

# Large-scale season-dependent effects of temperature and zooplankton on phytoplankton in the North Atlantic

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**ABSTRACT:** We analyzed 13 yr of monthly time series (1998 to 2010) of satellite-derived chlorophyll, sea-surface temperature and zooplankton abundance (copepod taxa from continuous plankton recorder surveys) in order to better understand the ecological processes that regulate the seasonal phytoplankton dynamics in different regions of the North Atlantic Ocean. Results showed large-scale, seasonally varying effects of temperature and zooplankton abundance on chlorophyll concentration. Specifically, we found positive temperature effects in most of the regions, which tended to be most pronounced in spring and early summer, especially in the warmer water regions. The situation changed in late summer (mostly July to September), when we detected a negative correlation between chlorophyll concentration and the abundance of copepod nauplii, suggesting top-down control by grazing when phytoplankton generally suffer nutrient limitation and low growth rate. Our results demonstrate that both physical (bottom-up) effects and zooplankton (top-down) effects alternate to shape the seasonal dynamics of phytoplankton in the North Atlantic.

**KEY WORDS:** Trophic control · Seasonal patterns · Sea-surface temperature · Plankton · Top-down · Bottom-up · Generalized additive models

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## INTRODUCTION

Marine phytoplankton contribute nearly 50% of the global primary production (Field et al. 1998) and play a vital role in regulating global carbon sequestration (Sabine et al. 2004), as well as serving as the ultimate base of the food web and, thus, fishery yields (Chassot et al. 2010). Marine phytoplankton generally fluctuate at seasonal and interannual time scales, and much effort has been devoted to address-

ing the ecological processes that regulate their dynamics (Hays et al. 2005). These ecological processes include physical and chemical drivers (e.g. temperature, light and nutrients), known as bottom-up regulation, and zooplankton grazing (or viral lysis), known as top-down processes. The relative importance of these 2 structuring forces has been studied by ecologists and oceanographers in the past few decades (Weisse 1991, Lapointe 1999, Reid et al. 2000, Lotze et al. 2001, Verity et al. 2002, Smith &

Lancelot 2004, Jaschinski & Sommer 2008), without arriving at definitive conclusions. This partly reflects that most of these processes are involved simultaneously, although with different relative contributions.

Several studies suggest that marine phytoplankton are primarily bottom-up controlled, when it comes to explaining both the seasonal cycle (Sverdrup 1953) and the interannual variation (Richardson & Schoeman 2004, Raitso et al. 2006, Stenseth et al. 2006, Irwin & Finkel 2008). However, other studies have suggested that phytoplankton dynamics are primarily driven by alterations in zooplankton grazing pressure (Strom et al. 2001, Deonaraine et al. 2006, Sommer & Sommer 2006, Kim et al. 2007, Strom et al. 2007, Chen et al. 2009, Behrenfeld 2010). In the Skagerrak system, a top-down relationship was found between *Calanus finmarchicus* and phytoplankton (Durant et al. 2013). Banse (1994) argued that copepod grazing had a major control on phytoplankton biomass, even in areas where nutrient inputs were substantial and phytoplankton growth rates were high. More recent evidence suggests that the type of trophic forcing could vary temporally and spatially. For example, a general spatially homogeneous bottom-up control, which characterized the base of the food web from 1958 to 1972 in the North Sea, was reported to change to a region-specific top-down control after 1972 (Llope et al. 2012). In the subtropical south-western Atlantic Ocean, a negative coupling between phytoplankton and zooplankton was only found during the austral spring (mostly September to November) (Fernandes et al. 2012).

To study the general importance of bottom-up and top-down factors in controlling phytoplankton biomass, there is a need for data with large spatial and temporal coverage. In the North Atlantic region, a source of spatially explicit data on plankton abundance is the Continuous Plankton Recorder (CPR) Program run by the Sir Alister Hardy Foundation for Ocean Sciences (SAHFOS) ([www.sahfos.org/](http://www.sahfos.org/)). The CPR Survey provides long-term, near-surface abundance data for plankton in the North Atlantic with a monthly resolution (Richardson et al. 2006). There is considerable evidence that CPR data capture a roughly consistent fraction of the *in situ* abundance of each zooplankton taxon and, thus, reflect the major patterns observed in the plankton (Batten et al. 2003a), as zooplankton biomass typically is dominated by taxa (medium-sized copepods and cladocerans) that are well sampled by the mesh of the CPR (Hays 1994). Seasonal cycles estimated from CPR data for relatively abundant taxa are repeatable each year, and are sufficiently resolved to detect the ear-

lier seasonal peaks in response to the warmer sea temperatures of recent years (Edwards & Richardson 2004). There is generally good agreement between zooplankton seasonal cycles measured by the CPR and by other samplers such as WP-2 nets (John et al. 2001). While the CPR can also give an estimate of the phytoplankton biomass (the phytoplankton colour index; PCI), we chose to use satellite-derived high-resolution ocean colour data for 2 reasons. Firstly, there is a close relationship between PCI and chlorophyll (chl; a widely used proxy for phytoplankton biomass) measured by satellite (Batten et al. 2003b, Raitso et al. 2005, McQuatters-Gollop et al. 2007). Secondly, while overall chlorophyll (PCI) is estimated from CPR samples, the exact nature of the PCI has been questioned because it is assessed visually by comparison with standard colour charts (Robinson & Hiby 1978) and is assigned 4 numerical values (0, 1, 2, 6.5). Having only 4 categories results in a rather coarse resolution of the phytoplankton variability relative to satellite-derived continuous chl data, especially on a seasonal scale. The extensive coverage and resolution of satellite data allow further conclusions to be drawn that are representative of large areas. To our knowledge, few studies have yet combined the high-quality satellite-derived chlorophyll data with (zooplankton) predator abundance data from the CPR.

Previous studies have generally approached the trophodynamics of plankton on an annual scale (Richardson & Schoeman 2004, Raitso et al. 2006, Stenseth et al. 2006, Irwin & Finkel 2008, Llope et al. 2012). However, aggregating data across seasons can mask seasonally dependent effects of factors (Persson et al. 2012). The aim of the present study was to assess whether seasonally varying effects of climate and predators on phytoplankton can be observed in the North Atlantic. Light obviously also plays an important role in controlling phytoplankton growth and abundance, and, while solar radiation clearly is unaffected by climate change, photosynthetic active radiation in the water column may nevertheless change in response to ice or cloud cover (Clement et al. 2009). The net combined effect of changes in temperature and light on primary production is hard to predict, however. Higher temperatures could cause greater stratification and reduced productivity due to reduced mixing and nutrient scarcity. In the case of light limitation, a higher degree of stratification could promote volume-specific primary production. Cloud cover would reduce surface radiation, but also prevent surface heat loss. Temperature itself also largely depends on the fate of photons in the water column

and thus light attenuation by particles or solutes. But it would be difficult to include all of these factors and beyond the scope of our work. Hence, we focus on the bottom-up effects of temperature on phytoplankton in this study.

To address this issue, monthly values of the satellite-derived chlorophyll *a* (chl) concentration (considered as a proxy for phytoplankton biomass), CPR-derived zooplankton abundance (copepod nauplii, total copepodites, *Calanus* copepodite stages I to IV and *Calanus* copepodite stages V and VI) and sea-surface temperature were extracted for 7 selected CPR standard areas in the North Atlantic (Beare et al. 2003) over 13 yr (1998 to 2010). These data were analyzed using a seasonally varying-coefficient generalized additive model (GAM) (Hastie & Tibshirani 1990, 1993) that allowed us to quantify how the associations among the predictor variables and the response varied as smooth functions of month-of-the-year.

## MATERIALS AND METHODS

### Data sources

**Study area.** Seven CPR standard areas (B2, B4, B5, B6, B7, C7 and D7 in Fig. 1), characterized by higher sampling frequency than other standard areas, were selected for this study. These areas cover both a longitudinal gradient centred at 61° N (B7–B2, with longitudes centred at 37° W, 26° W, 14° W, 3° W and 0° W, respectively), as well as a latitudinal gradient centred at 37° W (B7, C7 and D7, centred at latitudes 61° N, 57° N and 52.5° N, respectively). These areas have been used to describe plankton seasonal and interannual changes in the North Atlantic, to test hypotheses on the propagation of the effect of sea-surface warming up the plankton food web in the Northeast Atlantic (Richardson & Schoeman 2004) and to investigate the role of phytoplankton productivity, temperature and environmental stability on the control of copepod diversity (Nogueira et al. 2012). CPR samples are collected by means of a robust plankton filtering instrument towed by ships-of-opportunity along their standard routes (Hays 1994). The near-surface seawater (ca. 7 m depth) is filtered by a moving band of silk of 270 µm mesh size that collects plankton from the ambient water. Further information about counting and data processing, consistency and comparability of CPR sampling can be found elsewhere (Richardson et al. 2006).

**Chlorophyll data.** A 13 yr (1998 to 2010) record of monthly chlorophyll *a* concentration (chl, mg m<sup>-3</sup>)

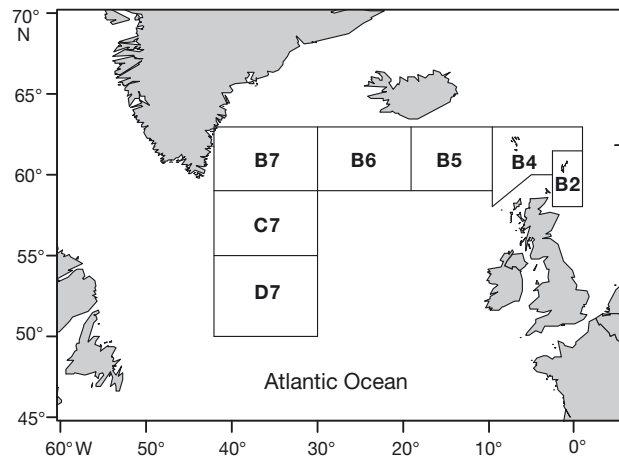


Fig. 1. Positions of the continuous plankton recorder (CPR) standard areas selected for the present study. These selected standard areas are characterized by higher sampling frequency than other standard areas. B7–B2 are distributed along a longitudinal gradient, while B7–D7 are distributed along a latitudinal gradient

data obtained from the European Space Agency's GlobColour project ([www.globcolour.info/](http://www.globcolour.info/)) were used in this analysis. The remotely sensed level-3 monthly chl data were derived using standard case I ocean water algorithms (Morel & Maritorena 2001), with a spatial resolution of 1°. Compared to data from a single sensor, the merged products have approximately twice the mean global coverage and lower uncertainties (Maritorena et al. 2010). For the standard areas in our analysis, satellite-derived chlorophyll data were unavailable up to 3 mo each year during midwinter (November, December and January in B2 and B4–B7; November and December in C7; December in D7).

**Zooplankton data.** Copepods are usually the main grazers of phytoplankton and the most important link between primary producers and higher trophic levels (Wiggert et al. 2005, Richardson 2008, Uye 2011). For our analysis, we used the monthly resolved record of abundances (ind. m<sup>-3</sup>) of different copepod groups and stages for the 13 yr period (1998 to 2010) corresponding to the available satellite-derived chlorophyll data. The categories 'copepod nauplii' (NAU) include nauplii of all copepods sampled. The categories 'total copepodites' (COP) include all copepodite stages of all copepods sampled. The categories '*Calanus* I to IV' (CAL1) and '*Calanus* V and VI' (CAL2) include, respectively, Copepodite Stages I to IV and V and VI of *Calanus finmarchicus*, *C. helgolandicus* and *C. glacialis*. Specifically, *C. finmarchicus* represents >70% of the copepod biomass in the western Atlantic, Labrador Basin and

south of Iceland, and >90% off the Newfoundland coast and in the southern Norwegian Sea (Planque & Batten 2000). These regions in which *C. finmarchicus* dominated the dry weight of zooplankton basically covered the 7 study areas (B2, B4–B7, C7 and D7 in Fig. 1) in our research. Average lengths of specimens in CAL1 and CAL2 have been reported to be 1.65 and 2.48 mm, respectively (Robertson 1968). Note that the different sub-categories represent functional rather than taxonomical groups of the dominant copepods.

**Sea-surface temperature data.** Monthly satellite-derived sea-surface temperature (SST, °C) data were obtained from the NOAA Extended Reconstructed SST (ERSST) V3b data set with a spatial resolution of 1° ([www.esrl.noaa.gov/psd/data/gridded/data.noaa.ersst.html](http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.ersst.html)). All chlorophyll, zooplankton and SST data were averaged spatially in these 7 standard regions.

### Statistical analysis

**Seasonal GAMs.** Seasonal plankton trophodynamics were analyzed using GAMs (Wood 2006, 2008) with the *mgcv* library in the R environment (v.2.11.1; R Development Core Team 2010). GAMs can disentangle the additive effects of different predictor variables on the response variable from the data without making strong assumptions about the shape of the response function (Hastie & Tibshirani 1990). Phytoplankton biomass was modelled as a function of season (month), phytoplankton biomass anomaly of the previous month, temperature anomaly and abundance anomalies of 4 different zooplankton variables. Both phytoplankton biomass and zooplankton abundance data were  $\log_{10}(N+1)$  transformed (where  $N$  is chlorophyll concentration [ $\text{mg m}^{-3}$ ] or zooplankton abundance [ $\text{ind. m}^{-3}$ ]). The predictor variables were centred by subtracting the monthly mean values from the observations. That way, the predictor variables measured the interannual anomalies around the mean seasonal values. The model formula was:

$$\text{chl}_{ij} = \mu + f_1(\text{Month}_j) + f_2(\text{Month}_j, \text{by} = \text{chl}_{i(j-1)}) + f_3(\text{Month}_j, \text{by} = \text{SST}_{ij}) + \begin{cases} f_4(\text{Month}_j, \text{by} = \text{NAU}_{ij}) \\ f_4(\text{Month}_j, \text{by} = \text{COP}_{ij}) \\ f_4(\text{Month}_j, \text{by} = \text{CAL1}_{ij}) \\ f_4(\text{Month}_j, \text{by} = \text{CAL2}_{ij}) \end{cases} + \varepsilon_{ij} \quad (1)$$

Here,  $\text{chl}_{ij}$  is the phytoplankton biomass for month  $j$  in year  $i$ .  $\text{chl}_{i(j-1)}$  is the chlorophyll anomaly for

month  $j-1$  in year  $i$ , and  $\text{SST}_{ij}$  (see Fig. 3),  $\text{NAU}_{ij}$  (see Fig. 5), and  $\text{COP}_{ij}$ ,  $\text{CAL1}_{ij}$  and  $\text{CAL2}_{ij}$  (Figs. S1, S2 and S3, respectively, in the Supplement at [www.int-res.com/articles/suppl/m502p025\\_supp.pdf](http://www.int-res.com/articles/suppl/m502p025_supp.pdf)) are centred predictor variables as explained above in 'Zooplankton data'.  $\mu$  is an intercept;  $f_1$ ,  $f_2$ ,  $f_3$  and  $f_4$  are smooth functions (natural cubic splines with a maximum of 4 degrees of freedom) of month (1, 2, ..., 12). The notation 'by=' indicates that the smooth function  $f$  is multiplied by the covariate indicated, e.g. chl for  $f_2$ .  $f_1$  is the month-dependent intercept.  $f_2$  quantifies the month-dependent effect of lagged chlorophyll. More specifically, this function gives the coefficient for a predictor effect that is linear for any given month, but variable in magnitude (and possibly sign) among months. Month (1, 2, ..., 12) is considered a numeric variable (not a categorical). The function thus shows how the association between the inter-annual fluctuations in the predictor and response changes across the season.  $f_3$  is the month-dependent effect function of temperature, and  $f_4$  is the month-dependent effect function of zooplankton.  $\varepsilon_{ij}$  is a normal distributed and independent noise term.

In order to select which zooplankton variable to include as a covariate ( $f_4$ , Eq. 1), we compared models with each zooplankton group respectively and then selected the formulation with the lowest Akaike's information criterion (AIC) value (Burnham & Anderson 2002). Then the non-significant terms ( $p > 0.05$ ) were removed one by one from the selected model using a stepwise approach. The residuals from the final model selected for each area were inspected using normal quantile-quantile probability plots, to check that they had an approximately normal distribution. Autocorrelation functions (acf) and partial autocorrelation functions (pacf) were also used to detect if there was autocorrelation among the residuals.

**Granger causality test.** The Granger causality test is a statistical hypothesis test for determining whether one variable is useful in forecasting another (Granger 1969), and can be used to investigate the potential causal pathways in a time series (Thurman & Fisher 1988). For example, a time series of SST is said to Granger-cause phytoplankton if it can be shown that the past SST values contain information that helps predict phytoplankton and is beyond the information contained in past values of phytoplankton alone.

### Model diagnostics

The residuals from the models did not show strong deviations from the normal distribution, and there

was no strong autocorrelation left in the residuals (Fig. S4 in the Supplement). We therefore considered the reported p-values and confidence bands to be robust. Illustrations of the month-dependent intercept and month-dependent autoregressive effect of lagged chlorophyll are shown in Figs. S5 & S6 in the Supplement.

## RESULTS

### Seasonal patterns of plankton in the North Atlantic

Both phytoplankton biomass and zooplankton abundance revealed strong seasonal patterns in the 7 study regions (Fig. 2). Phytoplankton biomass generally

showed 1 peak per annual cycle (i.e. unimodal cycles), increasing in March and reaching the peak in June (except B6 in July). For zooplankton, the total copepodites, *Calanus* I to IV and *Calanus* V and VI generally increased in February, which implied that copepods came from diapause in deeper water into the surface layer before the onset of the phytoplankton spring bloom. The older zooplankton stages (*Calanus* V and VI) peaked at the same time or later than the younger zooplankton stages (*Calanus* I to IV and total copepodites) in Regions B2–B6, and earlier only in Regions B7, C7 and D7. *Calanus* I to IV peaked before chlorophyll only in Regions B2–B6, but in the same month or later in Regions B7, C7 and D7 (Fig. 2). The nauplii generally increased in March and peaked 1 or 2 mo later than the *Calanus* copepodites.

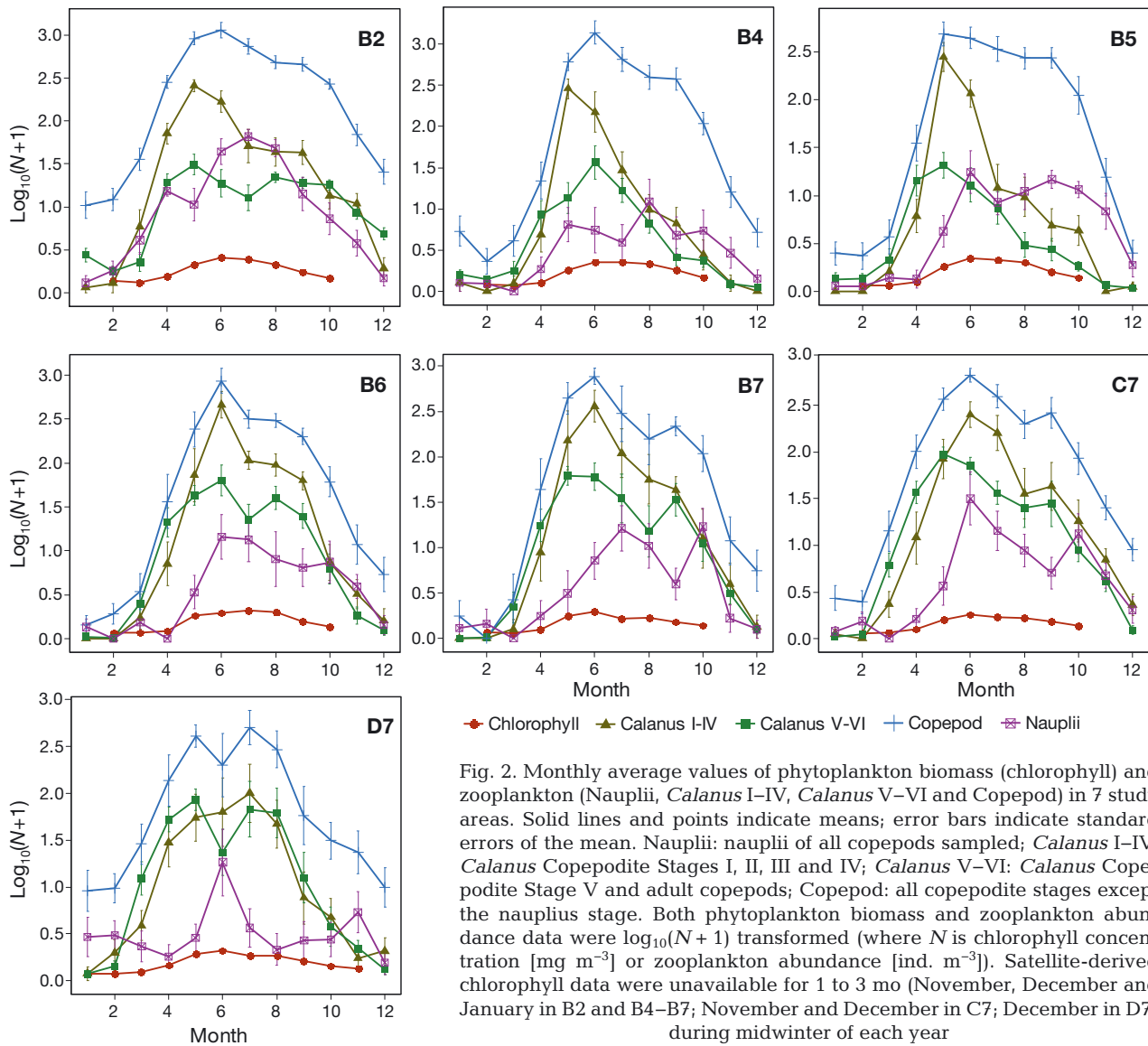


Fig. 2. Monthly average values of phytoplankton biomass (chlorophyll) and zooplankton (Nauplii, *Calanus* I–IV, *Calanus* V–VI and Copepod) in 7 study areas. Solid lines and points indicate means; error bars indicate standard errors of the mean. Nauplii: nauplii of all copepods sampled; *Calanus* I–IV: *Calanus* Copepodite Stages I, II, III and IV; *Calanus* V–VI: *Calanus* Copepodite Stage V and adult copepods; Copepod: all copepodite stages except the nauplius stage. Both phytoplankton biomass and zooplankton abundance data were  $\log_{10}(N+1)$  transformed (where  $N$  is chlorophyll concentration [ $\text{mg m}^{-3}$ ] or zooplankton abundance [ $\text{ind. m}^{-3}$ ]). Satellite-derived chlorophyll data were unavailable for 1 to 3 mo (November, December and January in B2 and B4–B7; November and December in C7; December in D7) during midwinter of each year

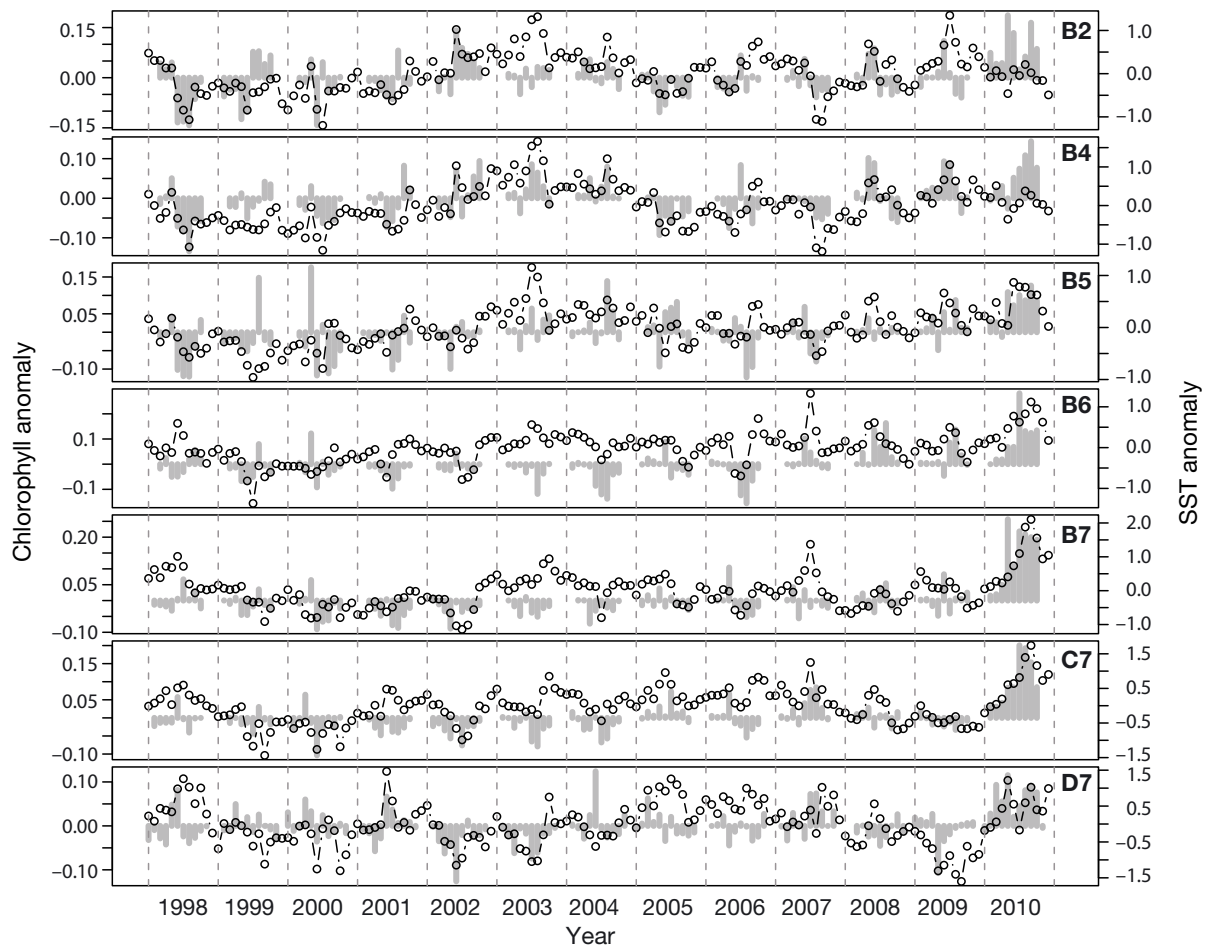


Fig. 3. Monthly anomalies of phytoplankton ( $\log_{10}[N + 1]$ , where  $N$  is chlorophyll concentration [ $\text{mg m}^{-3}$ ], bars) and sea-surface temperature (SST,  $^{\circ}\text{C}$ , circles) for the 7 study regions in the North Atlantic from 1998 to 2010

### Seasonal effects of SST on phytoplankton

Seasonally dependent effects of temperature on phytoplankton were assessed for each study region using a nonlinear interaction term between monthly SST anomaly and month ( $f_2$ , Eq. 1). There was general agreement between anomalies of phytoplankton and SST (Fig. 3). The results showed that temperature was a significant predictor for 5 out of the 7 regions studied ( $p < 0.001$  for B2, B4 and C7;  $p < 0.05$  for B7 and D7; Table 1). Positive relations between temperature and phytoplankton were found in all regions across all months (except B5), and the strength of this relation changed on a seasonal scale (Fig. 4). For 3 regions (B2, B4 and D7), the positive relation was strongest in spring; for 2 regions (B6 and B7), the positive relation was sustained through spring and early summer; for 1 region (C7), the positive relation was only observed in summer and autumn (Fig. 4).

### Seasonal effects of zooplankton on phytoplankton

GAMs were also used to identify the effects of zooplankton on phytoplankton ( $f_4$ , Eq. 1). Monthly anomalies of phytoplankton and copepod nauplius abundance for the 7 study regions in the North Atlantic are presented in Fig. 5. It seemed that there was an inverse relationship between phytoplankton and nauplii (Fig. 5), while no such pattern was observed between phytoplankton and older zooplankton stages (Figs. S1 to S3 in the Supplement). Our statistical analyses showed that only copepod nauplii turned out to be a significant predictor in explaining the variance of phytoplankton biomass for B5 ( $p < 0.001$ ), B6 ( $p < 0.01$ ) and C7 ( $p < 0.05$ ) (Table 1, Fig. 6). None of the other zooplankton variables (total copepodites, *Calanus* I to IV and V and VI) were selected as significant predictors of phytoplankton biomass in the final GAMs. Significant negative relations were found between copepod nauplii

Table 1. Results of the seasonal generalized additive models. Each line corresponds to 1 standard area in the North Atlantic (see Fig. 1). edf: estimated degree of freedom for smooth effect of month describing seasonal change in intercept or seasonally varying effect of a predictor variable;  $R^2$ : the proportion of variance in log chlorophyll concentration explained by the model. The statistical significance of the variable is indicated by: \*  $p < 0.05$ , \*\*  $p < 0.01$  and \*\*\*  $p < 0.001$ .  $MON_t$ : month at time  $t$ ;  $chl_{t-1}$ : chl  $a$  concentration at time  $t - 1$ ;  $SST_t$ : sea surface temperature at time  $t$ ;  $NAU_t$ : nauplius abundance at time  $t$

Region	Selected predictor variables (edf)			Mean intercept (SE)	$R^2$	n
B2	$MON_t$ (3.684)***	$chl_{t-1}$ (2.918)***	$SST_t$ (2.271)***	0.29 (0.006)	0.74	95
B4	$MON_t$ (3.416)***	$chl_{t-1}$ (2)**	$SST_t$ (2.363)***	0.26 (0.004)	0.838	93
B5	$MON_t$ (3.951)***			0.21 (0.006)	0.792	94
B6	$MON_t$ (3.14)***	$chl_{t-1}$ (2)***	$SST_t$ (2) <sup>0.05</sup>	0.22 (0.006)	0.729	74
B7	$MON_t$ (3.31)***	$chl_{t-1}$ (2)***	$SST_t$ (2)*	0.19 (0.006)	0.644	97
C7	$MON_t$ (3.902)***		$SST_t$ (3.042)***	0.16 (0.004)	0.812	101
D7	$MON_t$ (3.838)***	$chl_{t-1}$ (2)**	$SST_t$ (2)*	0.20 (0.004)	0.767	121

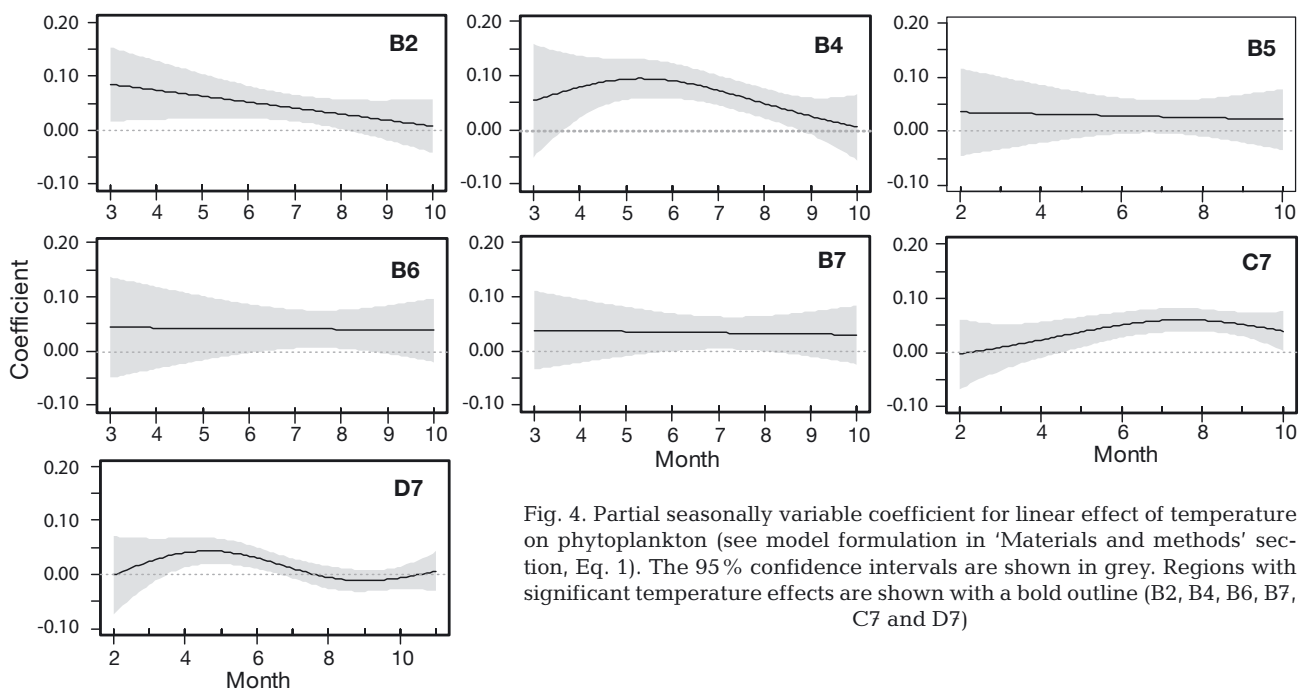


Fig. 4. Partial seasonally variable coefficient for linear effect of temperature on phytoplankton (see model formulation in 'Materials and methods' section, Eq. 1). The 95% confidence intervals are shown in grey. Regions with significant temperature effects are shown with a bold outline (B2, B4, B6, B7, C7 and D7)

and phytoplankton biomass in summer (July to September in B6 and C7; May to October in B5) (Fig. 6). This negative relation was strongest in August for B6 and C7, while, for Region B5, the negative relation was found through summer and autumn.

#### Causality relationships between SST/nauplii and phytoplankton

Potential causality between temperature, nauplii and chlorophyll was investigated with a Granger test. We found strong evidence for significant Granger causality in the relationship of SST on chlorophyll in all areas (Table S1 in the Supplement). Significant Granger causality in the relationship of nauplii on

chlorophyll was also found in the B6 and D7 areas (at 5% level), as well as in the B2 and C7 regions (at a 10% level), suggesting the copepod nauplii had a top-down effect on chlorophyll (Table S2 in the Supplement). Furthermore, we also found significant Granger causality in the relationship of chlorophyll on nauplii in Regions B2, C7 and D7.

#### DISCUSSION

Phytoplankton biomass is considered to be under 'bottom-up' control when environmental factors such as temperature, light, or nutrient concentrations limit their increase and under 'top-down' control when zooplankton grazing limits the algal stocks (Lehman

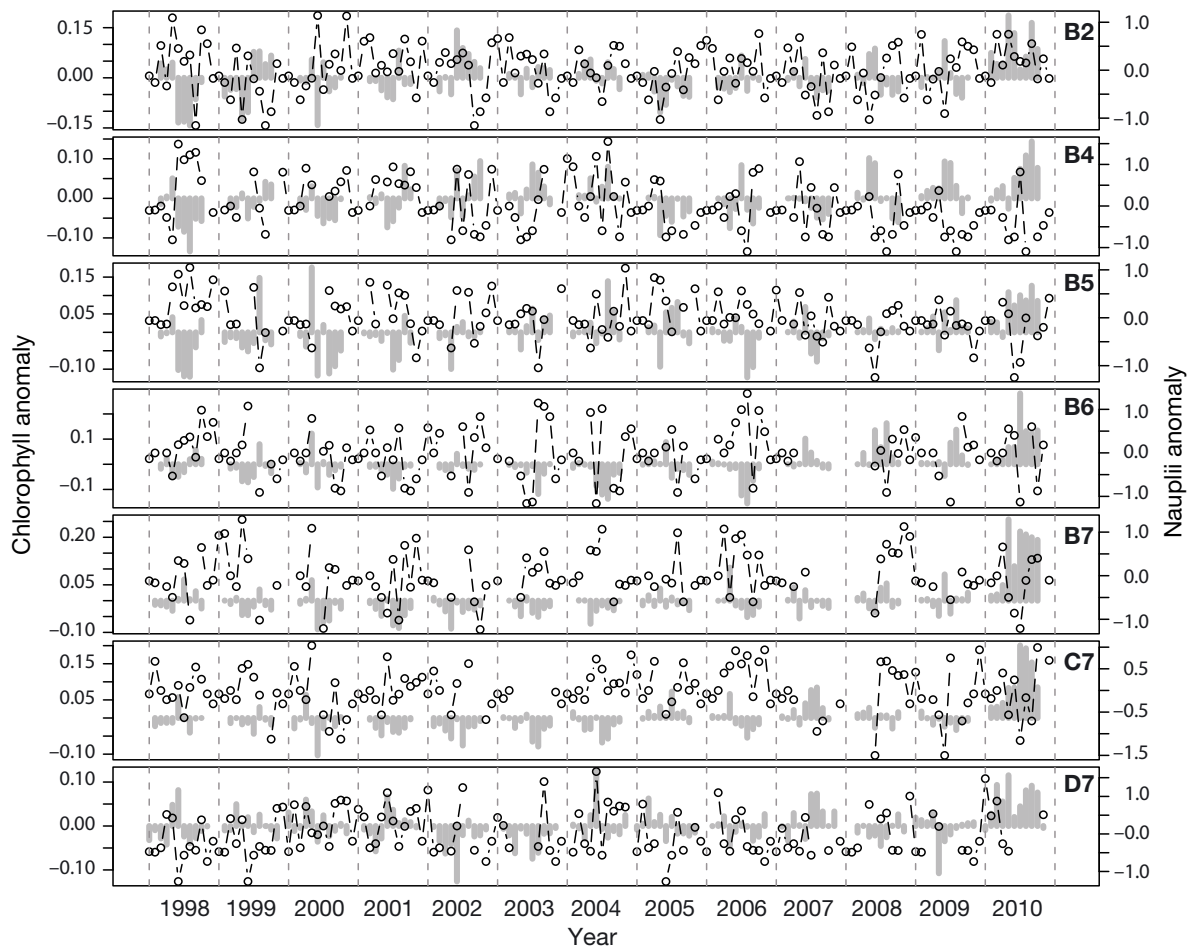


Fig. 5. Monthly anomalies of phytoplankton ( $\log_{10}[N + 1]$ , with  $N$  being chlorophyll concentration [ $\text{mg m}^{-3}$ ], bars) and copepod nauplius abundance ( $\log_{10}[N + 1]$ , where  $N$  is zooplankton abundance [ $\text{ind. m}^{-3}$ ], circles) for the 7 study regions in the North Atlantic from 1998 to 2010

1991, Verity & Smetacek 1996, Banse 1994). It is, however, hard to disentangle these effects, since the variations in time and space of the different factors are often confounded, and environmental factors such as temperature can also influence phytoplankton indirectly, for example, through effects on the zooplankton grazers. Further, as there are no time series of nutrients available, temperature functions as an indicator of nutrient availability as well. For the surveyed area, light, nutrients, grazing and viral lysis may all regulate phytoplankton biomass (Behrenfeld 2010). Richardson & Schoeman (2004) used CPR annual data to study the trophic interactions among plankton, and overall found bottom-up control in the Northeast Atlantic. In support of this finding, analysis of seasonal plankton dynamics along a cross-shelf gradient in the southern Bay of Biscay also gave clear evidence of bottom-up regulation; there was no support for top-down control (Stenseth et al. 2006). By

combining long-term data with a high seasonal and spatial resolution for selected CPR standard areas across the North Atlantic, our study reveals a more subtle pattern, where both temperature and zooplankton show seasonally varying effects on phytoplankton biomass.

Using annual CPR data from 20 Northeast Atlantic standard areas, Richardson & Schoeman (2004) found only 2 areas with significantly positive correlation between SST and phytoplankton biomass. In contrast, by using monthly SST and phytoplankton data in 7 study regions, we found significant positive correlations in 5 regions (B2, B4, B7, C7 and D7) (Table 1, Fig. 4). Temperature, as a bottom-up forcing, can affect the dynamics of marine phytoplankton both directly and indirectly (e.g. via mixing regimes, nutrient dynamics and grazing) (Mauri et al. 2007, Chavez et al. 2011). Temperature can influence phytoplankton growth directly through its effect on



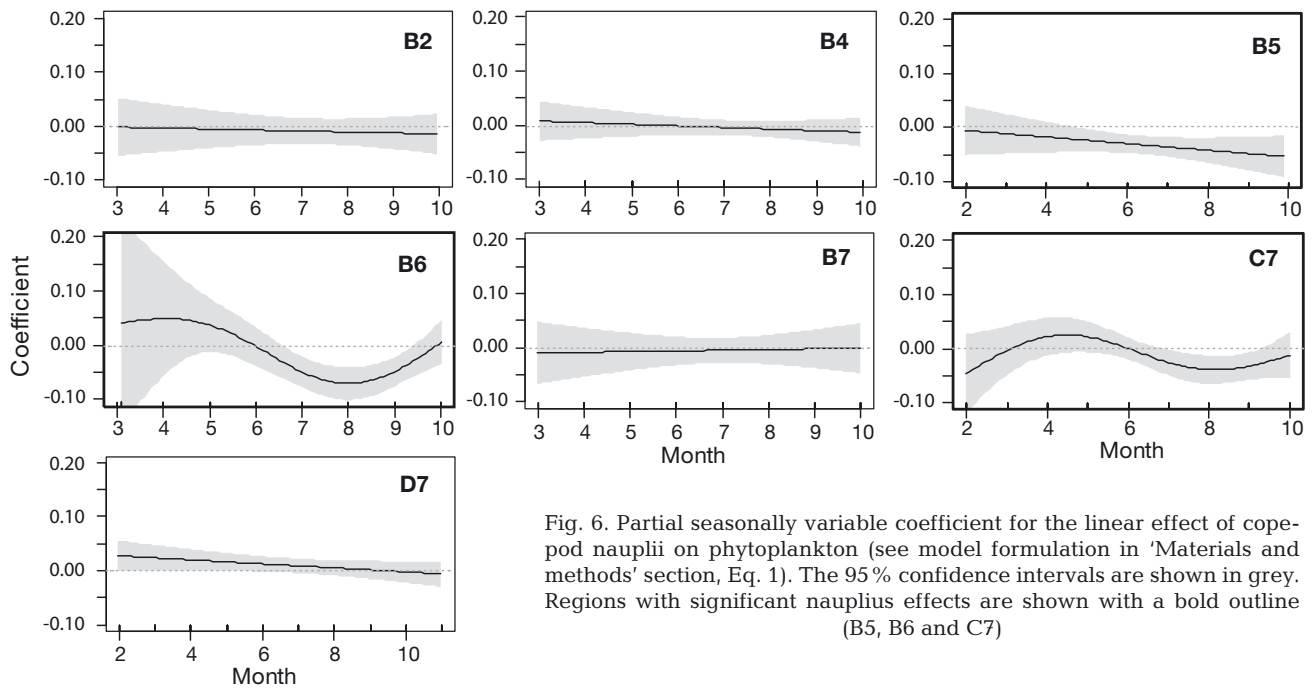


Fig. 6. Partial seasonally variable coefficient for the linear effect of copepod nauplii on phytoplankton (see model formulation in ‘Materials and methods’ section, Eq. 1). The 95 % confidence intervals are shown in grey. Regions with significant nauplius effects are shown with a bold outline (B5, B6 and C7)

metabolic rates of organisms; thus, higher temperatures could account for increased phytoplankton biomass by shortening the turnover time of the plankton. However, temperature can act as a proxy for other physical processes (changes in stratification, ambient light and nutrients) in regulating phytoplankton biomass (Li 2002). In high latitude oceans, increasing SSTs often cause increased thermal stratification, reduced mixing and, subsequently, declined surface nutrients and phytoplankton biomass (Doney 2006). Finally, temperature can also directly or indirectly affect the abundance and distribution of grazers and thus contribute to a net change of phytoplankton biomass (Helaouët & Beaugrand 2007). For example, models coupled with future projections indicated a reduction in abundance of *Calanus finmarchicus* at the southern edge (Georges Bank, the Scotian Shelf and the North Sea) and a potential increase at the northern edge of its spatial distribution (Reygondeau & Beaugrand 2011). Copepod growth, feeding and survival rates are also strongly driven by temperature (Speirs et al. 2006, Cook et al. 2007), which may affect the abundance of phytoplankton in any given stage. The net influence of temperature on phytoplankton thus depends on the relative magnitude of those positive and negative effects. Our analysis generally supported the view that the positive effects surpass the negative effects in the higher latitude Atlantic (50° to 65°N). Overall, this result agrees with the findings of Llope et al. (2009), Raitsois et al. (2006) and Irwin & Finkel (2008)

who found positive or nonlinear effects of temperature on phytoplankton in the North Sea and cold regions of the North Atlantic.

Furthermore, we found that the strengths of these positive effects vary throughout the year (Fig. 4). In C7, the strongest temperature effect was found in August, coinciding with the highest temperature in this region (Fig. S7 in the Supplement). In Regions B2, B4 and D7, however, the strongest effect of temperature was found in spring and early summer (Fig. 4). We hypothesize that this difference between regions and seasons may be related to differences in the relative roles of the various direct and indirect effects of temperature in different ocean regions and seasons. There are generally 2 turbulence–nutrient regimes associated with temperature (Bouman et al. 2003) in the North Atlantic: one is turbulent (vertically mixed)–nutrient-rich cool waters and the other is stratified–nutrient-poor warm waters. In general, stratification occurs already in May in the south (D7), then in the eastern regions (B2 and B4) and last in B7 (Fig. S8 in the Supplement). We note that Region C7—where the strongest positive temperature effect was found in summer—is among the colder water areas (Fig. S7) where stratification occurs late (Fig. S8). In contrast, the B2, B4 and D7 regions—where the strongest positive temperature effect was found in spring—are warmer water areas (Fig. S7) where the stratification occurs early (Fig. S8). At the start of the season, warming in temperate waters can enhance population growth of phytoplankton by

increasing stratification and residence time of the phytoplankton in the sunlit surface layers (Roemmich & McGowan 1995, Li 2002, Richardson & Schoeman 2004). Later in the season, phytoplankton growth is often nutrient limited; thus, increased temperature and stratification can have the opposite effect, by reducing import of nutrients from the lower layers. In cooler areas (e.g. C7), nutrient limitation during the growing season may be less severe, so that increased temperature and stratification have net positive effects on phytoplankton biomass throughout the growing season. In warmer water regions (e.g. B2, B4 and D7), increased temperature and stratification in summer may induce stronger nutrient limitation, which may cancel out the potential growth-promoting direct stimulus by elevated temperatures.

Zooplankton constitute a major link between primary producers and higher trophic levels and also act as major regulators of nutrient regeneration and export because of their importance in terms of both abundance and biomass (Richardson 2008). Still, their role in controlling phytoplankton biomass has remained a matter of controversy, partly because the peak biomass (and grazing pressure) of zooplankton coincides with nutrient depletion in late spring or summer. Recent evidence suggests that zooplankton contribute to a major loss in phytoplankton and can play an important role in regulating phytoplankton dynamics (Strom et al. 2001, 2007, Kim et al. 2007, Chen et al. 2009, Durant et al. 2013). However, direct evidence of the top-down effects of zooplankton on phytoplankton are rarely found in field studies (Micheli 1999, Richardson & Schoeman 2004, Stenseth et al. 2006, McGinty et al. 2012), not the least due to the aforementioned confounding factors. Our analysis provides statistical evidence of coupling between phytoplankton biomass and zooplankton abundance (nauplii) during late summer (mostly July to September) in B5, B6 and C7 (Fig. 6). The significant negative correlations between nauplius abundance and phytoplankton biomass in these regions provide support for top-down control by copepods on phytoplankton in late summer. These are areas where stratification occurs neither particularly early nor particularly late (Fig. S8), and we have no good explanation as to why these specific areas seem to be specially prone to top-down effects.

Given the generally higher biomass of copepodites over nauplii in the sea (Webber & Roff 1995), one would expect stronger grazing effects from the copepodites than from the nauplii. However, we found no relationships between the older copepod stages (total copepodites, *Calanus* I to IV and *Calanus* V and VI)

and phytoplankton. We hypothesize that this could partly be related to the size fraction of phytoplankton and the different optimal prey sizes of nauplii and copepods. In the North Atlantic Ocean, nanoplankton prevails all year long and contributes >70% to the mean chlorophyll *a* concentration (Alvain et al. 2008). Bruno et al. (1983) also revealed that nanoplankton, primarily small solitary flagellates, chlorophytes and diatoms dominated from May through September and accounted for 88.5% of the productivity and 88.1% of the standing crop (measured as chlorophyll *a*) in a temperate North Atlantic estuary. According to the size ratio relationship between planktonic predators and their prey (Hansen et al. 1994), the optimum prey size for copepod nauplii (100 to 500  $\mu\text{m}$ ) is about 5 to 25  $\mu\text{m}$  in length, which mainly includes nanoplankton (2 to 20  $\mu\text{m}$ ). Böttjer et al. (2010) showed that the nauplii of the dominant copepods ingested nanoplankton above all, which implies that copepod nauplii may be capable of exerting considerable grazing pressure on nanoplankton-sized prey. By contrast, the older copepod stages (copepodites and adults) exhibit an omnivorous diet of autotrophic and heterotrophic cells, including nanoflagellates, dinoflagellates, ciliates, diatoms and small copepod nauplii (Lampitt & Gamble 1982, Nakamura & Turner 1997, Vargas & González 2004). Another possible reason is related to sampling issues, as the CPR only samples the surface layers (ca. 7 m depth), and copepods dynamically select their habitat (depth) based on resource availability and predation pressure (Basedow et al. 2010). As nauplii are less able to migrate vertically, their abundance in the surface layers might hypothetically be a more accurate measure of total copepod density than the abundances of the older stages, which are more prone to migrate vertically. The third possible reason is that high (possibly size- or stage-specific) predation from various invertebrate and vertebrate predators on the copepods (Dalpadado et al. 2000, Eiane et al. 2002) led to dominance of the younger copepod stages in the area. The fact that the advanced stages of copepods decline before the phytoplankton does, suggests that predation rather than starvation is the major regulator. Note that nauplii are likely to be grossly underestimated by the coarse (270  $\mu\text{m}$ ) mesh size used in the CPR and that their sampled abundance only provides a relative index for their actual abundance, which cannot be directly compared to copepodite abundance.

In our analysis, bulk chlorophyll was used as an indicator of phytoplankton biomass. By lumping all phytoplankton together as a uniform group we no

doubt missed some of the dynamics, particularly with respect to the changes in the taxa present in the phytoplankton (Hinder et al. 2012) and the seasonal shifts in community composition in the North Atlantic (Barton et al. 2013), but this is an acceptable first-order approximation. Also, trophic interactions between life cycle stages of the copepods (for example, trophic cascades) might mask correlations between phytoplankton and copepodites in our analysis. In addition to more extended time series, further statistical analyses should aim at separating the various bottom-up and top-down impacts on different phytoplankton taxa, as well as addressing more thoroughly the possible interactions among the copepod stages. Finally, the complex interplay between temperature, stratification, nutrients, light and productivity is no doubt an important issue to address further, and a point of departure in this respect could be to include the effects of clouds on the temperature–light–production interactions.

To summarize, our results suggest that both temperature-related bottom-up effects and zooplankton top-down effects influence phytoplankton biomass, yet with different relative impacts over different areas and in different seasons. Our results thus provide an empirically based example of how climate changes (water warming) are likely to have contrasting effects on the plankton in different ocean areas and seasons and potentially involve feedbacks from the zooplankton to the phytoplankton.

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