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Succession of primary producers and micrograzers in a coastal ecosystem dominated by *Phaeocystis globosa* blooms

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The community structures and succession of phytoplankton, protozooplankton and copepods were studied from February 2007 to July 2009 in a coastal area of the eastern English Channel subject to *Phaeocystis globosa* blooms. While diatom blooms preceded *P. globosa* blooms each year, the community structure and stock of heterotrophic protists appeared to be related to the dominant *P. globosa* life cycle stages. In 2007, the dominance of large colonies (>100 μm, up to 316 μg C L^{-1}), which resulted in a high biomass of healthy free cells (up to 132 μg C L^{-1}), accompanied high spirotrich ciliate stocks (up to 58 μg C L^{-1}) and high abundances of the copepods *Acartia clausi* and *Temora longicornis* (up to 11 ind. L^{-1}). In 2008, the bloom which lasted a shorter period of time was dominated by large colonies (up to 328 μg C L^{-1}) and fewer free cells (up to 98 μg C L^{-1}). This corresponded with a lower abundance of grazers, with stocks of heterotrophic protists and copepods 1.6 times and 2.2 times lower, respectively. In 2009, the *P. globosa* bloom was again dominated by large colonies and <100 μm diatoms. This corresponded to a dominance of heterotrophic dinoflagellates among the protists (62% of the total heterotrophic protist biomass) and *Acartia clausi* (55% of the copepod abundance). Overall, heterotrophic dinoflagellates appeared to be likely the most important group of phytoplankton grazers.

KEYWORDS: *Phaeocystis globosa*; diatoms; micrograzer community; eastern English Channel

INTRODUCTION

In the North Sea and in the eastern English Channel, gelatinous colonies of *Phaeocystis globosa* Scherffel, 1900 (Prymnesiophyceae), several millimetre in size (Rousseau *et al.*, 2007), commonly dominate the phytoplankton community during spring, following the decline of an earlier diatom bloom (e.g. Lancelot *et al.*, 1998). *Phaeocystis globosa*, a species of ephemeral occurrence, alternates between a colonial stage in the earlier phase and solitary cells during the decline of the bloom (Rousseau *et al.*, 2007).

In the colonial form, *P. globosa* can represent over 90% of the phytoplankton biomass (Lancelot, 1995; Lamy *et al.*, 2009), and be responsible for the massive load of organic matter into the ambient water, often resulting in foam accumulation along the shoreline (Van Boekel *et al.*, 1992).

Generally speaking, phytoplankton blooms occur as a result of growth greatly exceeding mortality, often

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through escaping control by grazers (Strom 2002; Irigoien *et al.*, 2005). In the particular case of *P. globosa*, experimental and modelling studies suggest that in early stages of the bloom, solitary cells are well-grazed by the microzooplankton, but control ceases when colonies start to form (Verity, 2000). Culture experiments have shown that the smaller forms of *P. globosa*, free cells of 4–8 μm, can support the growth and reproduction of protists, but not copepods (Tang *et al.*, 2001). Furthermore, field studies of microzooplankton grazing during blooms of *Phaeocystis* have indicated high grazing rates (e.g. Stelfox-Widdicombe *et al.*, 2004). Thus, existing evidence supports a view that microzooplankton grazing could potentially impact *Phaeocystis* blooms. In contrast, several field studies focusing on mesozooplankton impact on *P. globosa* have reported grazing rates that vary from negligible, suggesting the unsuitability of *P. globosa* for many species of mesozooplankton (Hansen *et al.*, 1993; Gasparini *et al.*, 2000), to highly variable (Seuront and Vincent, 2008). These discrepancies may be attributable to the effects of colony size on susceptibility to copepod grazing (e.g. Verity, 2000) and/or copepods switching to heterotrophic food (Hansen and Van Boekel, 1991; Nejstgaard *et al.*, 2001). Overall, despite the existence of numerous studies dealing with *P. globosa* blooms, the identities and relative importance of the major groups of grazers remain obscure. In a model simulation study, Verity (Verity, 2000) postulated that transitions between life cycle stages of *P. globosa* may potentially be important to interactions between phytoplankton, micro- and mesozooplankton and that these interactions may depend on the match or mismatch of phytoplankton and grazer communities.

Here we attempt to clarify whether succession of the phytoplankton community corresponded to changes in the grazer community, especially with regard to heterotrophic protists. Our study covered 3 years of the critical period of phytoplankton growth and senescence in a coastal system (eastern English Channel) over a period of 2.5 years. Such an approach permits the identification of "regular and recurrent patterns from occasional and exceptional events" (Ribera d'Alcala *et al.*, 2004). We hypothesized that although the bloom is dominated by a single species, *P. globosa*, phytoplankton community composition preceding and following the bloom is likely to be variable, as well as the intensity of the bloom, and in particular the magnitude and the timing of *P. globosa* life stages (flagellated cells, colonies and free colonial cells). Because of their known potential as *P. globosa* grazers and because of the scarcity of studies in particular in the eastern English Channel, our study focused on the effects of phytoplankton variability on heterotrophic protists (ciliates and dinoflagellates) as well as including copepods, consumers of both phytoplankton and heterotrophic protists.

METHOD

Study site and sampling

Water samples were collected at the coastal station (50°40′75″N, 1°31′17″E, 20–25 m water depth) of the SOMLIT network (Service d'Observation du Milieu Littoral) in the eastern English Channel (Strait of Dover, Fig. 1). The eastern English Channel is characterized by its tidal range, between 3 and 9 m, and a residual circulation parallel to the coast, where the continental inputs are restricted to the coastal area and transported from south-west to north-east. This so-called coastal flow (Brylinski *et al.*, 1991) is separated from offshore waters by a tidally maintained frontal area (Brylinski and Lagadeuc, 1990). Sampling was always carried out at high tide. Sampling was conducted on 52 dates over the study period (22, 14 and 16 samples in 2007, 2008 and 2009, respectively). Sampling frequency was planned to be weekly, during the period of growth and senescence of the spring bloom and about every 2 weeks for the rest of the year. Actual sampling frequency varied with weather conditions in the channel and, thus, varied from a minimum of less than a week (3 days) to a maximum of 57 days (overall mean and median frequency of 17 and 14 days, respectively). Sub-surface sampling (2–3 m water depth) was conducted for phytoplankton and microzooplankton, and vertical hauls for mesozooplankton.

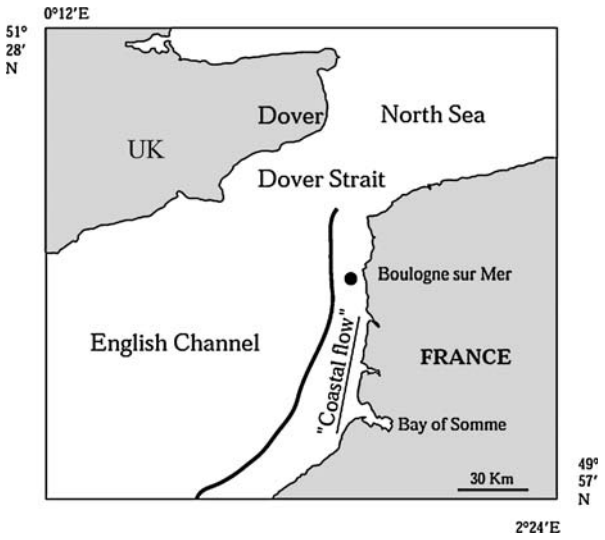

Fig. 1. Location of the SOMLIT station (closed circle).

Physico-chemical parameters and Chlorophyll *a* (Chl *a*)

Seawater temperature (T, °C) and salinity (S) were measured using a conductivity–temperature–depth profiling system (CTD Seabird SBE 25). Inorganic nutrient concentrations were determined from 100 mL samples with an Alliance Integral Futura Autoanalyser II for nitrate (NO_3^-), nitrite (NO_2^-), silicate [$(SiO_4)^{4-}$] and phosphate (PO_4^{3-}; Strickland and Parsons, 1972; Aminot and Kerouel, 2004). Chlorophyll *a* (Chl *a*) concentrations were measured on 90% (v/v) acetone-extracted particulate material isolated by filtration on GF/F glass-fibre filters (Whatman). Concentrations were determined by fluorescence using a 10-AU Turner Designs© fluorometer (Lorenzen, 1966). Particulate organic carbon (POC) was analysed by filtering (<150 mm Hg) duplicate 50–200 mL seawater samples through pre-combusted (4–5 h at 480°C) glass-fibre filters (Whatman GF/F, 25 mm). Analysis was performed on a NA2100 Frisons CHN analyser after drying filters at 60°C for 24 h and exposure to HCl 1 N vapours for 5 h.

Sample analysis

Phytoplankton

For microphytoplankton analysis, samples were fixed with Lugol-glutaraldehyde solution (1% v/v; Breton *et al.*, 2006) and examined using an inverted microscope (Nikon Eclipse TE2000-S) after sedimentation in 5–25 mL Hydrobios chambers. Diatom carbon biomass was calculated on the basis of cell concentration and specific biometry using the size-dependent relationship recommended by Menden-Deuer and Lessard (Menden-Deuer and Lessard, 2000). Carbon biomass of the *Phaeocystis globosa* colonies was calculated from biovolume measurements at ×100 or ×200 magnification, as previously described by Breton *et al.* (Breton *et al.*, 2006). The microphytoplankton was further divided in two size groups: (i) phytoplankton smaller than 100 μm (small colonies of *P. globosa* and diatoms) and (ii) phytoplankton larger than 100 μm (large colonies of *P. globosa* and large diatoms). To enumerate nanophytoplankton (<20 μm), 5–10 mL samples were preserved using borax-buffered formaldehyde (1% v/v). Samples were filtered onto black Nuclepore filters (pore size: 0.8 μm), stained with DAPI (Porter and Feig, 1980) within 5 h of sampling and stored at −20°C until counting. Cells were enumerated using a Leica FW4000 epifluorescence microscope at ×1000. To distinguish between phototrophic and heterotrophic cells, autofluorescence (chlorophyll) was determined under blue light excitation (BP 450–480 nm). Free colonial and flagellated *Phaeocystis* cells are easily distinguished based on their morphology. Colonial cells are in the size range of 4.5–8 μm, have an anterior longitudinal groove and lack filamentous appendages. Flagellated cells have a rounded shape, and are smaller than colonial cells, with a diameter of 3–5 μm (reviewed in Rousseau *et al.*, 2007). Phototrophic nanoplankton consisted almost exclusively of free *P. globosa* cells and cryptophytes (see Results section) and will be designated from now-on in the text as phototrophic nanoflagellates (PNF).

Nano-sized diatoms were counted along with microphytoplankton as described above. For each sample, at least 30 fields and at least 250 PNF were counted on each filter. To estimate PNF biomass, biovolume was calculated based on the linear dimensions (length and width) of cells using an image analyser with a camera mounted on the microscope. Biovolume was then converted to biomass according to Menden-Deuer and Lessard (Menden-Deuer and Lessard, 2000).

Heterotrophic protists

For heterotrophic protist enumeration, duplicate samples (250 mL) were placed in opaque glass bottles. One 250 mL sample was fixed with acid Lugol's solution (2% v/v) for quantitative counts, and the other with borax-buffered formaldehyde (1% v/v) for the determination of the trophic type of the ciliates, heterotroph or mixotroph, based on the presence or absence of sequestered chloroplasts. The samples were then stored at 4°C in the dark until analysis (most often within the following week and maximally 3 weeks later). Samples were further sedimented in 50 or 100 mL Hydrobios chambers for at least 24 h before enumeration using a Nikon Eclipse TE2000-S inverted microscope at ×200 or ×400 magnification. Lugol's fixed samples were enumerated and sized with phase contrast. The formaldehyde-fixed samples were examined using blue light excitation (DM 500 nm dichromic mirror, BP 450–480 nm excitation filter, BA 515 nm barrier filter and a 100 W mercury burner) to detect chlorophyll autofluorescence and to distinguish plastidic from non-plastidic ciliates. Ciliates were identified wherever possible to genus or species level following Kofoid and Campbell (Kofoid and Campbell, 1929) for tintinnid ciliates, the Plankton Ciliate Project (Plankton Ciliate Project, 2002) for spirotrich and other ciliates, and following Schiller (Schiller, 1931–1937), Gómez and Souissi (Gómez and Souissi, 2007a) and Maar *et al.* (Maar *et al.*, 2002) for heterotrophic dinoflagellates. Ciliates were further divided into three size groups (<20, 20–40, >40 μm) and dinoflagellates into five size groups (<10, 10–20, 20–40, 40–60, >60 μm).

Linear dimensions (length and width) were measured at ×400 magnification using an image analyser with a camera mounted on the microscope. Biovolumes of cells were calculated assuming the nearest geometrical shape; for this, a minimum of 10 cells (for rare tintinnids) and a maximum of 300 cells (for the most abundant *Strombidium* and *Strobilidium*) were measured. Biovolumes were converted to carbon biomass using a conversion factor of 190 fg C μm^{-3} for ciliates (Putt and Stoecker, 1989) and $0.760 \times volume^{0.819}$ pg C μm^{-3} (Stoecker *et al.*, 1994) for dinoflagellates.

Mesozooplankton

Zooplankton samples for the quantitative analysis were collected by means of vertical or sub-vertical hauls from the bottom to the surface, using a 200 μm mesh size WP2 net (UNESCO, 1968). The volume filtered was measured with a TSK flow-meter and mounted on the mouth of the net (0.25 m^{-2} mouth area). The filtered volume varied between 1 and 7 m^{-3}. The choice of mesh size, while preventing a quantitative study of copepod nauplii, was made as compromise between sampling small metazoa and limiting and/or delaying the clogging of the net in this eutrophic and turbid coastal area. Thus the lower values of filtered volume correspond to rapid clogging of the net by tripton or phytoplankton (e.g. *Phaeocystis globosa*). After each haul, the sample was preserved in a 5% buffered-formaldehyde seawater solution until laboratory analysis.

In the laboratory, all specimens were identified and counted in subsamples (1/10 to 1/30) of the whole sample. Zooplankton species were determined under a binocular microscope following Rose (Rose, 1933) for the copepods and the Plankton identification Leaflets (ICES, 1939–2001) for the other groups which were determined at different level (Phylum, Class, Order or Species). In order to facilitate comparison with phytoplankton and microzooplankton, for total copepods and for the two dominant key species for the area, *Acartia clausi* and *Temora longicornis* biomass was also estimated. Individual species-specific biomass for copepods was determined by measuring dry weights and converted into carbon units assuming a 40% carbon content (Gorsky *et al.*, 1988). A minimum of 400 copepods were used to calculate conversion factors (401, 1153 and 545 copepods for *Temora longicornis*, *Acartia clausi* and other copepods). The averages of carbon per individual copepod were 3.56 ± 1.73, 1.59 ± 0.41 and 2.34 ± 2.63 μg C $copepod^{-1}$ for *Temora longicornis*, *Acartia clausi* and other copepods, respectively. These empirical conversion factors determined from our samples were then used to convert abundance into biomass data.

Data analysis

To portray temporal patterns of different phytoplankton and heterotrophic compartments considered in this study, the method of cumulated function (Ibanez *et al.*, 1993) was used. This method can be applied to portray trends in data series with missing values and does not require special conditions. The calculation consists of subtracting a reference value (here for a biomass parameter, we used the annual mean of the series) from the data; the resulting residuals are then successively added, forming a cumulative function. Successive positive residuals produce an increasing slope indicating higher values than the overall mean, whereas successive negative residuals produce a decreasing slope indicating values lower than the overall mean. A succession of values similar to the mean shows no slope.

$$S_p = \sum_{i=1}^{p} x_t - p_k \quad (1)$$

where S_p is the consecutive terms of the cumulative sums, and x_t the value for each sampling date (t); p_k, the annual mean. Spearman correlations, were calculated using series of cumulative sums (S_p). These correlations have an informative rather than an absolute value since the terms of cumulative sums are autocorrelated. For this reason, correlations can be relevant only if the correlation coefficient (r) is highly significant ($P = 0.01$ so 1%) for the degrees of freedom considered.

Log–log plots of total phytoplankton, diatoms, colonies and free *P. globosa* cells were used to investigate linkages with grazers, in particular ciliates and dinoflagellates (Irigoien *et al.*, 2005).

RESULTS

Environmental parameters

Salinity ranged from 33 to 35 and the seawater temperature from 4.6 to 18.2°C (Fig. 2a). Concentrations of inorganic nutrients exhibited typical seasonal patterns for this temperate coastal area: highest concentrations were recorded at the end of winter before the onset of the phytoplankton bloom reaching 37.23 μM for $NO_3^- + NO_2^-$, 15.05 μM for $(SiO_4)^{4-}$, 0.77 μM for PO_4^{3-} in 2007 (Table I); nutrient concentrations always dropped dramatically at the end of spring. A decrease in the maximum value of inorganic nutrients was observed from 2007 to 2009 and this was more pronounced for $NO_3^- + NO_2^-$ concentrations (Table I). POC ranged from 114 to 1675 μg C L^{-1} in 2007 and from around 100 to 600 μg C L^{-1} in 2008 and 2009 (Table I).

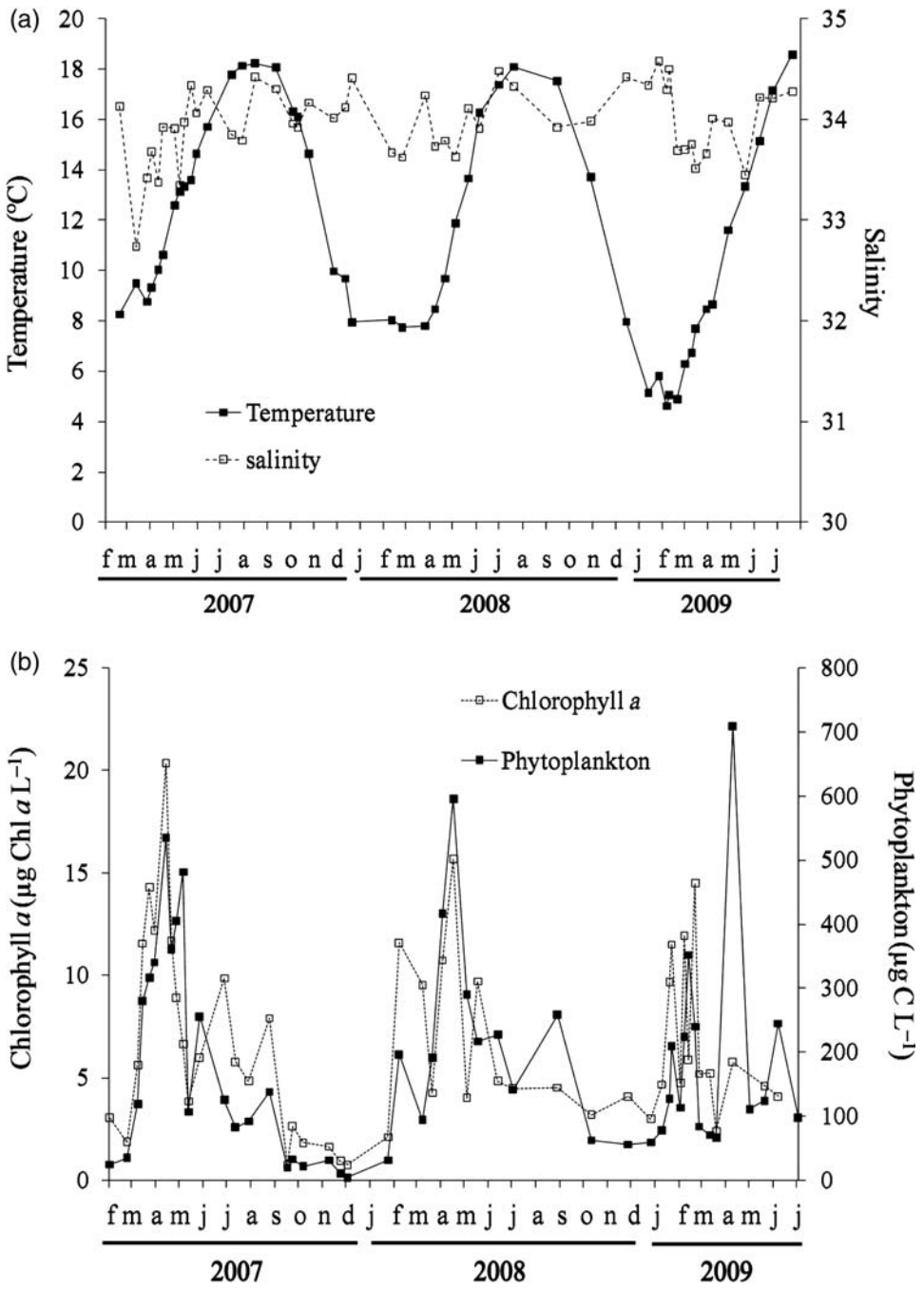

Fig. 2. Temporal variation of (**a**) temperature (°C) and salinity; (**b**) chlorophyll *a* (µg Chl*a* L^{-1}) and phytoplankton biomass (µg C L^{-1}) at SOMLIT station (eastern English Channel) from February 2007 to July 2009.

Phytoplankton

Chl *a* concentrations ranged from 0.8 to 20.3 µg Chl *a* L^{-1} (Table I) with minima during autumn/winter (October–February) and maxima in late spring (April–May, Fig. 2b). The peak value of Chl *a* concentration observed during spring coincided with the *P. globosa* bloom, except in 2009 when the Chl *a* maximum was due to diatoms and occurred before the peak of the phytoplankton biomass (Fig. 2b). Total phytoplankton biomass ranged from 2 to 638 µg C L^{-1}, with a maximum in spring and a minimum in autumn/winter (from October to February, Table II; Fig. 2b).

Based on our data, a highly significant empirical relationship between POC:Chl and Cphytoplankton:Chl

Table I: Environmental parameters from February 2007 to July 2009 in the eastern English Channel [min–max]

	2007	2008	2009
Seawater temperature (°C)	7.9–18.2	7.7–18.1	4.6–18.6
Salinity	32.7–34.4	33.5–34.5	33.4–34.6
$NO_3^- + NO_2^-$ (μM)	0.10–37.23	0.13–23.56	0.09–14.07
$(SiO_4)^{4-}$ (μM)	0.84–15.05	0.65–15.05	0.53–6.32
PO_4^{3-} (μM)	0.03–0.77	0.05–0.71	0.08–0.54
Chlorophyll *a* (μg L^{-1})	0.8–20.3	2.1–15.7	2.4–14.5
POC (μM)	114–1675	115–603	122–631

was calculated (COP = 92.0 + 47.6 [Chla], and Cphytoplankton = 29.4 + 23.6[Chla], $r^2 = 0.425$ and $r^2 = 0.552$ with $P < 0.0001$, respectively, data not shown).

Phaeocystis globosa blooms are ephemeral and at our study site occurred from late March to early May and lasted about 1 month each year (37, 27 and 29 days in 2007, 2008 and 2009, respectively, Fig. 3b and c). During the blooms, *P. globosa* represented up to 93% of the microphytoplankton and up to 100% of the nanophytoplankton biomass and large colonies (>100 μm) constituted most (56–93%) of the *P. globosa* biomass. With regard to inter-annual differences, from 2007 to 2009, maximum biomass values increased for *P. globosa* colonies (from 316 to 392 μg C L^{-1}) and free colonial cells (from 62 to 153 μg C L^{-1}), while flagellated cells decreased slightly (from 66 to 50 μg C L^{-1}; Fig. 3c).

Diatoms were always present with mean biomass values of 92% of total phytoplankton biomass over the study period. Diatom biomass ranged from 2 to 345 μg C L^{-1} (Table II). The mean of diatom biomass during the spring bloom (from March to May) was lowest in 2009 and highest in 2007 (Table III). The diatom 20–100 μm size class was the most important for all years and showed the highest biomass mean during the spring bloom in 2008 (Table III).

We distinguished three distinct assemblages of diatoms. The first group, composed of cells between 20 and 120 μm and characterized by *Pseudonitzschia* spp. and *Chaetoceros* spp., was present during *P. globosa* blooms and persisted during the post-bloom period until August. In 2009, the *Pseudonitzschia* spp. group also dominated the phytoplankton during the pre-bloom period (209 μg C L^{-1} in early March; Fig. 3a). The second group, characterized by diatoms forming colonies (>100 μm) such as *Skeletonema costatum* 5–20 μm length, *Brockmaniella brockmanii* and *Ditylum brightwelli* 20–120 μm length, marked the early spring period. The third group appeared from the end of summer to winter, composed of large fine-walled diatoms such as *Guinardia* spp., *Rhizosolenia* spp. and *Chaetoceros* spp.

Table II: Autotrophic and heterotrophic abundance and biomass [(min–max); mean ± SD], and percentage of total protist biomass and total metazoan abundance, from February 2007 to July 2009 in the eastern English Channel

Autotrophic and heterotrophic protists	Abundance (10^3 cells L^{-1})	Biomass (μg C L^{-1})	% biomass of microplankton	% biomass of nanoplankton
Total phytoplankton	[18–35341] 5280 ± 6479	[2.2–637.7] 177 ± 155	[40.0–97.1] 79.7 ± 14.5%	[2.9–60.0] 20.3 ± 14.5%
Diatom	[18–2382] 483 ± 504	[2.2–345.3] 109 ± 88	[6.7–100] 84.4 ± 27.9%	[0.21–100] 18.8 ± 19.7%
Phaeocystis globosa	[0–35079] 4785 ± 6458	[0–607.2] 66 ± 124	[0.00–93.3] 15.6 ± 27.9%	[0.00–99.8] 73.6 ± 23.0%
Total heterotrophic protist	[0.9–37.3] 8.8 ± 6.7	[0.6–61.1] 17.5 ± 15.0	[74.4–99.2] 88.6 ± 7.3%	[0.8–25.6] 11.4 ± 7.3%
Ciliate	[0.5–19.5] 3.4 ± 3.6	[0.4–58.1] 8.7 ± 11.7	[5.9–98.3] 52.1 ± 26.9%	[4.3–69.4] 26.6 ± 15.5%
Dinoflagellate	[0.3–32.4] 5.3 ± 5.4	[0.2–51.9] 8.8 ± 9.9	[1.7–94.1] 47.9 ± 26.9%	[30.6–95.7] 73.4 ± 15.5%
Copepods	**Abundance (ind. L^{-1})**	**Biomass (μg C L^{-1})**	**% abundance of mesozooplankton**	
Temora longicornis	[0.01–4.8] 0.8 ± 1.1	[0.02–17.1] 2.7 ± 3.8	[0.3–46.4] 16.3 ± 12.2%	
Acartia clausi	[0.01–4.6] 1.2 ± 1.3	[0.02–7.3] 1.9 ± 2.0	[0.7–59.2] 29.7 ± 16.7%	
Copepods	[0.03–10.9] 2.6 ± 2.6	[0.07–27.3] 6.4 ± 6.6	[1.6–95.4] 68.4 ± 22.4%	

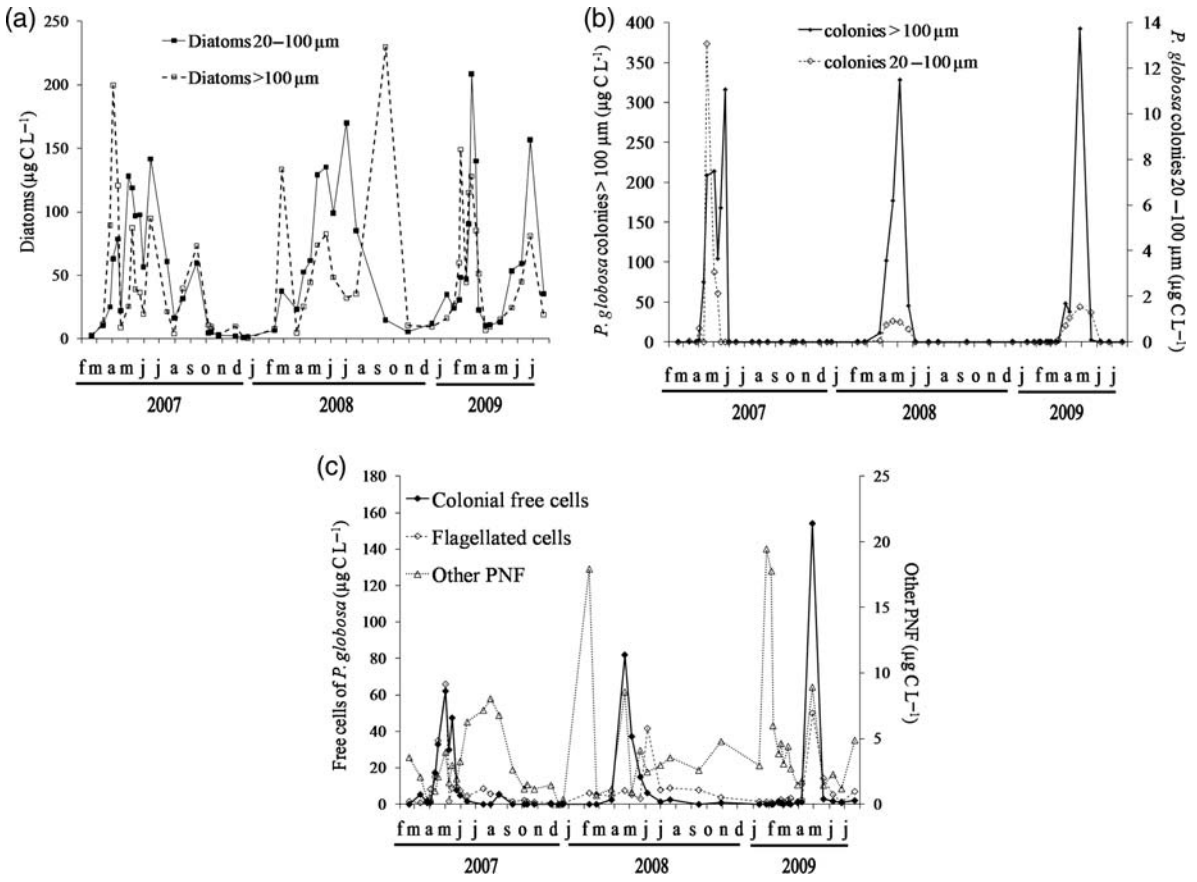

Fig. 3. Temporal variation of autotrophic biomass (µg C L^{-1}) at SOMLIT station (eastern English Channel) from February 2007 to July 2009: (**a**) diatoms 20–100 and >100 µm; (**b**) *Phaeocystis globosa* colonies 20–100 and >100 µm; (**c**) *P. globosa* colonial free cells, *P. globosa* flagellated cells and other phototrophic nanophytoplankton (other PNF).

Table III: Averages of biological stocks (biomass) during the spring bloom periods (from March to May) for 2007, 2008 and 2009 in the eastern English Channel

	2007	2008	2009
Autotrophic and heterotrophic protist biomass (µg C L^{-1})			
Total diatoms	139.5	127.3	115.7
Diatoms 20–100 µm	69.8	80.4	65.7
Diatoms >100 µm	63.9	46.2	45.7
Phaeocystis globosa	158.0	180.5	117.2
Free cells	47.3	47.3	47.9
Colonies	110.6	133.2	69.3
Colonies >100 µm	108.7	132.5	68.6
Heterotrophic protists	26.7	7.7	30.1
Mixotrophic ciliates	9.1	1.8	4.8
Heterotrophic ciliates	11.9	1.3	4.8
Dinoflagellates	5.7	4.6	20.5
Copepod biomass (µg C L^{-1})			
Total copepods	10.0	5.6	6.1
Acartia clausi	1.5	1.8	3.1
Temora longicornis	5.9	2.5	1.6

Heterotrophic protists (ciliates and dinoflagellates)

The biomass of heterotrophic protists over the study period showed low values during autumn–winter (0.6–20.0 µg C L^{-1}) and higher values during spring–summer (2.8–61.1 µg C L^{-1}). The overall biomass of protists during the spring bloom was similar in 2007 and 2009 and greater than that recorded for 2008 (Table III). Despite these differences, some common features were observed every year: (i) heterotrophic dinoflagellate biomass exceeded that of ciliates, except in spring 2007 (Fig. 4a), (ii) ciliates were almost equally divided between heterotrophs and mixotrophs (Fig. 4b).

Ciliate abundance and biomass over the study period ranged from 0.5 to 19.5 × 10^3 cells L^{-1} and from 0.4 to 58.1 µg C L^{-1}, respectively (Table II). High ciliate abundance and biomass were recorded in May 2007 and 2009, whereas in 2008 ciliate abundance and biomass were relatively low (<5.2 × 10^3 cells L^{-1} and

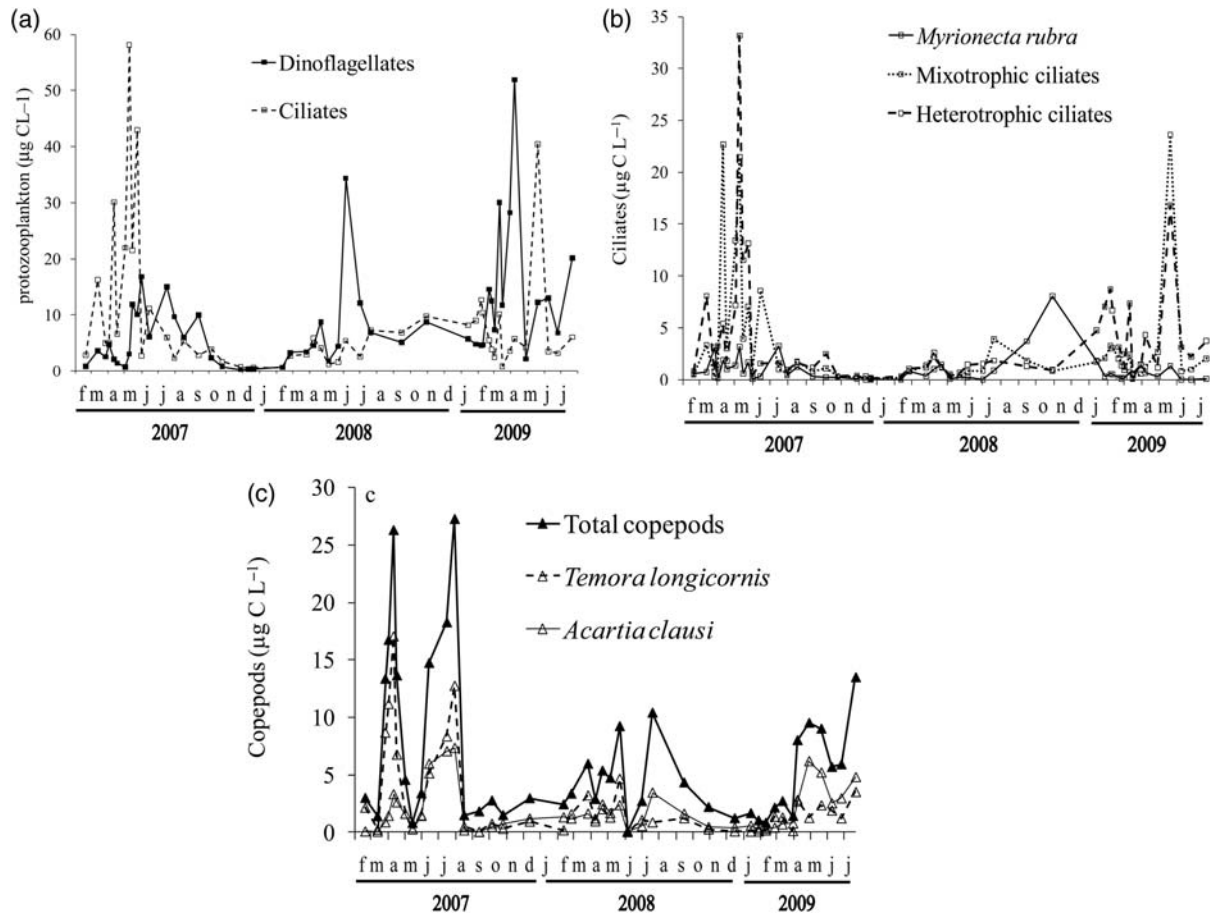

Fig. 4. Temporal variation of heterotrophic protist and copepod biomass (µg C L^{-1}) at SOMLIT station (eastern English Channel) from February 2007 to July 2009: (**a**) ciliates and dinoflagellates; (**b**) *Myrionecta rubra*, mixotrophic and heterotrophic ciliates; (**c**) total copepod, dominant copepod species *Temora longicornis* and *Acartia clausi*.

<10 µg C L^{-1}, Fig. 4a). The taxonomic composition of the ciliate community was largely invariant over the 2.5 years and was dominated (86% of abundance) by Spirotrichs of the genera *Strombidium, Strobilidium, Leegardiella, Tontonia* and the haptorid *Myrionecta rubra*. Among heterotrophic aloricate ciliates, *Strombidium lynni*, *Leegardiella sol* and *Strobilidium spiralis* were present in all samples. Scuticociliates were occasionally present during the study, in particular, after wind events in 2007 and 2008 (mean <1 µg C L^{-1}). Tintinnids were insignificant during the whole study and will not be further considered (max. 0.33 µg C L^{-1}; mean 0.02 µg C L^{-1}). Carnivorous ciliates, the suctorians (*Acineta* sp. and *Podophyra* sp.), were present in low numbers (up to 80 cells L^{-1}). The mixotrophic community was essentially composed by *Laboea strobila*, *Tontonia* spp., *Strombidium acutum* and *S. capitatum*. *Myrionecta rubra* was also present in large numbers and biomass (up to 4.32 × 10^3 cells L^{-1}, 8.02 µg C L^{-1}) during different seasons, without a marked seasonality (Fig. 4b). The biomass of heterotrophs and mixotrophs was in a similar range (from 0.1–34.3 and 0.1–24.6 µg C L^{-1}, respectively) to that of heterotrophs representing 55% and mixotrophs + *M. rubra* representing 45% of the mean ciliate biomass over the study period (Fig. 4b, Table II). The alternation of heterotrophs/mixotrophs was particularly noticeable in 2008 when outside of the period of dinoflagellate dominance, mixotrophic ciliates + *M. rubra* represented up to 62% of the ciliate biomass and 28% of the biomass of heterotrophic protists (Fig. 4b). The 20–40 µm size class (11.5 ± 3.7 × 10^3 µm^3) was the modal size-class for heterotrophs, while mixotrophs were dominated by the >40 µm size class (88.6 ± 35.4 × 10^3 µm^3). However, it should be noted that in spring 2009, *Tontonia* spp. alone represented 74.1% of the ciliate biomass and 51.9% of the ciliate abundance.

Dinoflagellate biomass ranged from 0.2 to 51.9 µg C L^{-1} (Table II; Fig. 4a) and increased from

2007 to 2009 (Table III) with the increase in the ratio of dinoflagellate to ciliate biomass average during the spring bloom from March to May, 0.3, 1.5 and 2.1 in 2007, 2008 and 2009, respectively, cf. Table III). The dinoflagellate community was composed almost exclusively of heterotrophic species. The most abundant species (84% of abundance and 86% of biomass) were the athecate forms such as *Gyrodinium spirale*, *Spatulodinium pseudonoctiluca*, *Gymnodinium* spp., while thecate dinoflagellates were dominated by *Protoperidinium* spp. and *Prorocentrum micans*. Dinoflagellates were particularly abundant during the pre-bloom period and at the end of the *Phaeocystis globosa* bloom, when they accounted from 72.8 to 93.5% and up to 86.3% of the heterotrophic protist biomass, respectively; they were also abundant during the summer (52.7–81.1% of the biomass). In 2007, the assemblage of <20 ($1.9 \pm 1.0 \times 10^3$ μm^3, *Protoperidinium* spp.) and 20–40 μm ($15.1 \pm 7.3 \times 10^3$ μm^3, *G. spirale*) size groups dominated the dinoflagellate community (48 and 44% of dinoflagellate abundance, respectively). In 2008, the larger size-class of 20–40 μm was dominant yet still composed of *Gyrodinium spirale* and *Protoperidinium* spp. accounting from 19 to 94% with a mean of 51% of the dinoflagellate biomass. In 2009, the >40 μm size class was dominant with the highest biomass (18–87% with mean of 46%).

Mesozooplankton

The abundance of mesozooplankton ranged from 0.6 to 13.9 ind. L^{-1} and was dominated by copepods (0.03–10.9 ind. L^{-1}) equal to 68.4 ± 22.4% of total abundance (Table II, Fig. 4c). Copepod biomass ranged from 0.07 to 27.3 μg C L^{-1} (mean 6.4 ± 6.6 μg C L^{-1}, Table II). The dominant copepod species were *Acartia clausi* and *Temora longicornis*, which accounted for 44.4 ± 18.8 and 23.3 ± 15.7% of copepod abundance and 31.4 ± 15.4 and 33.2 ± 18.7% of copepod biomass, respectively. Yet, we observed a change in relative abundances of these species during the spring bloom (from March to May). The *Acartia* to *Temora* ratio of average biomass values increased from 0.25 in 2007 to 1.9 in 2009 (Table III, Fig. 4c). *Paracalanus parvus* and *Centropages hamatus* were also present in lower abundances and accounted for 7.0 ± 5.4 and 13.6 ± 13.3% of total copepod abundance, respectively.

Pluteus and larvae of the urchin *Echinocardium cordatum* were present each year in spring during less than 1 week and occurred between the two maxima of copepods (Fig. 4). Their highest abundance was observed in May 2007 when they reached up to 11.3 ind. L^{-1} (up to 82% of zooplankton abundance) and they were absent during the rest of the year. Appendicularians *(Oikopleura dioica)* feeding essentially on picoplankton were also observed in low numbers (0–2.9 ind. L^{-1}, mean 15.3 ± 11.8% of the mesozooplankton abundance).

Temporal trends based on cumulative sums

The cumulative sums show temporal trends in terms of differences from overall averages, temporal variations not easily seen in figures such as Figs 3 and 4. We focused on the temporal trends of the three major types of consumers (ciliates, dinoflagellates and copepods) and autotrophs (Fig. 5a–i).

In 2007, the ciliate biomass was strongly related with all phytoplankton compartments (Fig. 5a–c, diatoms $r = 0.88$, *P. globosa* colonies $r = 0.97$ and free cells $r = 0.93$, $n = 21$, $P < 0.0001$). In 2008, no significant relation was observed with the phytoplankton and the ciliate cumulated sums values remained close to the average annual biomass (more or less parallel to the *x*-axis, Fig. 5a–c). In 2009, the ciliates related again with *P. globosa* colonies and free cells with a strong anomaly at the end of April (Fig. 5a and b) which corresponds to a highest ciliate biomass recorded in 2009 (Fig. 5a).

Dinoflagellates showed a remarkable co-variation with total phytoplankton biomass during the whole study ($r = 0.51$, $n = 51$, $P < 0.0002$; cf. Fig. 5d–f). Noteworthy is the fact that positive slopes in phytoplankton cumulative function were, in general, observed before those of dinoflagellates, except for *P. globosa* colonies and free cells in March 2007 (Fig. 5d–f). Overall, dinoflagellates appeared to be tightly linked to bulk phytoplankton stocks as well as stocks of *Phaeocystis* free cells, colonies as well as diatoms, despite changes in the composition of the diatom assemblages.

Copepod biomass was also related tightly with the phytoplankton biomass overall ($r = 0.70$, $n = 51$, $P < 0.0001$). However, in contrast to dinoflagellates, there were some marked anomalies with regard to temporal trends of *Phaeocystis* colonies and diatoms (Fig. 5g–i). In 2008, copepod cumulated sums remained close to the annual average but with a slight increase corresponding to the bloom of *P. globosa* colonies in May (Fig. 5h). Considering heterotrophic protists as prey, *Temora longicornis* were related to ciliate biomass ($r = 0.42$, $n = 51$, $P < 0.002$; data not shown) and *Acartia clausi* to heterotrophic dinoflagellate biomass ($r = 0.35$, $n = 51$, $P < 0.012$; data not shown).

General relationships

The plots of log-transformed data of biomass of major phytoplankton groups and their potential predators indicated curvilinear relationships. The biomass of total protists increased linearly with total phytoplankton and

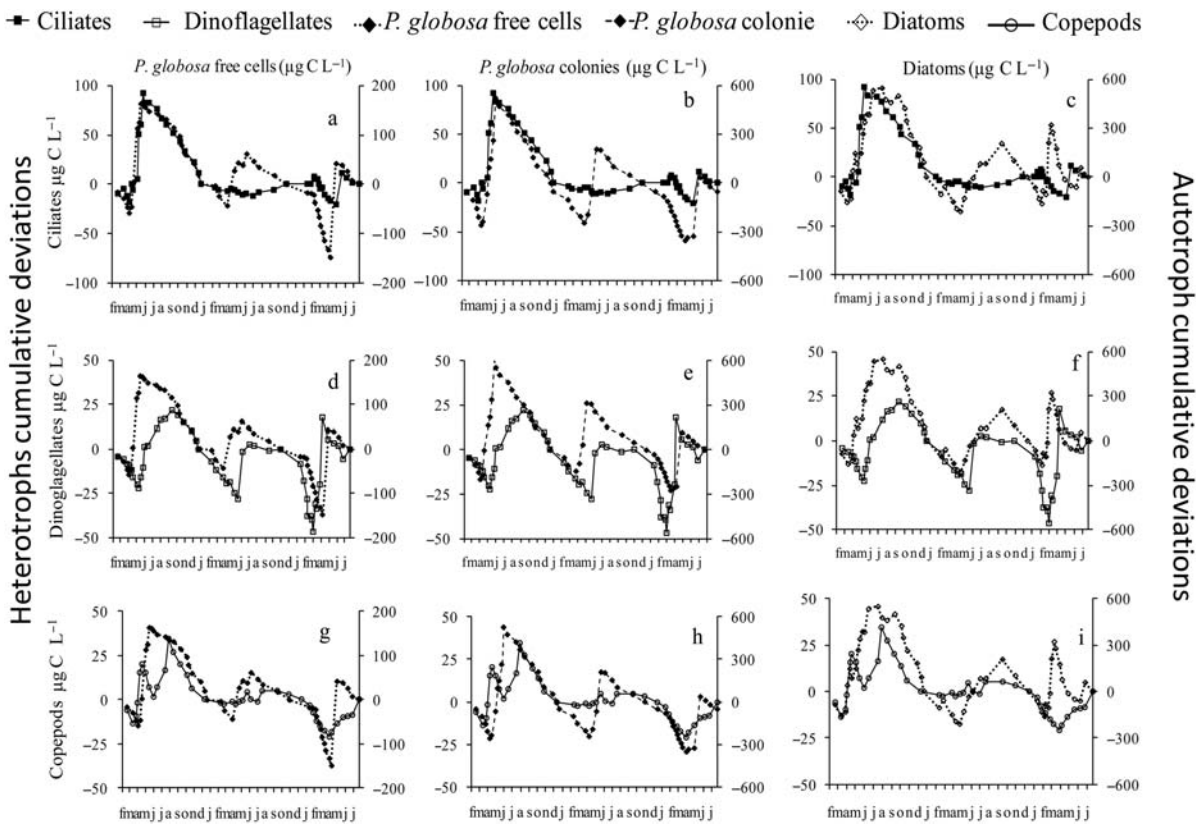

Fig. 5. Temporal trends of heterotroph and autotroph biomass (µg C L^{-1}) as cumulative sums. (**a**–**c**) Ciliates and phytoplankton, (**d**–**f**) heterotrophic dinoflagellates and phytoplankton and (**g**–**i**) copepods and phytoplankton.

levels around 70 µg C L^{-1} (Fig. 6a). The same type of relationship was observed with ciliates versus PNF and dinoflagellates versus diatoms levelling around 50 and 30 µg C L^{-1}, respectively (Fig. 6b and c). The calculated regressions for the linear part of the relations showed a stronger relation for total phytoplankton versus protists, followed by PNF versus ciliates and dinoflagellates versus diatoms (Fig. 6a–c). The relationship between dinoflagellates and *P. globosa* colonies suggested a curvilinear relationship, with dinoflagellate biomass decreasing for biomass higher than 1 µg C L^{-1} (Fig. 6d). The log–log plots of copepod biomass and auto- and heterotrophic protists did not show any significant relationship.

DISCUSSION

To our knowledge, this is the first study exploring a 2.5 years data of both primary producers and grazers in a system characterized by blooms of *Phaeocystis*. The primary aim of this study was to determine whether variations of the phytoplankton community corresponded with changes in the grazer community, especially with regard to heterotrophic protists. During our study, we observed phytoplankton successions typical of the eastern English Channel and in the Southern Bight of the North Sea with diatom blooms preceding *Phaeocystis* blooms (e.g. Breton *et al.*, 2000; Rousseau *et al.*, 2002; Seuront and Vincent, 2008; Guiselin, 2010). The phenomenon is generally ascribed as a succession in high nutrient coastal waters following silicate limitation of diatom production (e.g. Rousseau *et al.*, 2000) or alternatively, due to light limitation of diatoms (Peperzak *et al.*, 1998).

We found considerable variability in the *Phaeocystis* bloom as well as the diatom assemblages preceding and following the bloom, similar to previous studies in the same area. For example, Gomez and Souissi (Gomez and Souissi, 2008), based on sampling at approximately monthly intervals from 1998 to 2005, reported declines of the *P. globosa* spring bloom in offshore but not inshore waters and shifts in diatom assemblages (Gomez and Souissi, 2007b). During our study, the *P. globosa* concentrations were close to values of the 1998 *P. globosa* bloom (Gomez and Souissi, 2008; Table II). We encountered

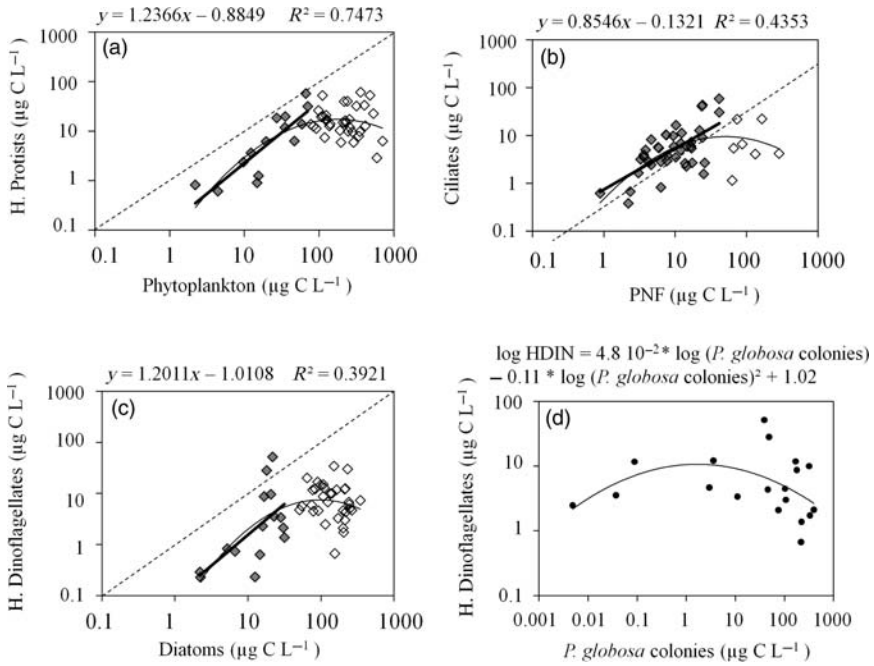

Fig. 6. Plots of log-transformed data of biomass of major phytoplankton groups and their potential protozoan predators. The dotted lines in (**a**), (**b**) and (**c**) indicate the 1:1 line. (a–c) Bold lines represent regressions for the linear part of the relation (grey rhombus), and the fine lines represent the polynomial model [grey and empty rhombus fitted with *R* software (http://www.r-project.org/)]. (**d**) The full line represents the polynomial model given above the figure.

variability in bloom duration, composition in terms of colony sizes and relative importance of non-colonial cells, as well as changes in the diatom assemblages, in particular the diatom group of *Pseudonitzschia* spp. present usually during and after the bloom (Rousseau *et al.*, 2002; Guiselin, 2010), appeared before the *P. globosa* bloom in 2009. Moreover, change in the dynamics of *P. globosa* life stages was also observed from 2007 to 2009: increases of maximum biomass of free cells (Fig. 3c), fewer small colonies (20–100 µm) and a slight increase of large colonies (Fig. 3b).

Along with variability in the phytoplankton, we found marked changes among the grazer communities, in terms of both compositional shifts and changes in abundance. In the heterotrophic protist community, the most obvious difference was a shift from a dominance of spirotrich ciliates in 2007 to dinoflagellates, largely *Gyrodinum spirale*, dominating the protist community in 2008 and 2009. The ciliate community was, overall, similar in abundance and composition to those found in other systems subject to *Phaeocystis* blooms. For example, Verity *et al.* (Verity *et al.*, 1993) reported ciliate abundances during the spring bloom in the North Atlantic of 1.9–17.2 cells mL^{-1}. The composition of ciliates was comparable to that found in Kattegat (Levinsen and Nielsen, 2002) and the proportion of mixotrophic species + *M. rubra* we found (45% of the ciliate biomass) similar to the values recorded for the North Sea (28 and 53% of the ciliate biomass nearshore and offshore, respectively; Stelfox-Widdicombe *et al.*, 2004). The relatively low ciliate abundances found in 2008 and 2009 compared to 2007 correspond with lower concentrations of free cells of *Phaeocystis* (Figs 3c and 4a), known to support ciliate growth (Tang *et al.*, 2001) as well as lower concentrations of copepods (Fig. 4c), the major predators of ciliates (e.g. Stoecker and Capuzzo, 1990; Christaki and Van Wambeke, 1995; reviewed by Calbet and Saiz, 2005).

Perhaps, the most remarkable finding of our study is with regard to heterotrophic dinoflagellates, largely the species putatively identified as *Gyrodinium spirale*. Biomass trends of heterotrophic dinoflagellates closely tracked those of diatoms as well as colonies of *Phaeocystis* (Fig. 5e and f). The biomass of heterotrophic dinoflagellates, in carbon units, was consistently about 10% of autotrophic biomass (Figs 3 and 4a) and they may have been the major consumers of phytoplankton. Heterotrophic dinoflagellates typically display low growth efficiencies and require relatively high prey concentrations, relative to ciliate microzooplankton (Hansen, 1992; Strom and Morello, 1998). However, they are capable of rapid growth given sufficient prey. In laboratory experiments, *Protoperidinium* species feeding on diatoms have daily division rates ranging from 0.5 to 2 per day

(Menden-Deuer *et al.*, 2005) and *Gyrodinium spirale*, feeding on other dinoflagellates, divides about once per day rate in the presence of phytoplankton prey concentrations typical of our study site, above 100 μg C L^{-1}, with gross growth efficiencies ranging from about 10 to 20% (Kim and Jeong, 2004). Employing these growth parameters, rough estimates suggest then a possibly major role for heterotrophic dinoflagellate as phytoplankton grazers at our study site. While heterotrophic dinoflagellates are known to be important grazers of diatoms (Sherr and Sherr 2007), our data suggest a significant role as consumers of *Phaeocystis* as well.

Copepods dominated the mesozooplankton assemblage (68.4%, Table II) with the usual copepod species found in the eastern English Channel and in the North Sea (Brylinski, 1986; Breton, 2000; Rousseau *et al.*, 2000). Abundances of copepods (0.03–10.9 ind. L^{-1}, Table II) were similar to those previously recorded for the study site, November 1995 to July 1997 (Breton, 2000). In our samples, *Acartia clausi* and *Temora longicornis* were the most abundant species found during this study (Table II). Brylinski (Brylinski, 2009) reported that *T. longicornis* habitually dominate copepod abundance during the spring and *A. clausi* during the summer.

During our study period, *T. longicornis* showed a decrease from 2007 to 2009 that corresponded with the decrease of *P. globosa* bloom duration, fewer large *Phaeocystis* colonies (>100 μm) and lower ciliate biomass (Table III). It is tempting to relate the decrease in *Temora longicornis* to declines in ciliate biomass ($r = 0.42$; cf. Results), as this species is thought to feed selectively on ciliates and discriminate against both *Phaeocystis* (Hansen and Van Boekel, 1991; Hansen *et al.*, 1993) as well as dinoflagellates (Vincent and Hartmann, 2001). The species which replaced *Temora longicornis*, *Acartia clausi*, while known to ingest ciliates (Gismervik and Andersen, 1997), apparently does not selectively prey on them in natural populations (Tiselius, 1989). The correlation between *A. clausi* and dinoflagellate biomass can be attributed to *A. clausi* preference for dinoflagellates over phytoplankton (Vargas and Gonzalez, 2004; Leising *et al.*, 2005a, b). With regard to the impact of copepod grazing on the communities of heterotrophic protists and phytoplankton, some rough estimates can be made based on maximal reported clearance rates, 40 mL day^{-1} *Temora*$^{-1}$ (Tiselius, 1989) and 30 mL day^{-1} *Acartia*$^{-1}$ (Gismervik and Andersen, 1997) and our peak copepod abundances (Fig. 4c). Such calculations suggest a weak control, clearing at most about 15% of the water column per day in 2008 and 2009 in the *Acartia* dominated years compared to 2007 in which peak populations of *Temora* may have been capable of clearing about 50% of the water column per day. Nauplii of the two dominant copepod species were not quantitatively sampled in this work, and we can speculate that nauplii maxima usually occur a few weeks before adult maxima and they can eventually have an important grazing impact in phytoplankton; since in cultures, they can feed on the same range of prey as the adults (e.g. *Isochrysis galbana* of about 12 μm and *Rhodomonas marina* 5–7 μm) (S. Souissi, Wimereux Marine Station, personal communication).

The log–log plots displayed curvilinear relationships between phytoplankton and predator. Irigoien *et al.* (Irigoien *et al.*, 2005), using a large scale data set, observed the same type of relationship, observing a plateau of microzooplankton biomass with increasing phytoplankton biomass at around 50 mg C m^{-3}, which they attributed to the presence of unfavourable prey and/or predation by mesozooplankton. In our study, microzooplankton also levelled at around this same value range (70 mg C m^{-3} Fig. 6a). In the plots of ciliates versus PNF and dinoflagellates versus diatoms, protistan biomass levelled at lower levels (Fig. 6b and c; 50 and 30 mg C m^{-3}, respectively) suggesting predation of copepods on microzooplankton which may have favoured further phytoplankton accumulation. The log–log relation between dinoflagellates and *P. globosa* colonies (Fig. 6d) indicated that while small colonies (representative of low biomass) may be suitable prey for dinoflagellates, larger colonies (representative of high biomasses) are more difficult to consume. Given that large colonies are unsuitable for copepods, this could intensify predation on dinoflagellates (Fig. 6d). The cumulated sum analysis showed some significant temporal relationships between copepods and phytoplankton and between copepods and heterotrophic protists. While phytoplankton and protists have similar growth rates, the absence of log–log relation between copepods and protists (autotrophic and heterotrophic) can be attributed to the time lags between the appearance of prey and the predator (of the order of days to weeks).

The more than 2 years sampling allowed assessment of the variability found in a "regular and recurrent event", the phytoplankton blooms of the eastern English Channel. We found differences in the phytoplankton blooms as well differences in the grazer assemblages, notably a marked variability from 1 year to the other in abundances of ciliate microzooplankton and the identity of the dominant copepod species. In contrast, heterotrophic dinoflagellates appear to be a relatively consistent assemblage in terms of both their aggregate biomass compared to phytoplankton, and their species composition. Heterotrophic dinoflagellates likely represent the primary consumers of phytoplankton, but there is also indication that they suffer

enhanced predation pressure by copepods particularly when large *Phaeocystis* colonies dominate the phytoplankton assemblages.

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