JOURNAL OF PLANKTON RESEARCH | VOLUME 34 | NUMBER 3 | PAGES 236–244 | 2012

Seasonal and interannual coupling between sea surface temperature, phytoplankton and meroplankton in the subtropical south-western Atlantic Ocean

LOHENGRIN DIAS DE ALMEIDA FERNANDES*, JUREMA QUINTANILHA, WANDA MONTEIRO-RIBAS, ELIANE GONZALEZ-RODRIGUEZ AND RICARDO COUTINHO
DEPARTAMENTO DE OCEANOGRAFIA, IEAPM, INSTITUTO DE ESTUDOS DO MAR ALMIRANTE PAULO MOREIRA, RUA KIOTO, 253, PRAIA DOS ANJOS, ARRAIAL DO CABO, RJ 28930-000, BRAZIL

*CORRESPONDING AUTHOR: lohengrin@ieapm.mar.mil.br, lohengrin.fernandes@gmail.com

Received July 1, 2011; accepted in principle December 7, 2011; accepted for publication December 13, 2011

Corresponding editor: Mark J. Gibbons

Meroplankton abundance (Bivalve larvae, Cirripede larvae and other non-identified larvae), phytoplankton biomass and sea surface temperature (SST) from a 15-year time series (1995−2009) in the Cabo Frio region, south-western Atlantic Ocean, were analysed to assess temporal patterns of co-variation. Weekly zooplankton sampling included vertical hauls (∼20 m) with a 100 μm net, taken in triplicate. All data were standardized to monthly within-year anomalies ($n = 180$), monthly between-year anomalies ($n = 12$) and annual anomalies ($n = 15$). Monthly and annual anomalies were compared by means of cross-correlation analyses, and trends were estimated by linear regression in time series after removing serial dependence. The degree of coupling between phytoplankton and meroplankton was estimated from the analysis of their interannual changes during the seasonal maxima of these variables. The three variables displayed a strong seasonality, and there is evidence of coupling between phytoplankton biomass and meroplankton abundance, dominated by bivalves and cirripedes, during the austral spring (mostly September to November). Meroplankton abundance was positively correlated to SST and negatively to phytoplankton; the latter correlation suggested that a sudden supply of meroplankton larvae can contribute to controlling phytoplankton biomass during the upwelling season. In contrast, annual changes in SST and phytoplankton biomass fail to account for the interannual variation in larval supply.

KEYWORDS: meroplankton; phytoplankton; time series; upwelling; top-down control; benthic-pelagic coupling

INTRODUCTION

Plankton assemblages in coastal areas include many meroplanktonic forms, since most marine benthic species are thought to include at least one larval planktonic phase in their development (Marcus and Boero, 1998; Pechenik, 1999). During this period of its lifecycle,

doi:10.1093/plankt/fbr106, available online at www.plankt.oxfordjournals.org. Advance Access publication January 13, 2012

which varies from 1 week to 2 years (Belgrano *et al.*, 1995; Anger, 2001), any larva competes for resources available in the environment with other planktonic organisms, while avoiding predation (McConaugha, 1988). The seasonal reproductive pulse can lower the individual chance of predation, while it can increase between-species competition (Morgan and Christy, 1997). Many benthic species have one major peak of hatching coincident with warmer water temperatures, implying shorter development time (Hoegh-Guldberg and Pearse, 1995; Kirby *et al.*, 2007; O'Connor *et al.*, 2007; Kirby *et al.*, 2008), or with spring phytoplankton blooms, involving greater food availability and diminished competition (Starr *et al.*, 1990; Martin *et al.*, 1996; Highfield *et al.*, 2010). Increases in seasonal phytoplankton due to favourable conditions are usually followed by a higher zooplankton abundance, implying a top-down control of phytoplankton communities (Sommer and Sommer, 2006). Micro- and mesozooplankton, including copepods, and other crustacean, protistan and gelatinous suspension feeders, are usually considered to be the main grazers of phytoplankton (Azam *et al.*, 1983; Stibor *et al.*, 2004). Benthic suspension feeders and meroplanktonic stages have received far less attention (Cloern, 1982; Kirby *et al.*, 2007, 2008). Results of the few studies concerning the relative importance of grazing by meroplankton have shown that some groups, such as Polychaete larvae and nauplii of *Balanus* sp., may consume twice as many diatoms as the globally abundant nauplii of the copepod *Calanus* spp. (Martin *et al.*, 1996; Turner *et al.*, 2001).

The favoured scenario for seasonal coupling between zooplankton phenology, mostly copepods, and phytoplankton abundance, the match–mismatch hypothesis (Cushing, 1990; Edwards and Richardson, 2004; Durant *et al.*, 2007), has been extended at the present time to other less-studied groups. The relative importance of meroplankton in top-down control and match–mismatch can be underestimated, since there are difficulties in larval identification of organisms from field samples. Some studies have shown that many larvae are opportunistic and can prey on pico-, nano- and microplankton, and that selection for prey size also occurs (Rivkin *et al.*, 1986; Martin *et al.*, 1996; Turner *et al.*, 2001). Additionally, there is a large body of evidence supporting synchrony between spawning of larvae and increases in phytoplankton biomass (Starr *et al.*, 1990; Mura *et al.*, 1996; Kirby *et al.*, 2008; Nixon *et al.*, 2009), which suggests a relatively greater importance of meroplankton in relation to the match–mismatch hypothesis (Edwards and Richardson, 2004).

Marine plankton assemblages in the Cabo Frio region have been studied over the past 30 years, in part due to the occurrence of a coastal wind-induced upwelling, which improves productivity in this area relative to other subtropical marine ecosystems in the South Atlantic (Valentin, 1984a,b; Valentin *et al.*, 1987). Most of the shelf waters in the western region of the tropical South Atlantic Ocean (SAO) are oligotrophic with low productivity in relation to the upwelling region associated with the Benguela Current in the eastern region (Gonzalez-Silvera *et al.*, 2004). The most productive areas in the subtropical SAO are sparse and associated with river-plumes, upwelling zones or shelf-break fronts, where input of new nutrients fuel primary productivity and the food web (Boltovskoy, 1981; Brandini *et al.*, 1997). Upwelling in the SAO is related to periodic breaks in vertical stability, which bring nutrient-rich deep waters to the euphotic zone and improve phytoplankton production (Valentin, 1984a). A few days after upwelling begins, micro- and mesozooplankton secondary productivity quickly increases as a result of bottom-up stimuli (Valentin, 1984b; Carvalho and Gonzalez-Rodriguez, 2004; Guenther *et al.*, 2008).

The response of the biological system to a sudden supply of nutrients (upwelling) and grazers (larval pool) is complex, as it involves the time scales of growth of all components of the ecosystem (Carr, 1998). Additionally, the size distribution of the organisms and coupling between primary and secondary producers are strongly affected by the frequency of input and seasonality (Hofmann and Ambler, 1988; Carr, 1998; Pugnetti *et al.*, 2008) and could be used to track and predict the impact of global changes to the ecosystem (Edwards and Richardson, 2004).

Seasonality is less marked in tropical and subtropical environments, and the larval pool may be affected by coastal processes, such as upwelling. On an interannual scale, secondary production of benthic species is related to global changes, and the meroplankton may therefore be used to track and predict the evolution of productivity. Recent evidence suggests that many of the meroplanktonic life stages are even more sensitive to climate change than their holozooplanktonic neighbours living permanently in the plankton (Piontkovski *et al.*, 2006; Richardson, 2008). It has been proposed that more comprehensive studies and long time-series data focusing on holo- and meroplankton are essential in the near future, mainly for the benefit of modelling global change.

This study aimed to address the relative importance of the larval pool in controlling phytoplankton biomass on both a seasonal and interannual scale. Among the many possible questions concerning the coupling/decoupling between zooplankton and phytoplankton, we focused on the following main hypotheses: (i) the seasonal increase in phytoplankton biomass relative to upwelling events is controlled by increased grazing pressure during peaks of the larval pool; and (ii) interannual changes in phytoplankton biomass and sea surface temperature (SST) may affect meroplankton phenology.

METHOD

Sampling

Plankton samples were taken weekly from October 1994 at Cabo Frio Island, Arraial do Cabo, Brazil (23°S 042.01°W). Details of the study site can be found in Guenther *et al.* (Guenther *et al.*, 2008). Data from January 1995 to December 2009 (15 years) were included in this study. On each sampling date, three sub-surface (~1 m depth) horizontal hauls of three minutes each were performed in sequence, totalling 2262 samples (mesh size = 100 μm, mouth opening = 40 cm diameter). Missing data from the time series (27 weeks), due to bad weather conditions, were interpolated from adjacent values.

Phytoplankton biomass was estimated by the chlorophyll *a* concentration (mg m^{-3}) from water samples taken at ±1 m depth using a Nansen bottle. SST (±1 m) was measured using a reversing thermometer mounted in the Nansen bottle. Chlorophyll *a* was measured according to Parsons *et al.* (Parsons *et al.*, 1984). Meroplankton abundance (N m^{-3}) was estimated from three subsamples taken with a Stempel pipette (2.97 mL). The veliger larvae of Bivalvia Mytilidae and the nauplii of Cirripedia were sorted and counted. Other less frequent and less abundant larvae, namely Echinodermata, Bryozoa, Annelida, Ascidiacea, Bivalvia non-Mytilidae and Decapoda larvae, were grouped together with Bivalvia and Cirripedia, and counted as "Meroplankton" (information provided as Supplementary Table SI). Only two species of Mytilidae are dominant at the study site, *Brachydontes solisianus* and *Perna perna* (Monteiro-Ribas *et al.*, 2006), while there are more species of Cirripedia. All laboratory procedures were performed by the same two individuals throughout the years to ensure consistency of correct identification.

Data analyses

Seasonality of chlorophyll *a*, SST and total meroplankton abundance was assessed by means of monthly between-year averages ($n = 12$) and monthly within-year anomalies ($n = 180$), calculated over the entire time series (12 months × 15 years). Interannual trends were examined using the matrix of monthly anomalies ($n = 180$) and annual anomalies ($n = 15$). Trends were obtained by least-square linear regression, and a Durbin–Watson test was performed in order to check for serial autocorrelation in the residuals of the regression analysis (Durbin, 1970). In cases of significant serial correlation of residuals, the effective number of independent values was corrected accordingly (Quenouille, 1952; Mackenzie and Köster, 2004; Highfield *et al.*, 2010; and references therein). A Student's *t*-test was used to determine whether the slope of the linear model was significantly different from zero. A Box–Jenkins autocorrelation function was used to assess the temporal dependence of months and years (Box and Jenkins, 1976), after removing the serial dependency of data (Kirby *et al.*, 2007). The relationships between monthly averages of meroplankton abundance, chlorophyll *a* and SST were addressed by means of cross-correlation analyses (Piontkovski *et al.*, 2006). Data normality was tested using a Shapiro–Wilk W test and data were log-transformed when necessary (Shapiro *et al.*, 1968). The timing of the seasonal peak of chlorophyll *a*, Mytilidae and Cirripedia was estimated according to the central tendency, and following the uni- or bimodal distribution. Details can be found in Edwards and Richardson (Edwards and Richardson, 2004). The interannual variation in the month of seasonal peak, or months when bimodal, was correlated through Pearson's Product Moment to reveal the phenological relationship between the bloom of phytoplankton and the timing of the larval pool.

RESULTS

SST over the past 15 years ranged over a relatively large amplitude, ranging from 19.1°C at the end of winter up to 26.7°C at the end of summer. A non-significant ($P > 0.05$) slope was observed throughout the SST time series, and the residual analysis showed high serial autocorrelation in SST time series (DW < 2, $r_{\text{lag1}} = 0.64$, $P < 0.01$, Table I). Positive and negative annual SST anomalies in the Cabo Frio region were frequent every 3 years from 1995, suggesting some interannual regularity in the time series (Figs 1 and 2, blue band). The strongest negative annual SST anomaly was observed in 1996/97. After removing the serial dependency on data by first-order differencing, higher but non-significant autocorrelation was observed for SST, with a lag of 3 years ($r_{\text{lag3years}} = 0.41$, $P = 0.06$, Fig. 2).

Chlorophyll *a* raw data throughout time series varied from 0.03 to 4.1 mg m^{-3}. Strong decreases in phytoplankton biomass were revealed by the negative annual anomalies that occurred in 2001 and 2008 (Fig. 1),

Table I: Overall average and standard deviation (SD) of weekly raw data over the last 15 years (1995–2009) and linear trend analysis (slope) of monthly anomalies of chlorophyll a*, total meroplankton and SST*

	Raw data		Monthly anomalies			
Time series (1995–2009)	Overall average	SD	Durbin–Watson parameter	Serial correlation	Trend slope	Trend *P*-value
Chlorophyll *a*	1.0	0.6	1.5	0.23	−0.0007	0.60
Meroplankton	434	392	1.4 ($P < 0.05$)	0.28	−0.0001	0.94
SST	22.6	1.4	0.7 ($P < 0.01$)	0.64	0.0012	0.39

The Durbin–Watson test was performed to reveal potential significant serial autocorrelation on time-series data.

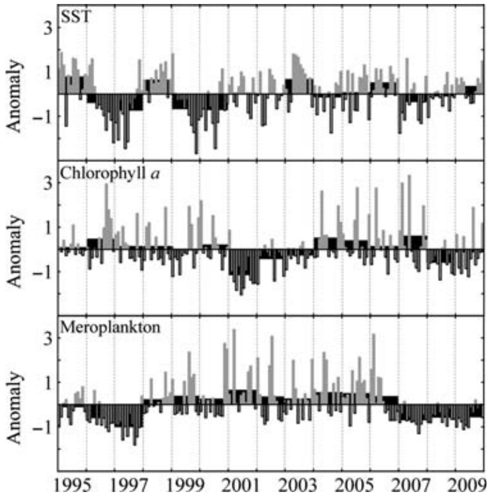

Fig. 1. Monthly anomalies (positive in gray and negative in white) of SST (top), chlorophyll *a* (middle) and meroplankton abundance (bottom), superimposed on annual anomalies (both positive and negative as black bars) from 1995 to 2009.

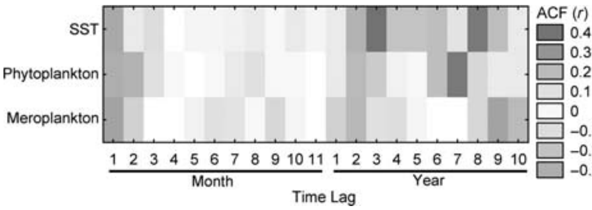

Fig. 2. Correlogram of Box–Jenkins autocorrelation function (ACF) calculated over the detrended (first order differential) monthly within-year anomalies (time-lag ranges from 1 to 11 months) and monthly between-year anomalies (time-lag range from 1 to 10 years). Higher positive autocorrelations are shown in blue and higher negative autocorrelations are shown in red. (The colour version of the figure is available at online supplementary data.)

although a non-significant trend slope was found. The autocorrelation function for chlorophyll *a* was non-significant ($P > 0.05$) for the first-order differenced data (Table I), although it slightly reflected the lag of 2 and 7 years in phytoplankton biomass ($r_{\text{lag2}} = 0.20$, $P = 0.09$, $r_{\text{lag7}} = 0.36$, $P = 0.12$, Fig. 2). Analysis of interannual changes in chlorophyll *a* failed to reveal a single trend in time series, and the largest peaks were seen in 1996, 2000, 2004 and 2007. Some of these peaks coincided with low meroplankton abundance (1996 and 2007), but there was no significant interannual cross-correlation (Table II).

Total meroplankton abundance ranged from 0 to about 12000 N m^{-3}, and the highest abundance in 2001 was concurrent with the onset of the decrease in phytoplankton biomass. In contrast, negative annual anomalies were seen in 1996–97 and again in 2007–09 (Fig. 1). Such as SST and chlorophyll *a*, interannual changes in the larval pool in 1995–2009 could not be summarized in a single trend (Tables I and II).

While our results failed to reveal any significant interannual trend in either SST, phytoplankton biomass or meroplankton abundance, seasonality was clearly evident in monthly between-year anomalies (Fig. 3). Warmer waters (>23°C) occurred in March and April, at the end of summer and beginning of autumn. At the same time (March), the first peak of larval abundance appeared followed by a strong decrease in phytoplankton biomass (April). After this period, SST and meroplankton abundance started to fall until September, while chlorophyll *a* reached its highest value (monthly between-year average ~ 1.2 mg m^{-3}, Fig. 3). Phytoplankton blooms were evident during the austral spring, when the lowest SST suggested that upwelling reached its maximum intensity (monthly between-year average <22°C). At the end of the spring (November), a second peak of larval abundance appeared and the phytoplankton biomass strongly decreased in the following month (<0.9 mg m^{-3}). The relationship between phytoplankton biomass, meroplankton abundance and SST led to a highly significant seasonal cross-correlation, but delayed by 1 month for chlorophyll *a* (Table II, Fig. 4).

Unidentified nauplii of Cirripedia and Mytilidae veligers were the most abundant group throughout the time series, averaging respectively 39 and 19% of total meroplankton abundance. Both groups usually peak

Table II: Interannual and seasonal cross-correlation between annual ($n = 15$) and monthly between-year ($n = 12$) anomalies of SST, chlorophyll a *(Chl* a*) and total meroplankton (Mero)*

	Annual ($n = 15$)			Seasonal		
	r	Lag	P-value	r	Lag	P-value
SST vs. Chl *a*	−0.20	0	0.47	−0.70	1	0.01
SST vs. Mero	0.28	0	0.32	0.56	0	0.06
Mero vs. Chl *a*	−0.23	0	0.41	−0.84	1	0.003

Only the highest correlation value and correspondent lag are shown. Lag in year for annual and month for seasonal.

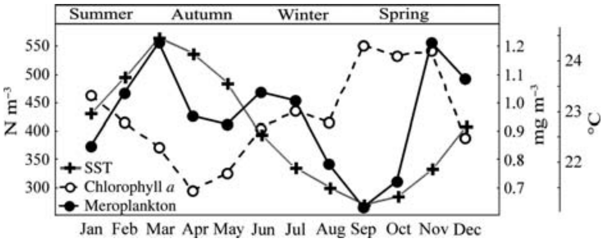

Fig. 3. Monthly between-year average of SST (plus symbol), chlorophyll *a* (open circles) and meroplankton abundance (black circles).

twice per year (Fig. 5a), although only one main peak was evident in each of 1997 and 2007. The first seasonal peak of Mytilidae and Cirripedia was concurrent at the end of austral summer and beginning of autumn, but the second peak showed a higher interannual and intergroup variation (Fig. 5b). Only this second peak of larval abundance in both groups was negatively correlated to the interannual changes in chlorophyll *a* (Fig. 5b).

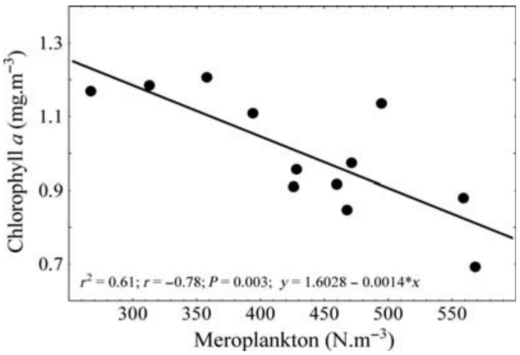

Fig. 4. Relationship between monthly between-year average of meroplankton abundance and lagged chlorophyll *a* (1 month delayed).

DISCUSSION

The Cabo Frio region is characterized by dominance of the warm Tropical Water in the upper 200 m, mainly during the austral autumn and winter, when southern winds are unfavourable for upwelling (Valentin *et al.*, 1987; Lima *et al.*, 1996; Lorenzzetti and Gaeta, 1996). The 1995–2009 time series shows high SST and low chlorophyll *a* anomalies early in the year, at the end of summer and at the beginning of autumn (March and April), and these seem to have driven the first peak of the larval pool. Under the influence of this warm and oligotrophic water, the phytoplankton assemblages are usually dominated by small cells (<2 μm) (Platt *et al.*, 1983; Li and Platt, 1987) and productivity is not as high as during upwelling (Carvalho and Gonzalez-Rodriguez, 2004; Guenther and Valentin, 2008). Therefore, primary biomass seems to be simultaneously nutrient- and grazing-limited (Gonzalez-Rodriguez *et al.*, 1992; Guenther *et al.*, 2008), and high abundance of larvae must have further reduced the phytoplankton biomass under oligotrophic conditions. In contrast, the high rate of zooplankton metabolism that occurs in warm oligotrophic oceans may also contribute to the regeneration of nutrients used by phytoplankton, and therefore to provide fuel supporting primary productivity (Banse, 1995). Our results are based on the meroplankton and phytoplankton relationship, and do not take into account other grazers and prey species, but suggest that meroplankton grazing during the larval pool peak at the end of summer was more effective in reducing rather than enhancing phytoplankton growth via nutrient regeneration.

According to some studies on grazing upon natural and cultured assemblages of phytoplankton, the ingestion of prey may be highly selective among holo- and meroplankton (Hart, 1991; Martin *et al.*, 1996). It has been argued that, according to their morphology and behaviour, many larvae may actively select prey by size, locomotion etc. (Rivkin *et al.*, 1986; Strathmann and Grünbaum, 2006). Polychaete larvae and nauplii of *Balanus* sp., for example, have a more herbivorous behaviour and may consume twice as many diatoms as the globally abundant nauplii of the copepod *Calanus* spp. (Martin *et al.*, 1996; Turner *et al.*, 2001).

From a classical point of view, larger zooplankton (>200 μm), mostly copepods, are the major grazers upon phytoplankton and are therefore the most important link between primary and secondary production (Wiggert *et al.*, 2005; Richardson, 2008; Uye, 2010). A second approach considers the mixo- and heterotrophic microplankton as the main consumers of

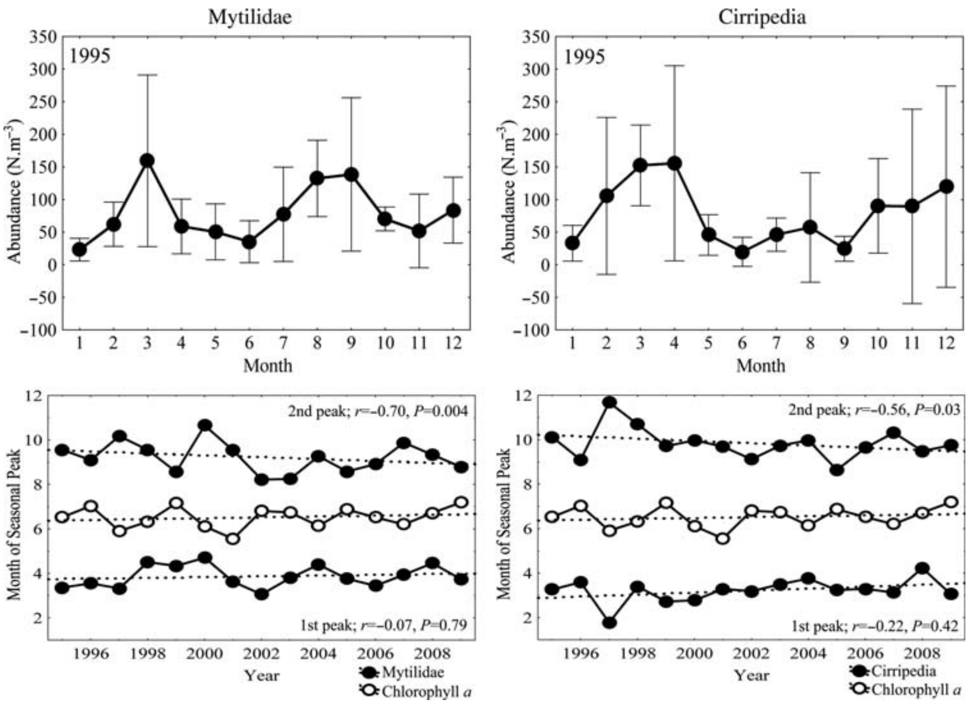

Fig. 5. Seasonal changes in phenology of meroplankton. (**a**) Examples of seasonal cycles for *Mytilidae veliger* and *Cirripedia nauplius*; and (**b**) interannual variability in the seasonal peak for *Mytilidae veliger*, *Cirripedia nauplius* and chlorophyll *a*.

the small autotrophic phytoplankton (Azam *et al*., 1983; Huskin *et al*., 2001): this approach has been modified in a more comprehensive model of food webs to address the way in which community production is diverted through its size-structured components (Martin *et al*., 1996; Calbet *et al*., 2001; Turner *et al*., 2001; Calbet and Landry, 2004; Schnetzer and Caron, 2005). During the summer peak of the larval pool, when warm water improves larval development, the food for meroplankton would possibly be insufficient given the small amount of phytoplankton in the Tropical Water, but potential other sources were outside the scope of our study. In some ecosystems where there is insufficient time to sustain larval development, larval supply is not so directly coupled to phytoplankton production. For example, under light-limited conditions, where high rates of primary production occur for only a few months, some larvae prefer to assimilate organic solutes and ingest bacteria, while actively excluding phytoplankton from the diet (Rivkin *et al*., 1986).

Even though the phenology of meroplankton and phytoplankton were directly related to each other, the very low primary biomass could not have driven the first seasonal peak of larval supply that occurred at the end of summer. Accordingly, it was most likely triggered by another stronger cue, such as increasing temperature. Many parameters of plankton communities, such as size structure and taxonomic composition, are regulated by their physical and chemical environment, and temperature is probably the most important physical variable structuring marine ecosystems (Richardson, 2008). Warmer temperatures, within the thermal niche limits of a species, can improve larval survival by speeding development and shortening the time spent in the planktonic stage (Hoegh-Guldberg and Pearse, 1995; O'Connor *et al*., 2007; Kirby *et al*., 2008). In Bivalvia, for example, increases in temperature shorten the duration of the larval phase more than do increases in food availability (Mackie, 1984). The seasonal pattern of meroplankton abundance followed that of SST closely enough to suggest that the summer larval peak was triggered by temperature. After the summer, both meroplankton abundance and SST gradually fell to their lower values in the spring (September), when upwelling became more frequent and intense.

The frequency of nutrient input by upwelling strongly affects both size distribution of organisms and coupling between primary and secondary productivity (Hofmann and Ambler, 1988). At the same time, upwelling may occur frequently enough to decrease mesozooplankton growth and to reduce the grazing pressure (Carr, 1998). Under low-grazing pressure and more frequent nutrient inputs, when the responses of phytoplankton should be stronger (Peña *et al*., 1994), primary productivity was further fuelled and the biomass of phytoplankton was strongly increased, but mainly during the spring. In the Cabo Frio region, when coastal upwelling is more frequent, new nutrients and larger cells brought to the euphotic zone quickly change the composition of phytoplankton and fuels primary productivity (Gonzalez-Rodriguez *et al.*, 1992; Kiørboe, 1993). Therefore, the size-structured food web in the region becomes more autotrophic and favourable to larger species (Guenther *et al.*, 2008), including large meroplankton. The spring bloom of phytoplankton in the region was clearly evident in the time series, and even a summer bloom has been reported (Valentin, 1984a). The same result was observed throughout the time series and suggests that phenology of phytoplankton and meroplankton in the Cabo Frio region was strongly affected by the frequency and intensity of upwelling. Our results reveal that the later the bloom of phytoplankton occurred, the earlier was the second peak of larval release. Years that had a clear spring bloom of phytoplankton, such as 1996 and 1999, led to a fast response of Mytilidae and Cirripedia and then to an increased larval pool. In contrast, when the major bloom of phytoplankton occurred earlier, as a summer bloom, the larval hatching was delayed until the end of the year. Under conditions of maximum upwelling, the phytoplankton assemblage is usually dominated by large cells, mostly diatoms that should increase the efficiency of grazing by mesozooplankton relative to microplankton (Pitcher *et al.*, 1991; Irigoien *et al.*, 2005; Zarauz *et al.*, 2009). During the spring bloom, the herbivorous food web is usually established, and a greater number of larvae are able to fulfil their metabolic and dietary requirements, and then to survive. The second peak in the larval pool that occurs from August to November quickly increases the grazing pressure and lowers the phytoplankton biomass in the following month (December), similarly to the first peak during the summer. Based on a physical−biological coupled model, Carbonel and Valentin (Carbonel and Valentin, 1999) showed that the strength and duration of the phytoplankton bloom under upwelling conditions in the Cabo Frio region is directly influenced by the grazing rate. These changes may be related to both seasonal and interannual shifts in the size-structured food web, which may affect the coupling between phytoplankton biomass and larval abundance. The recruitment success that depends in some way on the larval pool, among other processes (Broitman *et al.*, 2008; Pineda *et al.*, 2009), should also be dependent on the phenology of primary producers in the plankton system. Thus, interannual and seasonal changes in phytoplankton biomass and SST, which play a significant role in the larval pool, may also affect the adult benthic population.

The high-meroplankton−low-phytoplankton and low-meroplankton−high-phytoplankton years could suggest a negative relationship between groups, but the non-significant cross-correlation found between annual anomalies leads us to ascribe more importance to changes at a lower scale. On an annual or even longer scale, any change in the average phytoplankton biomass in pelagic ecosystems could be modulated by the net growth of its constituents. Peaks of larval release can in fact play a role in controlling the net growth of phytoplankton, but predominantly immediately after hatching, when larval density is high. As larvae grow, the majority are thought to be predated or exported (Thorson, 1950), while some settle (Pineda *et al.*, 2009), after which the net growth of phytoplankton could quickly increase again if not nutrient-limited and if the ingestion by other grazers remains at a low rate. The relative importance of meroplankton larvae in marine pelagic environments fluctuates, becoming greater at certain times of the year, when the larvae comprise a large percentage of the total zooplankton community (Highfield *et al.*, 2010). At such times, the meroplankton assemblages are usually dominated by one or a few species, and may act as a single functional group in the system, such as in the coastal upwelling area of Cabo Frio. In contrast, when considering a long time series, many unrelated species may peak at different moments, thus reflecting low-level interannual patterns. Similarly, the abundance and biomass of zooplankton, as a whole, usually show highly variable temporal patterns, which tend to mask any clear seasonal signal (Calbet *et al.*, 2001). Therefore, the interannual coupling between SST, phytoplankton biomass and larval pool was probably hidden by the succession of meroplankton species during 1995−2009 in the Cabo Frio region: the seasonal coupling suggests that marine pelagic phenology is even more sensitive to and therefore tracks changes in the ecosystem of the region.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org.

ACKNOWLEDGEMENTS

The authors would like to thank all those who have worked on the sampling and laboratory analysis, mainly the Chemical Group of IEAPM, and also the staff of the Department of Oceanography. We also thank Dr Daniela Bartholo, Dr Walquiria Pessanha and the two anonymous reviewers for critical reviews.

FUNDING

We thank FAPERJ – Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro for financial support (E26/110.220/2011).

REFERENCES

Anger, K. (2001) *The Biology of Decapod Crustacean Larvae*. Crustacean Issues. Vol. 14. A.A. Balkema, Swets and Zeitlinger, Lisse, The Netherlands.

Azam, F., Fenchel, T., Field, J. G. *et al*. (1983) The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog Ser.*, **10**, 257–263.

Banse, K. (1995) Zooplankton: pivotal role in the control of ocean production: I. Biomass and production. *ICES J. Mar. Sci.*, **52**, 265–277.

Belgrano, A., Legendre, P., Dewarumez, J. *et al*. (1995) Spatial structure and ecological variation of meroplankton on the French-Belgian coast of the North Sea. *Mar. Ecol. Prog. Ser.*, **128**, 43–50.

Boltovskoy, D. (1981) Caracteristicas biologicas del Atlantico Sudoccidental. In Boltovskoy, D. (ed.), *Atlas del Atlántico Sudoccidental y métodos de trabajo con el zooplancton marino*. INIDEP, Mar del Plata, pp. 239–251.

Box, G. E. P. and Jenkins, G. W. (1976) *Time Series Analysis: Forecasting and Control*. Holden-Day, San Francisco.

Brandini, F. P., Lopes, R. M., Gutseit, K. S. *et al*. (eds) (1997) *Planctonologia na plataforma continental do Brasil: diagnose e revisão bibliográfica*. MMA, CIRM, FEMAR, Rio de Janeiro.

Broitman, B. R., Blanchette, C. A., Menge, B. A. *et al*. (2008) Spatial and temporal patterns of invertebrate recruitment along the west coast of the United States. *Ecol. Monogr.*, **78**, 403–421.

Calbet, A., Garrido, S., Saiz, E. *et al*. (2001) Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. *J. Plankton Res.*, **23**, 319–331.

Calbet, A. and Landry, M. R. (2004) Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnol. Oceanogr.*, **49**, 51–57.

Carbonel, C. A. A. and Valentin, J. L. (1999) Numerical modelling of phytoplankton bloom in the upwelling ecosystem of Cabo Frio (Brazil). *Ecol. Model.*, **116**, 135–148.

Carr, M. E. (1998) A numerical study of the effect of periodic nutrient supply on pathways of carbon in a coastal upwelling regime. *J. Plankton Res.*, **20**, 491–516.

Carvalho, W. F. and Gonzalez-Rodriguez, E. (2004) Development of primary and bacterial productivity in upwelling waters of Arraial do Cabo region, RJ (Brazil). *Braz. J. Oceanogr.*, **52**, 35–45.

Cloern, J. E. (1982) Does the benthos control phytoplankton biomass in south San Francisco Bay? *Mar. Ecol. Prog. Ser.*, **9**, 191–202.

Cushing, D. H. (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Mar. Biol.*, **26**, 249–293.

Durant, J. M., Hjermann, D. Ø., Ottersen, G. *et al*. (2007) Climate and the match or mismatch between predator requirements and resource availability. *Clim. Res.*, **33**, 271–283.

Durbin, J. (1970) Testing for serial correlation in least-squares regression when some of the regressors are lagged dependent variables. *Econometrica*, **38**, 410–421.

Edwards, M. and Richardson, A. J. (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, **430**, 881–884.

Gonzalez-Rodriguez, E., Valentin, J. L., Andre, D. L. *et al*. (1992) Upwelling and downwelling at Cabo Frio (Brazil): comparison of biomass and primary production responses. *J. Plankton Res.*, **14**, 289–306.

Gonzalez-Silvera, A., Santamaria-del-Angel, E., Garcia, V. M. T. *et al*. (2004) Biogeographical regions of the tropical and subtropical Atlantic Ocean off South America: classification based on pigment (CZCS) and chlorophyll-*a* (SEAWIFS) variability. *Cont. Shelf Res.*, **24**, 983–1000.

Guenther, M., Gonzalez-Rodriguez, E., Carvalho, W. *et al*. (2008) Plankton trophic structure and particulate organic carbon production during a coastal downwelling-upwelling cycle. *Mar. Ecol. Prog Ser.*, **363**, 109–119.

Guenther, M. and Valentin, J. L. (2008) Bacterial and phytoplankton production in two coastal systems influenced by distinct eutrophication processes. *Oecol. Bras.*, **12**, 172–178.

Hart, M. W. (1991) Particle captures and the method of suspension feeding by echinoderm larvae. *Biol. Bull.*, **180**, 12–27.

Highfield, J. M., Eloire, D., Conway, D. *et al*. (2010) Seasonal dynamics of meroplankton assemblages at station L4. *J. Plankton Res.*, **32**, 681–691.

Hoegh-Guldberg, O. and Pearse, J. S. (1995) Temperature, food availability, and the development of marine invertebrate larvae. *Am. Zool.*, **35**, 415–425.

Hofmann, E. E. and Ambler, J. W. (1988) Plankton dynamics on the outer southeastern U.S. Continental Shelf. Part II: a time-dependent biological model. *J. Mar. Res.*, **46**, 883–917.

Huskin, I., Anadón, R., Woodd-Walker, R. S. *et al*. (2001) Basin-scale latitudinal patterns of copepod grazing in the Atlantic Ocean. *J. Plankton Res.*, **23**, 1361–1371.

Irigoien, X., Flynn, K. J. and Harris, R. P. (2005) Phytoplankton blooms: a 'loophole' in microzooplankton grazing impact. *J. Plankton Res.*, **27**, 313–321.

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

Kirby, R. R., Beaugrand, G., Lindley, J. A. *et al*. (2007) Climate effects and benthic–pelagic coupling in the North Sea. *Mar. Ecol. Prog. Ser.*, **330**, 31–38.

Kirby, R. R., Beaugrand, G. and Lindley, J. A. (2008) Climate-induced effects on the meroplankton and the benthic-pelagic ecology of the North Sea. *Limnol. Oceanogr.*, **53**, 1805–1815.

Li, W. K. W. and Platt, T. (1987) Photosynthetic picoplankton in the ocean. *Sci. Prog*, **71**, 117–132.

Lima, I. D., Garcia, A. E. C. and Möller, O. O. (1996) Ocean surface processes on the southern Brazilian shelf: characterization and seasonal variability. *Cont. Shelf Res.*, **16**, 1307–1317.

Lorenzzetti, J. A. and Gaeta, S. A. (1996) The Cape Frio upwelling effect over the south Brazil bight northern sector shelf waters: a study using AVHRR images. *Int. Arch. Photogramm. Remote Sens.*, **31**, 448–453.

Mackenzie, B. R. and Köster, F. W. (2004) Fish production and climate: sprat in the Baltic Sea. *Ecology*, **85**, 784–794.

Mackie, G. L. (1984) Bivalves. In Wilbur, K. M., Tompa, A. S., Verdonk, N. H. and van den Biggelaar, J. A. M. (eds), *The Mollusca: Reproduction*. Vol. 7. Academic Press, London, UK, pp. 352–418.

Marcus, N. H. and Boero, F. (1998) Minireview: the importance of benthic-pelagic coupling and the forgotten role of life cycle in coastal aquatic systems. *Limnol. Oceanogr.*, **43**, 763–768.

Martin, D., Pinedo, S. and Sardá, R. (1996) Grazing by meroplanktonic polychaete larvae may help to control nanoplankton in the NW Mediterranean littoral: *in situ* experimental evidence. *Mar. Ecol. Prog. Ser.*, **143**, 239–246.

McConaugha, J. R. (1988) Export and reinvasion of larvae as regulators of estuarine decapod populations. *Am. Fish. Soc. Symp.*, **3**, 90–103.

Monteiro-Ribas, W. M., Rocha-Miranda, F., Romano, R. C. and Quintanilha, J. (2006) Larval development of *Brachydontes solisianus* (Bivalvia, Mytilidae), with notes on differences between its hinge system and that of the mollusk *Perna perna*. *Braz. J. Biol.*, **66**, 109–116.

Morgan, S. G. and Christy, J. H. (1997) Planktivorous fishes as selective agents for reproductive synchrony. *J. Exp. Mar. Biol. Ecol.*, **209**, 89–101.

Mura, M. P., Agustí, S., del Giorgio, P. A. *et al.* (1996) Loss-controlled phytoplankton production in nutrient-poor littoral waters of the NW Mediterranean: *in situ* experimental evidence. *Mar. Ecol. Prog Ser.*, **130**, 213–219.

Nixon, S. W., Fulweiler, R. W., Buckley, B. A. *et al.* (2009) The impact of changing climate on phenology, productivity, and benthic–pelagic coupling in Narragansett Bay. *Estuarine Coastal Shelf Sci.*, **82**, 1–18.

O'Connor, M. I., Bruno, J. F., Gaines, S. D. *et al.* (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proc. Natl Acad. Sci.*, **104**, 1266–1271.

Parsons, T. R., Maita, Y. and Lalli, C. M. (1984) *A Manual of Chemical and Biological Methods for Seawater Analysis*. Pergamon press, Oxford.

Pechenik, J. A. (1999) On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Mar. Ecol. Prog. Ser.*, **177**, 269–297.

Peña, M. A., Lewis, M. R. and Cullen, J. J. (1994) New production in the warm waters of the tropical Pacific Ocean. *J. Geophys. Res.*, **99**, 14255–14268.

Pineda, J., Reyns, N. B. and Starczak, V. R. (2009) Complexity and simplification in understanding recruitment in benthic populations. *Popul. Ecol.*, **51**, 17–32.

Piontkovski, S., O'Brien, T. D., Umani, S. *et al.* (2006) Zooplankton and the North Atlantic Oscillation: a basin-scale analysis. *J. Plankton Res.*, **28**, 1039–1046.

Pitcher, C. C., Walker, D. R., Mitchell-Innes, B. A. *et al.* (1991) Short-term variability during an anchor station study in the southern Benguela upwelling system: phytoplankton dynamics. *Prog Oceanogr.*, **28**, 39–64.

Platt, T., Subba Rao, D. V. and Irwin, B. (1983) Photosynthesis of picoplankton in the oligotrophic ocean. *Nature*, **301**, 702–704.

Pugnetti, A., Bazzoni, A. M., Beran, A. *et al.* (2008) Changes in biomass structure and trophic status of the plankton communities in a highly dynamic ecosystem (Gulf of Venice, northern Adriatic Sea). *Mar. Ecol.*, **29**, 367–374.

Quenouille, M. H. (1952) *Associated Measurements*. Butterworths, London.

Richardson, A. J. (2008) In hot water: zooplankton and climate change. *ICES J. Mar. Sci.*, **65**, 279–295.

Rivkin, R. B., Bosch, I., Pearse, J. S. *et al.* (1986) Bacterivory: a novel feeding mode for asteroid larvae. *Science*, **233**, 1311–1314.

Schnetzer, A. and Caron, D. A. (2005) Copepod grazing impact on the trophic structure of the microbial assemblage of the San Pedro Channel, California. *J. Plankton Res.*, **27**, 959–971.

Shapiro, S. S., Wilk, M. B. and Chen, H. J. (1968) A comparative study of various tests of normality. *J. Am. Stat. Assoc.*, **63**, 1343–1372.

Sommer, U. and Sommer, F. (2006) Cladocerans versus copepods: the cause of contrasting top–down controls on freshwater and marine phytoplankton. *Oecologia*, **147**, 183–194.

Starr, M., Himmelman, J. H. and Therriault, J. C. (1990) Direct coupling of marine invertebrate spawning with phytoplankton blooms. *Science*, **247**, 1071–1074.

Stibor, H., Vadstein, O., Lippert, B. *et al.* (2004) Calanoid copepods and nutrient enrichment determine population dynamics of the appendicularian *Oikopleura dioica*: a mesocosm experiment. *Mar. Ecol. Prog. Ser.*, **270**, 209–215.

Strathmann, R. R. and Grünbaum, D. (2006) Good eaters, poor swimmers: compromises in larval form. *Integr. Comp. Biol.*, **46**, 312–322.

Thorson, G. (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev. Cambridge Philos. Soc.*, **25**, 1–45.

Turner, J. T., Levinsen, H., Nielsen, T. G. *et al.* (2001) Zooplankton feeding ecology: grazing on phytoplankton and predation on protozoans by copepod and barnacle nauplii in Disko Bay, West Greenland. *Mar. Ecol. Prog. Ser.*, **221**, 209–219.

Uye, S. (2010) Human forcing of the copepod–fish–jellyfish triangular trophic relationship. *Hydrobiologia*, **666**, 71–83.

Valentin, J. L. (1984a) Analyse des paramètres hydrobiologiques dans la remontée de Cabo Frio (Brésil). *Mar. Biol.*, **82**, 259–276.

Valentin, J. L. (1984b) Spatial structure of the zooplankton community in the Cabo Frio region (Brazil) influenced by coastal upwelling. *Hydrobiologia*, **113**, 183–199.

Valentin, J. L., Andre, D. L. and Jacob, S. A. (1987) Hydrobiology in the Cabo Frio (Brazil) upwelling: two dimensional structure and variability during a wind cycle. *Cont. Shelf Res.*, **7**, 77–88.

Wiggert, J. D., Haskell, A. G. E., Paffenhöfer, G.-A. *et al.* (2005) The role of feeding behaviour in sustaining copepod populations in the tropical ocean. *J. Plankton Res.*, **27**, 1013–1031.

Zarauz, L., Irigoien, X. and Fernandes, J. A. (2009) Changes in plankton size structure and composition, during the generation of a phytoplankton bloom, in the central Cantabrian Sea. *J. Plankton Res.*, **31**, 193–207.