{-2} d^{-1}, the phytoplankton contribution to the daily diet of mesozooplankton can increase approximately 5 times. Therefore, in the moderate productive regions the amount of mesozooplankton carbon biomass per unit of phytoplankton carbon would be higher than in oligotrophic regions. Suggested reasons for these discrepancies are that in oligotrophic regions the length of the trophic chains are extended and mesozooplankton (copepods) only take 3 to 7% of available phytoplankton, while in productive regions, where the trophic chain is short, this consumption reaches 15 to 30%.

Gasol et al. (1997) summarised the available data to estimate the pyramid of biomass (organic carbon) from 10 well-studied open ocean communities of the Atlantic, Pacific, Indian, and Mediterranean Sea, from the northern arctic to the southern subtropical latitudes. The authors concluded that the mesozooplankton:phytoplankton ratio declines with an increase of phytoplankton biomass, and the average value of this ratio is about 0.5 in the plankton of low productive regions (Gasol et al. 1997, their Fig. 4). The ratio (in organic carbon) range was from 0.15 to 0.70 in the upper 200 m layer in the Indian Ocean (Tranter 1973), which is similar to that in the Atlantic Ocean.

Measurements carried out at a geographically fixed station in the Arabian Sea (21° N, 64° E) showed that this ratio varied from 0.6 to 5.5 (Kumar et al. 2001). These seasonal differences were due to low annual variability of mesozooplankton biomass (ranging from 1.5 to 2.2 g C m^{-2}) although phytoplankton biomass varied from 0.4 to 2.2 g C m^{-2}. Between 24° N and 10 to 15° N phytoplankton varied from 1.1 to 2.2 g C m^{-2} during the southwest monsoon, and from 1.3 to 1.5 g C m^{-2} in the northeast monsoon (Shalopyonok et al. 2001). At that phytoplankton concentration, mesozooplankton biomass should be 0.5 to 0.8 g C m^{-2}, according to Eq. (5). Annually averaged mesozooplankton biomass is in the range from 0.75 to 1 g C m^{-2} (Rudjakov et al. 1997).

Table 4. Averaged primary production, phyto-, mesozooplankton biomass and rates of primary production to phytoplankton biomass over the biogeochemical provinces of the Atlantic Ocean. PP: primary production from Longhurst et al. (1995); Phyto: phytoplankton biomass (0–100 m); MZ: mesozooplankton biomass (0–100 m)

Province	Mean annual values			
	PP g C m^{-2} d^{-1}	Phyto g C m^{-2}	PP:Phyto d^{-1}	MZ g C m^{-2}
West and east subtropical gyre	0.30	1.20	0.25	0.28
Tropical gyre	0.29	1.17	0.25	0.74
Western tropical Atlantic	0.36	1.26	0.29	0.80
Eastern tropical Atlantic	0.43	1.32	0.32	0.96
South Atlantic gyre	0.21	1.04	0.20	0.24
Coastal provinces	1.4	2.50	0.56	1.5

Overall, in the upper 100 m layer, in the 6 studied provinces (Table 4) the mesozooplankton comprises approximately 50% of phytoplankton biomass. This layer is the major biotope for phytoplankton algae. In the tropical regions of the Atlantic Ocean, the ratio between mesozooplankton biomass in the 0–100 m to 0–500 m layer was equal to 0.5–0.7 (Lenz et al. 1993). If we accept an average value of 0.6, then it can be said that phyto- and mesozooplankton biomass are approximately equal in the upper 500 m layer.

Chlorophyll-zooplankton relations

Correlation between chlorophyll in the upper 5 m and chlorophyll, phytoplankton, and mesozooplankton biomass in the 0 to 200 m layer were calculated for the Pacific (40° N to 40° S) and the Atlantic Ocean (20° N to 40° S). Estimates of phyto- and mesozooplankton were made at the same stations and usually from the same (180 l) bottles sampled at 12 to 24 depths in the upper 200 m layer (Vinogradov et al. 1999). According to their calculations, equation parameters were as follows:

$$B_{MZ} = 1.16\ \mathrm{chl}^{0.433} \quad (r^2 = 0.52,\ p = 0.0000,\ n = 99) \tag{7}$$

$$B_{P} = 1.47\ \mathrm{chl}^{0.448} \quad (r^2 = 0.46,\ p = 0.0000,\ n = 95) \tag{8}$$

$$\mathrm{chl}_{(0-200)} = 49.43\ \mathrm{chl}^{0.374} \quad (r^2 = 0.67,\ p = 0.0000,\ n = 92) \tag{9}$$

where B_P and B_{MZ} are phyto- and mesozooplankton biomass in g C m^{-2} (0 to 200 m), Chl is chlorophyll concentration in the upper 5 m layer (mg m^{-3}), $\mathrm{Chl}_{(0-200)}$ is chlorophyll concentration in the upper 200 m layer (mg m^{-2}). From Eqs. (7) and (8) one notices that B_{MZ} does not increase linearly with B_P. Dividing Eq. (7) by Eq. (8), then the B_{MZ}:B_P ratio would not depend upon phytoplankton in the range from 0.2 to 4.0 g C m^{-2} and the derived ratio would be approximately 0.8. These Pacific-related values are somewhat higher than those observed in the Atlantic Ocean. However, in the Pacific Ocean they are for the 200 m layer. For the Pacific Ocean regions, the ratio of mesozooplankton biomass through different depths (sampled layers) was quantified by the equation (Tseitlin et al. 1997a):

$$k = (z_1/z_2)^{0.48} \tag{10}$$

where k is the coefficient transferring biomass in the $0–z_2$ m layer into the biomass in the $0–z_1$ m layer. According to this equation, biomass (mg m^{-2} wet biomass) in the 200 m layer is 1.4 times higher than that in the 100 m layer. When the major phytoplankton biomass is in the 100 m layer, the ratio B_{MZ}:B_P will be 0.6. This ratio results from Eq. (7) being divided by 1.4, and this figure being further divided by Eq. (8). The value is close to the values obtained for NATR, WTRA, ETRA, and GUN. However, it is 2 to 3 times higher than that in NAST and SATL. Differences are due to estimates of phytoplankton biomass. Eqs. (8) & (9) indicate that in the 200 m layer, the chlorophyll:carbon (chl:c) ratio decreases from 0.04 to 0.03 with an increase of chlorophyll concentration from 0.05 to 5.0 mg m^{-3} in the upper layer. These data do not corroborate well with a stated concept of nutrient impact on chlorophyll concentration (Geider et al. 1997). When phytoplankton is limited by nutrients the chl:c ratio decreases. In oligotrophic waters this ratio differs from that measured in the other oceanic regions.

In nutrient-depleted tropical waters, such as the north Pacific Ocean, the chl:c ratio within the mixed layer was 0.008 and declined to 0.04 at greater depth (Campbell et al. 1994). The values do not strongly diverge from the data obtained in the Atlantic Ocean on chlorophyll concentration and phytoplankton biomass in June (1992) in the EUMELI programme. During this period the sum of chl *a* and divinyl-chl *a* in oligotrophic waters was 34.6 mg m^{-2} and phytoplankton biomass measured with the flow cytometer on cell abundance and carbon content in the cell was 2.0 g C m^{-2} (Partensky et al. 1996). The comparison of these values results in a chl:c in oligotrophic waters of 0.017. From the above data one can assume that the phytoplankton biomass in oligotrophic regions, as reported by Vinogradov et al. (1999), is underestimated by 2 to 3 times.

Shushkina et al. (1997, their Table 1) summarised the annual data on average plankton biomass in the World's Ocean. They presented average data which suggest that where chl *a* from satellites is <0.1 mg m^{-3}, phytoplankton biomass is 0.42 g C m^{-2} and mesozooplankton is 0.3 g C m^{-2} in the upper 200 m layer of tropical oligotrophic waters. In the case of mesotrophic waters, values were 0.1 to 0.3 mg m^{-3} for chl *a*, 0.56 g C m^{-2} for phytoplankton and 0.95 g C m^{-2} for mesozooplankton. The mesozooplankton biomass exceeded that of phytoplankton according to these data in mesotrophic regions. The annual average mesozooplankton biomass we obtained for these chlorophyll concentrations (i.e. 0.1 to 0.3 mg m^{-3}) was 0.45 and 0.90 g C m^{-2}. These values were obtained as follows. Using Eq. (1) we determined the total chlorophyll value in the 0 to 100 m layer. This value was multiplied by 60 which gave phytoplankton biomass in carbon units (g C m^{-2}). These values were substituted in Eq. (5) & (6) in order to obtain zooplankton biomass in carbon units for 2 seasons. The annual mean was obtained from the above numbers. This mean corresponds fairly well with the estimate given by Shushkina et al. (1997).

The mesozooplankton:phytoplankton ratio is different, which also is due to discrepancy in estimates of the phytoplankton biomass. Thus, if the chl *a* concentration per unit surface is calculated by Eq. (9) and divided by the phytoplankton biomass given by Shushkina et al. (1997), the chl *a* to carbon ratio is 0.03 for ultra-oligotrophic and 0.05 for mesotrophic regions. This level has only been observed for phytoplankton at the lower part of the photosynthetic zone (Furuya 1990, Li et al. 1992, Campbell et al. 1994). In the upper 10 m layer, with low nutrients, values of the chl *a* to carbon ratio achieve 0.01 to 0.007 (Buck et al. 1996, Taylor et al. 1997) and were on average 0.015 for the 200 m layer.

Seasonal cycles

Cushing (1975) has postulated that there are 3 patterns of seasonal cycles in phyto-zooplankton relationships. The first is seen in Antarctic waters, where there is 1 summer peak of phyto- and zooplankton. The second is typical for temperate regions, where there are 2 peaks, a major one in spring and a less developed one in autumn. The seasonal peaks are not well developed in the third type, which is typical for tropical regions. We have analysed seasonal changes of primary production by Longhurst (1998), phyto- and mesozooplankton biomass in carbon units (Fig. 7) using remotely sensed seasonal measurements of chl *a* from the upper layer (Longhurst 1995) and mesozooplankton:chl *a* ratios (Fig. 5). In order to do that, an average surface concentration was calculated for the upper 100 m layer and multiplied by 60. From Eqs. (3) to (6), mesozooplankton biomass was calculated for each province. These enabled an estimate to be calculated of the dynamics of the biomass in tropical regions where field data are scarce. It should be noticed that the sharp decline of the curves between summer to winter seasons in Fig. 7 is related to the method of data analysis, where only 2 (i.e. not all 4) seasons were defined.

The maximum of phyto and zooplankton biomass in the province of the NAST and SATL occurs in the winter-spring period. During this time, the phytoplankton biomass (1.2 to 1.8 g C m^{-2}) was 1.5 to 2.0 times greater than that in the summer-autumn period, and for zooplankton biomass about 2 times. Similar seasonal patterns of zooplankton biomass have been reported for the Sargasso Sea, near Bermuda (Menzel & Ryther 1961, Madin et al. 2001) and for the northwestern Atlantic Ocean (40 to 45° N), based on copepod abundance measurements (Planque et al. 1997). The measurements of phytoplankton biomass are in reasonable agreement with the chl *a* data. From a transect carried out in August to September from 20° W,

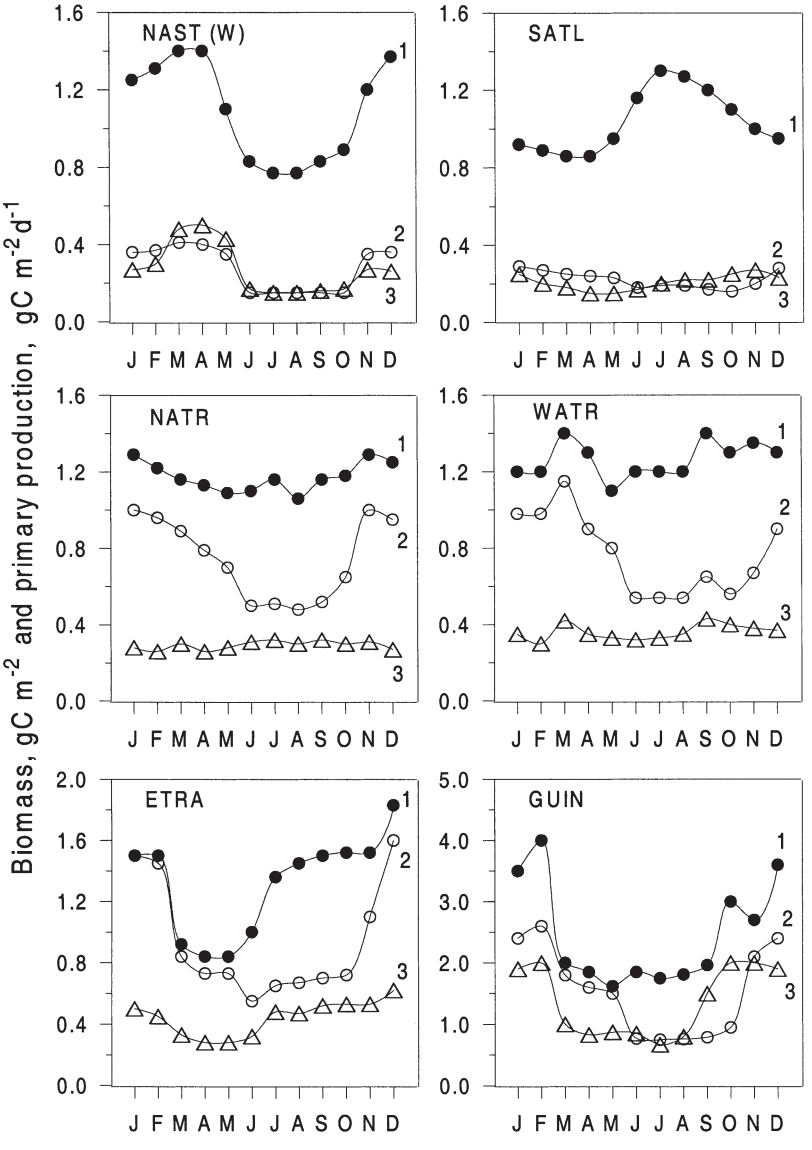

Fig. 7. Seasonal cycle of primary production (3) described by Longhurst (1998) and phyto- (1) and mesozooplankton (2) biomass in individual provinces calculated with Eqs. (1) to (6) from the CZCS chlorophyll concentration (Longhurst 1995)

between 25° and 45° N, Buck et al. (1996) quantified the phytoplankton biomass as 1.07 g C m^{-2}. They achieved this by counting the algae using a flow cytometer, and from carbon measurements of individual cells. We calculated the phytoplankton biomass from the chl *a* August values as 0.92 g C m^{-2} (Fig. 7). Mesozooplankton biomass was measured as 0.82 g C m^{-2}, in April, along 20° W at 33° N by Lenz et al. (1993), and when calculated from the chl *a* values it was 0.6 g C m^{-2}. Similar values of mesozooplankton biomass (0.4 g C m^{-2}) and phytoplankton biomass (1.4 g C m^{-2}) were obtained for the northern province (20° W, 47° N) at the end of April (Harrison et al. 1993, Lochte et al. 1993).

Seasonal variations of phytoplankton and mesozooplankton biomass over the year do not exceed 2 times in the provinces of the western and tropical gyres (Fig. 7). In these provinces, where a weak upwelling takes place, the production cycle for biomass has a low amplitude. In the eastern tropical ocean, where seasonal changes of upwelling and hydrographic conditions are well developed (Longhurst 1993), changes in phyto- and mesozooplankton can reach 2- to 3-fold (Fig. 7). Minimal values of zooplankton biomass were observed in March to May (0.4 to 0.6 g C m^{-2}) and increased in December to 1.6 g C m^{-2}. Gruzov (1973) and Borgne (1977) reported similar seasonal cycles for this region. From the equator to 12° S, zooplankton biomass changes from 0.3 to 0.6 g C m^{-2} during spring and by the end of autumn it was 1.0 to 1.5 g C m^{-2}. The characteristic seasonal cycles in the phytoplankton biomass are in good agreement with the large-scale changes of primary production and mesozooplankton biomass.

In general, our analysis indicated that the seasonal dynamics of phyto- and mesozooplankton biomass were fairly similar in the subtropical and tropical provinces. Differences are observed in the amplitude of biomass fluctuations, which are greater in regions where nutrient enrichment takes place in the upper layer. For the large area of the eastern tropical Pacific, logarithmic values of primary production, chlorophyll and mesozooplankton biomass were positively correlated with each other in each season and area (Blackburn 1981). The main point of interest is that the phyto- and mesozooplankton biomass seasonal changes were generally similar and small in the tropical Atlantic and Pacific Oceans.

Phytoplankton specific production

Estimates of the plankton biomass of the World's Ocean have a useful role for assessments of the carbon cycle. Annual values of phytoplankton production among oceanic provinces range from 0.2 to 0.4 g C m^{-2} d^{-1} (Table 4). This carbon flux is driven by a phytoplankton biomass of 1.0 to 1.3 g C m^{-2}. On average, phytoplankton biomass in the oceanic provinces turns over once per 3 to 5 d. The specific daily production of phytoplankton (yearly average) is relatively constant over different latitudes: it varies between 0.2 and 0.3 d^{-1} in the upper 100 m layer. In coastal provinces, where the concentration of nutrients is high, the specific production is higher, at 0.5 d^{-1}. Therefore, mesozooplankton biomass might differ several times with the same primary production level.

CONCLUSION

The concept of biogeochemical provinces was applied to the field measurements on chlorophyll and mesozooplankon in the tropical and subtropical regions obtained in the past 40 yr. This allowed us to derive trends of mesozooplankton-phytoplankton relationships within the provinces, which could be used to restore macroscale mesozooplankton biomass distributions from remotely sensed chlorophyll data.

General patterns were obtained between chlorophyll concentrations and mesozooplankton biomass on an ocean basin scale. The ratio of the total biomass of phyto- and mesozooplankton, in carbon units, varied from 6 to 1 in the 0 to 100 m layer and on average, the phytoplankton biomass exceeded twice that of mesozooplankton. The seasonal cycles of phyto- and zooplankton biomass for the 6 provinces of the tropical and subtropical zones were qualitatively comparable. There were nonlinear relationships between mean chlorophyll concentration within the 0 to 10 m layer and mesozooplankton biomass within the 0 to 100 m layer, which indicated that a different amount of phytoplankton carbon biomass corresponds to mesozooplankton biomass. In the moderate productive regions, the amount of mesozooplankton carbon biomass per unit of phytoplankton carbon would be higher than in oligotrophic regions. Relationships were established between primary production, phytoplankton and mesozooplankton biomass for the 6 oceanic provinces.

Acknowledgements. This work was funded by NSF grant #DEB-0203622, NASA grant #NAG 5-3113 and the UK Darwin Initiative grant #162/8/251.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: November 24, 2000; Accepted: November 19, 2002
Proofs received from author(s): March 7, 2003