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

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Abstract:

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 ($>100\ \mu\text{m}$, $375\ \mu\text{g C L}^{-1}$) which resulted in a high biomass of healthy free cells ($163\ \mu\text{g C L}^{-1}$) accompanied high spirotrich ciliate stocks (up to $58\ \mu\text{g C L}^{-1}$) and high abundances of the copepods *Acartia clausi* and *Temora longicornis* (up to $11\ \text{ind L}^{-1}$). In 2008, the bloom which lasted a shorter period of time, was dominated by large colonies ($328\ \mu\text{g C L}^{-1}$), and fewer free cells ($131\ \mu\text{g C L}^{-1}$). 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 $<100\ \mu\text{m}$ 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.

INTRODUCTION

In the North Sea and in the eastern English Channel, gelatinous colonies of *Phaeocystis globosa* Scherffel, 1900 (Prymnesiophyceae) several mm 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). *P. 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 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 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

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2 46 cells of 4-8 μm , can support the growth and reproduction of protists, but not copepods (Tang et al.,
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4 47 2001). Furthermore, field studies of microzooplankton grazing during blooms of *Phaeocystis* have
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6 48 indicated high grazing rates (e.g., Stelfox-Widdicombe et al., 2004). Thus, existing evidence
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8 49 supports a view that microzooplankton grazing could potentially impact *Phaeocystis* blooms. In
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10 50 contrast, several field studies focusing on mesozooplankton impact on *P. globosa* have reported
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12 51 grazing rates that vary from negligible, suggesting the unsuitability of *P. globosa* for many species
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14 52 of mesozooplankton (Hansen et al., 1993; Gasparini et al., 2000), to highly variable (Seuront and
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16 53 Vincent, 2008). These discrepancies may be attributable to the effects of colony size on
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18 54 susceptibility to copepod grazing (e.g., Verity, 2000) and/or copepods switching to heterotrophic
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20 55 food (Hansen and Van Boekel, 1991; Nejstgaard et al., 2001). Overall, despite the existence of
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22 56 numerous studies dealing with *P. globosa* blooms, the identities and relative importance of the
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24 57 major groups of grazers remains obscure. In a model simulation study, Verity (2000) postulated that
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26 58 transitions between life cycle stages of *P. globosa* may potentially be important to interactions
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28 59 between phytoplankton, micro- and mesozooplankton and that these interactions may depend on
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30 60 the match or mis-match of phytoplankton and grazer communities.
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32 61 Here we attempt to clarify whether succession of the phytoplankton community corresponded to
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34 62 changes in the grazer community, especially with regard to heterotrophic protists. Our study covered
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36 63 3 years of the critical period of phytoplankton growth and senescence in a coastal system (eastern
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38 64 English Channel) over a period of 2.5 years. Such an approach permits the identification of "regular
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40 65 and recurrent patterns from occasional and exceptional events" (Ribera d'Alcala et al., 2004). We
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42 66 hypothesized that although the bloom is dominated by a single species, *P. globosa*, phytoplankton
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44 67 community composition preceding and following the bloom is likely to be variable, as well as the
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46 68 intensity of the bloom, and in particular the magnitude and the timing of *P. globosa* life stages
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48 69 (flagellated cells, colonies, and free colonial cells). Because of their known potential as *P. globosa*
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50 70 grazers and because of the scarcity of studies in particular in the eastern English Channel, our study
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52 71 focused on the effects of phytoplankton variability on heterotrophic protists (ciliates and
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54 72 dinoflagellates) as well as including copepods, consumers of both phytoplankton and heterotrophic
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56 73 protists.
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53 75 **METHOD**

55 76 **Study site and Sampling**

Water samples were collected at the coastal station (50° 40' 75 N, 1° 31' 17E, 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 days and 14 days, respectively). Sub-surface sampling (2-3 m water depth) was conducted for phytoplankton and microzooplankton, and vertical hauls for mesozooplankton.

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 nutrients concentrations were determined from 100 mL samples with an Alliance Integral Futura Autoanalyser II for nitrate (NO₃⁻), nitrite (NO₂⁻), silicate [(SiO₄)⁴⁻] and phosphate (PO₄³⁻; 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 analyzed by filtering (<150 mm Hg) duplicate 50 to 200 mL seawater samples through pre-combusted (4 to 5 h at 480°C) glass fibre filters (Whatman GF/F, 25 mm). Analysis was performed on a NA2100 Frisons CHN analyzer after drying filters at 60°C for 24 h and exposure to HCl 1 N vapors for 5 h.

Sample Analysis

Phytoplankton: For microphytoplankton floristic 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

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2 109 biomass was calculated on the basis of cell concentration and specific biometry using the size-
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4 110 dependent relationship recommended by Menden-Deuer and Lessard (2000). Carbon biomass of the
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6 111 *Phaeocystis globosa* colonies was calculated from biovolume measurements at x100 or x200
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8 112 magnification, as previously described by Breton et al. (2006). The microphytoplankton was further
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10 113 divided in two size groups: (i) Phytoplankton smaller than 100 µm (small colonies of *P. globosa*,
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12 114 and diatoms) and (ii) phytoplankton larger than 100 µm (large colonies of *P. globosa* and large
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14 115 diatoms). To enumerate nanophytoplankton (< 20 µm) 5 to 10 mL samples were preserved using
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16 116 borax buffered formaldehyde (1% v/v). Samples were filtered onto black Nuclepore filters, (pore
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18 117 size: 0.8 µm) and stained with DAPI (Porter and Feig, 1980) within 5 h of sampling and stored at –
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20 118 20°C until counting. Cells were enumerated using a Leica FW4000 epifluorescence microscope at
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22 119 x1000. To distinguish between phototrophic and heterotrophic cells, autofluorescence (chlorophyll)
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24 120 was determined under blue light excitation (BP 450-480 nm). Free colonial and flagellated
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26 121 *Phaeocystis* cells are easily distinguished based on their morphology. Colonial cells are in the size
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28 122 range of 4.5– 8 µm, have an anterior longitudinal groove and lack filamentous appendages.
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30 123 Flagellated cells have a rounded shape, and are smaller than colonial cells, with a diameter of 3–5
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32 124 µm (reviewed in Rousseau et al. 2007). Phototrophic nanoplankton consisted almost exclusively of
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34 125 free *P. globosa* cells and cryptophytes (see results) and will be designated from now-on in the text
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36 126 as phototrophic nanoflagellates (PNF).
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38 127 Nano-sized diatoms were counted along with microphytoplankton as described above. For each
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40 128 sample, at least 30 fields and at least 250 phototrophic nanoflagellates (PNF) were counted on each
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42 129 filter. To estimate PNF biomass, biovolume was calculated based on the linear dimensions (length
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44 130 and width) of cells using an image analyser with a camera mounted on the microscope. Biovolume
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46 131 was then converted to biomass according to Menden-Deuer and Lessard (2000).
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48 132 Heterotrophic protists: For heterotrophic protist enumeration, duplicate samples (250 mL) were
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50 133 placed in opaque glass bottles. One 250 mL sample was fixed with acid Lugol's solution (2% v/v)
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52 134 for quantitative counts, and the other with borax buffered formaldehyde (1% v/v) for determination
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54 135 of the trophic type of the ciliates, heterotroph or mixotroph, based on the presence or absence of
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56 136 sequestered chloroplasts. The samples were then stored at 4°C in the dark until analysis (most often
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58 137 within the following week and maximally 3 weeks later). Samples were further sedimented in 50 or
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60 138 100 mL Hydrobios chambers for at least 24 h before enumeration using an Nikon Eclipse TE2000-S
inverted microscope at 200x or 400x 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 to 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 Kofoed and Campbell (1929) for tintinnid ciliates, the Planktonic Ciliate Project (<http://www.liv.ac.uk/ciliate/intro.htm>), University of Liverpool, 2002, for spirotrich and other ciliates, and following Schiller (1931-1937), Gomez and Souissi (2007) and Maar et al. (2002) for heterotrophic dinoflagellates. Ciliates were further divided into 3 size groups (<20, 20-40, >40 μm) and dinoflagellates in 5 size groups (<10, 10-20, 20-40, 40-60, >60 μm). Linear dimensions (length and diameter) were measured at x400 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 x volume^{0.819} pg C μm^{-3} (Stoecker et al., 1994) for dinoflagellates.

Mesozooplankton: Zooplankton samples for 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, mounted on the mouth of the net (0.25 m² mouth area). The filtered volume varied between 1 m³ and 7 m³. 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 (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 2 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 $2.34 \pm 2.63 \mu\text{g C copepod}^{-1}$ 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 show no slope.

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

S_p = consecutive terms of the cumulative sums

x_t = value for each sampling date (t)

p_k = 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°C 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 $\text{NO}_3^- + \text{NO}_2^-$, 15.05 μM for $(\text{SiO}_4)^{4-}$, 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 $\text{NO}_3^- + \text{NO}_2^-$ concentrations (Table I). POC ranged from 114 to 1675 $\mu\text{g C L}^{-1}$ in 2007 and from around 100 to 600 $\mu\text{g C L}^{-1}$ in 2008 and 2009 (Table I)

Phytoplankton

Chlorophyll *a* (chl *a*) concentrations ranged from 0.8 to 20.3 $\mu\text{g Chl a L}^{-1}$ (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 $\mu\text{g C L}^{-1}$, 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 was calculated ($\text{COP} = 92.0 + 47.6 [\text{Chl a}]$, and $\text{Cphytoplankton} = 29.4 + 23.6[\text{Chl a}]$, $r^2 = 0.425$ and $r^2 = 0.552$ with $p < 0.0001$ respectively, figures not shown).

Phaeocystis globosa blooms are ephemeral and at our study site occurred from late March to early May and lasted about one month each year (37, 27 and 29 days in 2007, 2008 and 2009, respectively, Fig. 3b,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 to 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 $\mu\text{g C L}^{-1}$) and free colonial cells (from 62 to 153 $\mu\text{g C L}^{-1}$) while flagellated cells decreased slightly (from 66 to 50 $\mu\text{g C L}^{-1}$; 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 $\mu\text{g C L}^{-1}$ (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).

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2 232 We distinguished 3 distinct assemblages of diatoms. The first group, composed of cells
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4 233 between 20-120 μm and characterized by *Pseudonitzschia* spp., and *Chaetoceros* spp., was present
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6 234 during *P. globosa* blooms and persisted during the post-bloom period until August. In 2009 the
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8 235 *Pseudonitzschia* spp. group also dominated the phytoplankton during the pre-bloom period (209 μg
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10 236 C L^{-1} in early March; Fig. 3a). The second group, characterized by diatoms forming colonies (> 100
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12 237 μm) such as *Skeletonema costatum* 5-20 μm length, *Brockmaniella brockmanii* and *Ditylum*
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14 238 *brightwelli* 20-120 μm length, marked the early spring period. The third group appeared from the
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16 239 end of summer to winter, composed of large fine-walled diatoms such as *Guinardia* spp.,
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18 240 *Rhizosolenia* spp. and *Chaetoceros* spp.

18 241 **Heterotrophic protists (ciliates and dinoflagellates)**

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20 242 The biomass of heterotrophic protists over the study period showed low values during autumn-
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22 243 winter (0.6 to 20.0 $\mu\text{g C L}^{-1}$) and higher values during spring-summer (2.8 to 61.1 $\mu\text{g C L}^{-1}$). The
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24 244 overall biomass of protists during the spring bloom was similar in 2007 and 2009 and greater than
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26 245 that recorded for 2008 (Table III). Despite these differences, some common features were observed
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28 246 every year: a) heterotrophic dinoflagellate biomass exceeded that of ciliates, except in spring 2007
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30 247 (Fig. 4a), b) ciliates were almost equally divided between heterotrophs and mixotrophs (Fig. 4b).

31 248 Ciliate abundance and biomass over the study period ranged from 0.5 to 19.5 $10^3 \text{ cells L}^{-1}$
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33 249 and from 0.4 to 58.1 $\mu\text{g C L}^{-1}$, respectively (Table II). High abundance and biomass were recorded
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35 250 in May 2007 and 2009, while in 2008 ciliate abundance and biomass were relatively low ($< 5.2 \cdot 10^3$
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37 251 cells L^{-1} and $< 10 \mu\text{g C L}^{-1}$, Fig. 4a). The taxonomic composition of the ciliate community was
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39 252 largely invariant over the 2.5 years and was dominated (86% of abundance) by Spirotrichs of the
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41 253 genera *Strombidium*, *Strobilidium*, *Leegardiella*, *Tontonia* and the haptorid *Myrionecta rubra*.
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43 254 Among heterotrophic aloricate ciliates, *Strombidium lynni*, *Leegardiella sol*, and *Strobilidium*
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45 255 *spiralis* were present in all samples. Scuticociliates were occasionally present during the study in
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47 256 particular after wind events in 2007 and 2008 (mean $< 1 \mu\text{g C L}^{-1}$). Tintinnids were insignificant
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49 257 during the whole study and will not be further considered (max. 0.33 $\mu\text{g C L}^{-1}$; mean 0.02 $\mu\text{g C L}^{-1}$).
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51 258 Carnivorous ciliates, the suctorians (*Acineta* sp. and *Podophyra* sp.) were present in low numbers
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53 259 (up to 80 cells L^{-1}). The mixotrophic community was essentially composed by *Laboea strobila*,
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55 260 *Tontonia* spp, *Strombidium acutum* and *S. capitatum*. *Myrionecta rubra* was also present in large
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57 261 numbers and biomass (up to 4.32 $10^3 \text{ cells L}^{-1}$, 8.02 $\mu\text{g C L}^{-1}$) during different seasons, without a
58
59 262 marked seasonality (Fig. 4b). The biomass of heterotrophs and mixotrophs was in a similar range
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57 263 (from 0.1-34.3 and 0.1-24.6 $\mu\text{g C L}^{-1}$, 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 ($11.5 \pm 3.7 \cdot 10^3 \mu\text{m}^3$) was the modal size-class for heterotrophs while mixotrophs were dominated by the >40 μm size class ($88.6 \pm 35.4 \cdot 10^3 \mu\text{m}^3$). 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 $\mu\text{g C L}^{-1}$ (Table II; Fig. 4a) and increased from 2007 to 2009 (Table III) with the increase of 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, 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 pseudonociluca*, *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 to 81.1% of the biomass). In 2007 the assemblage of <20 ($1.9 \pm 1.0 \cdot 10^3 \mu\text{m}^3$, *Protoperidinium* spp.) and 20-40 μm ($15.1 \pm 7.3 \cdot 10^3 \mu\text{m}^3$, *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 to 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 to 10.9 ind. L^{-1}) equal to $68.4\% \pm 22.4$ of total abundance (Table II, Fig. 4c). Copepod biomass ranged from 0.07 to 27.3 $\mu\text{g C L}^{-1}$ (mean $6.4 \pm 6.6 \mu\text{g C L}^{-1}$, Table II). The dominant copepod species were *Acartia clausi* and *Temora longicornis*, which accounted for $44.4 \pm 18.8\%$ and $23.3 \pm 15.7\%$ of copepod abundance and $31.4 \pm 15.4\%$ and $33.2 \pm 18.7\%$ of copepod biomass, respectively. Yet, we observed a change in relative abundances of these species during the spring

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2 296 bloom (from March to May). The *Acartia* to *Temora* ratio of average biomass values increased from
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4 297 0.25 in 2007 to 1.9 in 2009 (Table III, Fig. 4c). *Paracalanus parvus* and *Centropages hamatus* were
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6 298 also present in lower abundances and accounted for 7.0 ± 5.4 and $13.6 \pm 13.3\%$ of total copepod
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8 299 abundance, respectively.
9 300 Pluteus and larvae of the urchin *Echinocardium cordatum* were present each year in spring during
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11 301 less than 1 week and occurred between the two maxima of copepods (Fig. 4). Their highest
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13 302 abundance was observed in May 2007 when they reached up to 11.3 ind. L^{-1} (up to 82% of
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15 303 zooplankton abundance) and they were absent during the rest of the year. Appendicularians
16 304 (*Oikopleura dioica*) feeding essentially on picoplankton, were also observed in low numbers (0 to
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18 305 2.9 ind. L^{-1} , mean $15.3 \pm 11.8\%$ of the mesozooplankton abundance).
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22 307 **Temporal Trends based on cumulative sums**

23 308 The cumulative sums show temporal trends in terms of differences from overall averages, temporal
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25 309 variations not easily seen in figures such as Figures 3 and 4. We focused on the temporal trends of
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27 310 the three major types of consumers (ciliates, dinoflagellates and copepods) and autotrophs (Fig. 5a-
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29 311 i).

30 312 In 2007 the ciliate biomass was strongly related with all phytoplankton compartments (Fig
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32 313 5a-c, diatoms $r = 0.88$, *P. globosa* colonies $r = 0.97$ and free cells $r = 0.93$, $n = 21$, $p < 0.0001$). In
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34 314 2008, no significant relation was observed with the phytoplankton and the ciliate cumulated sums
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36 315 values remained close to the average annual biomass (more or less parallel to the x-axis, Fig. 5a-c).
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38 316 In 2009, the ciliates related again with *P. globosa* colonies and free cells with a strong anomaly at
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40 317 the end of April (Fig. 5a-b) which corresponds to a highest ciliate biomass recorded in 2009 (Fig.
41 318 5a).
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43 319 Dinoflagellates showed a remarkable co-variation with total phytoplankton biomass during
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45 320 the whole study ($r = 0.51$, $n = 51$, $p < 0.0002$; c.f. Fig. 5 d, e, f). Noteworthy is the fact that positive
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47 321 slopes in phytoplankton cumulative function were in general observed before those of
48 322 dinoflagellates, except for *P. globosa* colonies and free cells in March 2007 (Fig. 5d-f). Overall,
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50 323 dinoflagellates appeared to be tightly linked to bulk phytoplankton stocks as well as stocks of
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52 324 *Phaeocystis* free cells, colonies as well as diatoms, despite changes in the composition of the diatom
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54 325 assemblages.

55 326 Copepod biomass was also related tightly with the phytoplankton biomass overall ($r = 0.70$,
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57 327 $n = 51$, $p < 0.0001$). However, in contrast to dinoflagellates there were some marked anomalies with
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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 levels around $70 \mu\text{g C L}^{-1}$ (Fig. 6a). The same type of relationship was observed with ciliates vs PNF and dinoflagellates vs diatoms levelling around 50 and $30 \mu\text{g C L}^{-1}$, respectively (Fig. 6b,c). The calculated regressions for the linear part of the relations, showed a stronger relation for total phytoplankton vs protists, followed by PNF vs ciliates and dinoflagellates vs diatoms (Fig. 6, a,b,c). The relationship between dinoflagellates and *P. globosa* colonies suggested a curvilinear relationship, with dinoflagellate biomass decreasing for biomass higher than $1 \mu\text{g C L}^{-1}$ (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 (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

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2 360 and shifts in diatom assemblages (Gomez and Souissi, 2007). During our study, the *P. globosa*
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4 361 concentrations were close to values of the 1998 *P. globosa* bloom (Gomez and Souissi, 2008; Table
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6 362 II). We encountered variability in bloom duration, composition in terms of colony sizes and relative
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8 363 importance of non-colonial cells, as well as changes in the diatom assemblages, in particular the
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10 364 diatom group of *Pseudonitzschia* spp. present usually during and after the bloom (Rousseau et al.,
11 365 2002; Guiselin, 2010), appeared before the *P. globosa* bloom in 2009. Moreover change in the
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13 366 dynamics of *P. globosa* life stages was also observed from 2007 to 2009: increases of maximum
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15 367 biomass of free cells (Fig. 3c), fewer small colonies (20-100 μm) and a slight increase of large
16 368 colonies (Fig. 3b).

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18 369 Along with variability in the phytoplankton, we found marked changes among the grazer
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20 370 communities, in terms of both compositional shifts and changes in abundance. In the heterotrophic
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22 371 protist community, the most obvious difference was a shift from a dominance of spirotrich ciliates in
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24 372 2007 to dinoflagellates, largely *Gyrodinium spirale*, dominating the protist community in 2008 and
25 373 2009. The ciliate community was, overall, similar in abundance and composition to those found in
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27 374 other systems subject to *Phaeocystis* blooms. For example, Verity et al. (1993) reported ciliate
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29 375 abundances during the spring bloom in the North Atlantic of 1.9 - 17.2 cells mL^{-1} . The composition
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31 376 of ciliates was comparable to that found in Kattegat (Levinsen and Nielsen, 2002) and the
32 377 proportion of mixotrophic species + *M. rubra* we found (45% of the ciliate biomass) similar to the
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34 378 values recorded for the North Sea (28% and 53% of the ciliate biomass nearshore and offshore
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36 379 respectively; Stelfox-Widdicombe et al., 2004). The relatively low ciliate abundances found in 2008
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38 380 and 2009 compared to 2007 correspond with lower concentrations of free cells of *Phaeocystis* (Fig.
39 381 3c; Fig. 4a), known to support ciliate growth (Tang et al., 2001) as well as lower concentrations of
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41 382 copepods (Fig. 4c), the major predators of ciliates (e.g., Stoecker and Capuzzo, 1990; Christaki and
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43 383 Van Wambeke, 1995; reviewed by Calbet and Saiz 2005).

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45 384 Perhaps the most remarkable finding of our study is with regard to heterotrophic
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47 385 dinoflagellates, largely the species putatively identified as *Gyrodinium spirale*. Abundance trends of
48 386 heterotrophic dinoflagellates closely tracked those of diatoms as well as colonies of *Phaeocystis*
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50 387 (Fig. 5e,f). The biomass of heterotrophic dinoflagellates, in carbon units, was consistently about
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52 388 10% of autotrophic biomass (see Fig. 3 and Fig. 4a) and they may have been the major consumers of
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54 389 phytoplankton. Heterotrophic dinoflagellates, typically display low growth efficiencies and require
55 390 relatively high prey concentrations, relative to ciliate microzooplankton (Hansen, 1992; Strom and
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57 391 Morello, 1998). However, they are capable of rapid growth given sufficient prey. In laboratory
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experiments, *Protoperidinium* species feeding on diatoms have daily division rates ranging from 0.5 - 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 $100 \mu\text{g L}^{-1}$, 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 & Sherr 2007), our data suggests 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 (Breton 2000, Rousseau et al. 2000, Brylinski 1986). Abundances of copepods ($0.03 - 10.9 \text{ ind. L}^{-1}$, 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 (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 ($> 100 \mu\text{m}$) 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., 2005 a,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, $40 \text{ mL d}^{-1} \text{ Temora}^{-1}$ (Tiselius, 1989) and $30 \text{ mL d}^{-1} \text{ Acartia}^{-1}$, (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 2 dominant copepod species were not quantitatively sampled

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2 424 in this work, we can speculate that nauplii maxima usually occur a few weeks before adult maxima
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4 425 and they can eventually have an important grazing impact in phytoplankton; since in cultures they
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6 426 can feed on the same range of prey as the adults (e.g. *Isochrysis galbana* of about 12 μm and
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8 427 *Rhodomonas marina* 5-7 μm) (S. Souissi, Wimereux Marine Station, personal communication).
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11 429 The log-log plots displayed curvilinear relationships between phytoplankton and predator. Irigoien
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13 430 et al. (2005) using a large scale data set, observed the same type of relationship, observing a plateau
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15 431 of microzooplankton biomass with increasing phytoplankton biomass at around 50 mg C m^{-3} ; which
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17 432 they attributed to the presence of unfavourable prey and/or predation by mesozooplankton. In our
18 433 study microzooplankton also levelled at around this same value range (70 mg C m^{-3} Fig 6a). In the
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20 434 plots of ciliates vs PNF and dinoflagellates vs diatoms, protistan biomass levelled at lower levels
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22 435 (Fig. 6b, c; 50 and 30 mg C m^{-3} , respectively) suggesting predation of copepods on
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24 436 microzooplankton which may have favoured further phytoplankton accumulation. The log-log
25 437 relation between dinoflagellates and *P. globosa* colonies (Fig. 6d) indicated that while small
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27 438 colonies (representative of low biomass) may be suitable prey for dinoflagellates, larger colonies
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29 439 (representative of high biomasses) are more difficult to consume. Given that large colonies are
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31 440 unsuitable for copepods, this could intensify predation on dinoflagellates (Fig. 6d). The cumulated
32 441 sum analysis showed some significant temporal relationships between copepods and phytoplankton
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34 442 and between copepods and heterotrophic protists. While phytoplankton and protists have similar
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36 443 growth rates, the absence of log-log relation between copepods and protists (autotrophic and
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38 444 heterotrophic) can be attributed to the time lags between the appearance of prey and the predator (of
39 445 the order of days to weeks).
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43 447 The more than two year's sampling allowed assessment of the variability found in a "regular
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45 448 and recurrent event", the phytoplankton blooms of the eastern English Channel. We found
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47 449 differences in the phytoplankton blooms as well differences in the grazer assemblages, notably a
48 450 marked variability from one year to the other in abundances of ciliate microzooplankton and the
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50 451 identity of the dominant copepod species. In contrast, heterotrophic dinoflagellates appear to be a
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52 452 relatively consistent assemblage in terms of both their aggregate biomass compared to
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54 453 phytoplankton, and their species composition. Heterotrophic dinoflagellates likely represent the
55 454 primary consumers of phytoplankton, but there is also indication that they suffer enhanced predation
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pressure by copepods particularly when large *Phaeocystis* colonies dominate the phytoplankton assemblages.

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39 631 **Table and Figure legends**

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41 632
42
43 633 Table I: Environmental parameters from February 2007 to July 2009 in the eastern English Channel
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45 634 [min – max]. Numbers in parenthesis indicate the number of samples per year.
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48 636 Table II: Autotrophic and heterotrophic abundance and biomass ([min – max]; mean ± sd), and % of
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50 637 total protist biomass and total metazoan abundance, from February 2007 to July 2009 in the eastern
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52 638 English Channel.
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55 640 Table III: Averages of biological stocks (biomass or abundance) during the spring bloom periods
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57 641 (from March to May) for 2007, 2008 and 2009 in the eastern English Channel.
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Figure 1: Location of the SOMLIT station (●)

Figure 2: Temporal variation of (a) temperature ($^{\circ}\text{C}$) and salinity; (b) chlorophyll *a* ($\mu\text{g Chl } a \text{ L}^{-1}$) and phytoplankton biomass ($\mu\text{g C L}^{-1}$) at SOMLIT station (eastern English Channel) from February 2007 to July 2009.

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

Figure 4: Temporal variation of heterotrophic protist and copepod biomass ($\mu\text{g C L}^{-1}$) 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* abundances.

Figure 5: Temporal trends of heterotroph and autotroph biomass ($\mu\text{g C L}^{-1}$) as cumulative sums. (a to c) ciliates and phytoplankton, (d to f) heterotrophic dinoflagellates and phytoplankton and (g to i) copepods and phytoplankton.

Figure 6: Plots of log transformed data of biomass of major phytoplankton groups and their potential protozoan predators. The dotted line in panels a, b and c indicates the 1:1 line. (a,b and 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 represent the polynomial model given above the figure.

671 Table I

	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]

Table II

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

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675 Table III

	2007	2008	2009
Autotrophic and heterotrophic protist biomass ($\mu\text{g C L}^{-1}$)			
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
<i>Phaeocystis globosa</i>	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 ($\mu\text{g C L}^{-1}$)			
Total Copepods	10.0	5.6	6.1
<i>Acartia clausi</i>	1.5	1.8	3.1
<i>Temora longicornis</i>	5.9	2.5	1.6

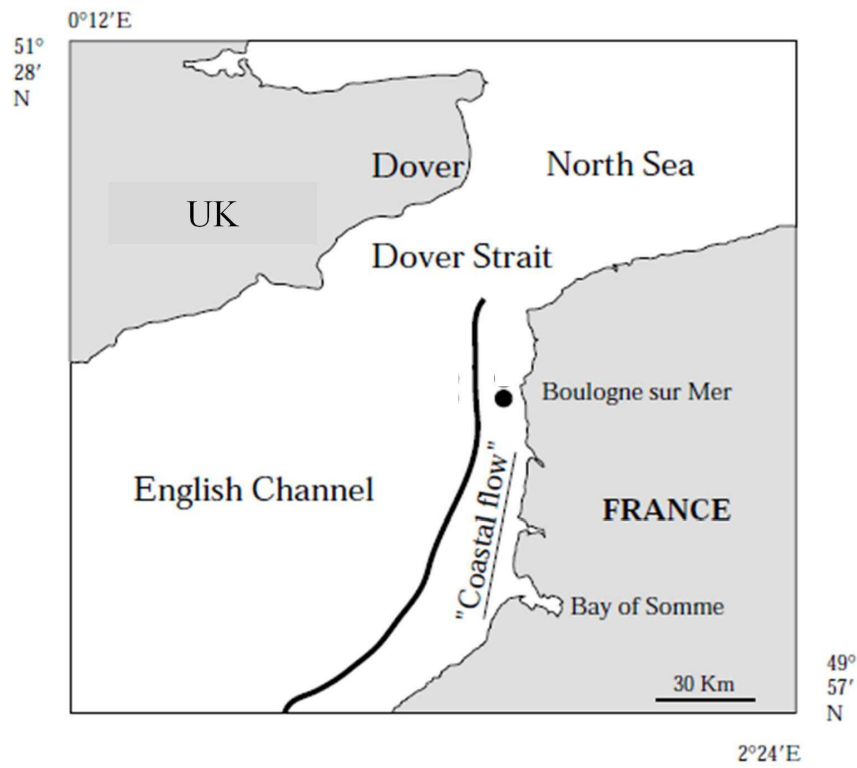


Fig. 1

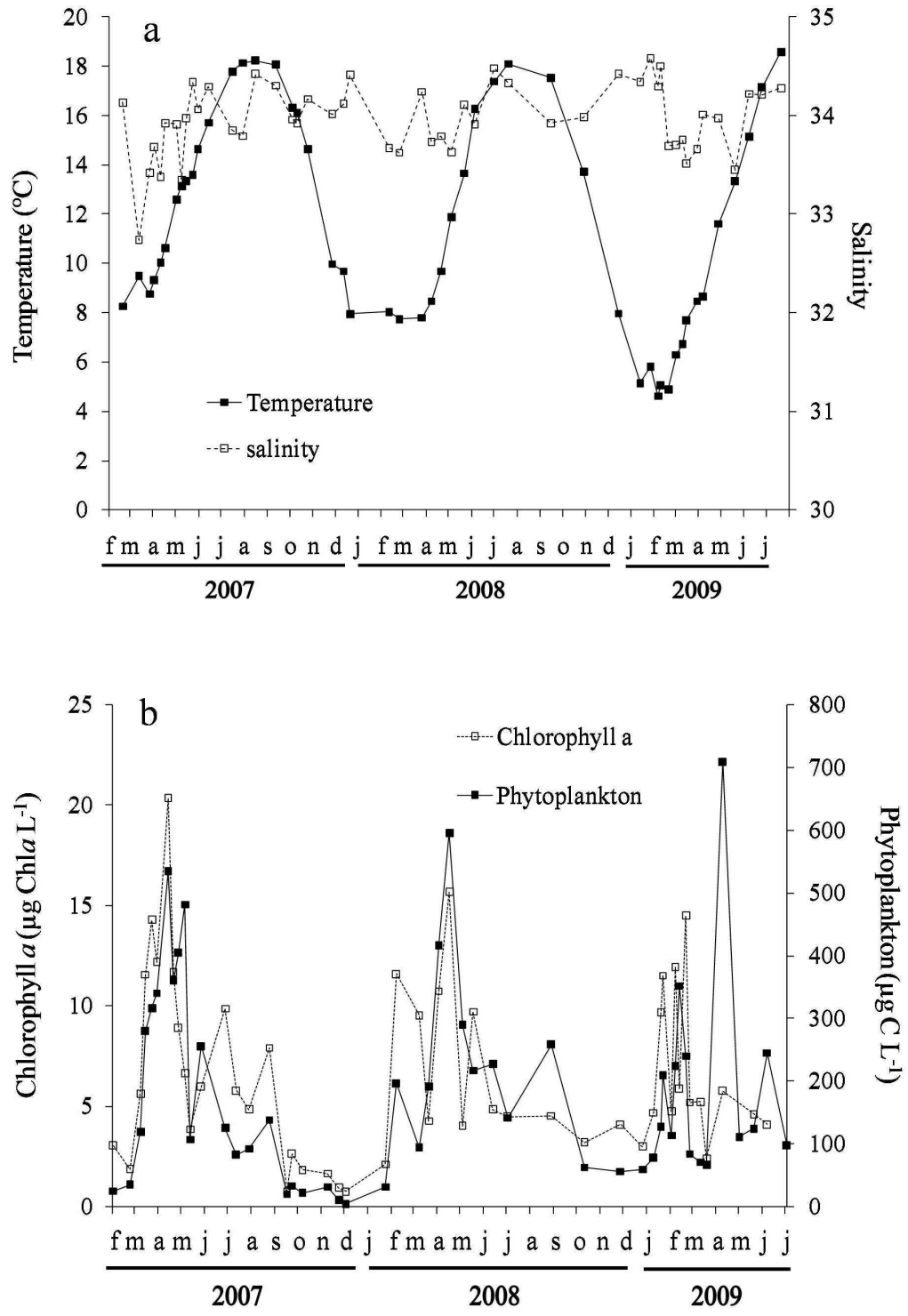


Fig. 2

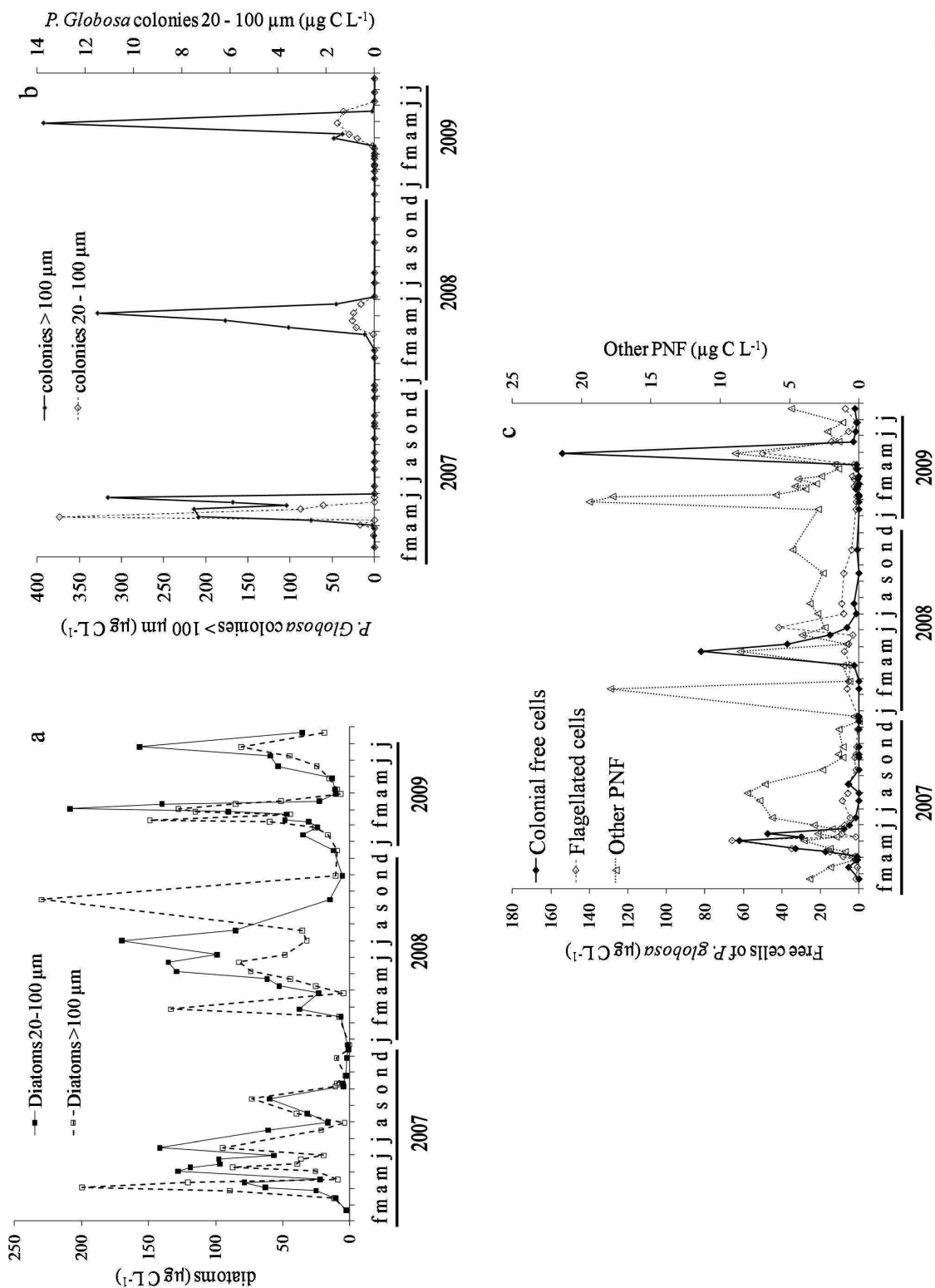


Fig. 3

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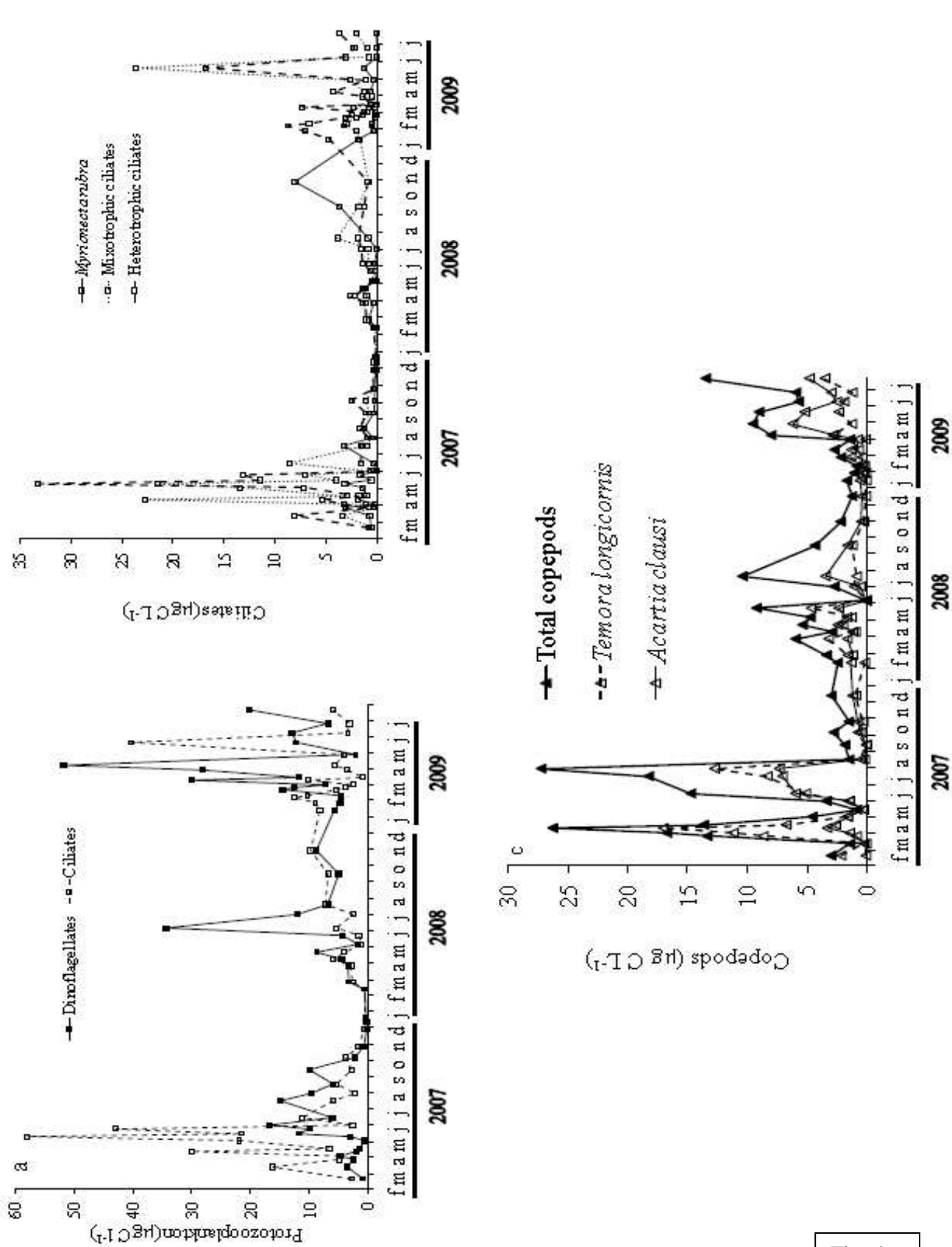


Fig. 4

Autotroph cumulative deviations

■ Ciliates ◆ *P. globosa* free cells ◆ *P. globosa* colonies ◆ Diatoms — Copepods

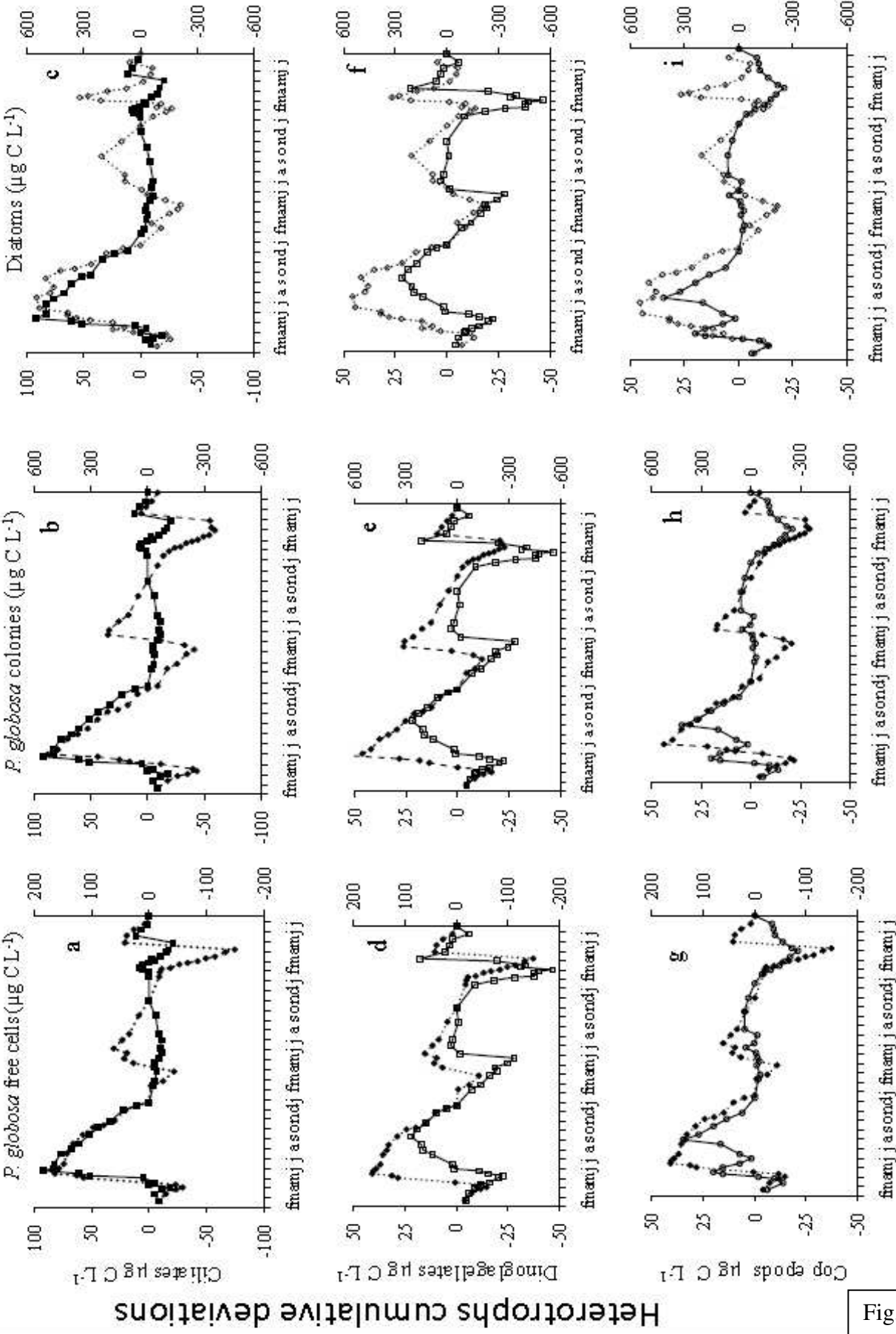


Fig. 5

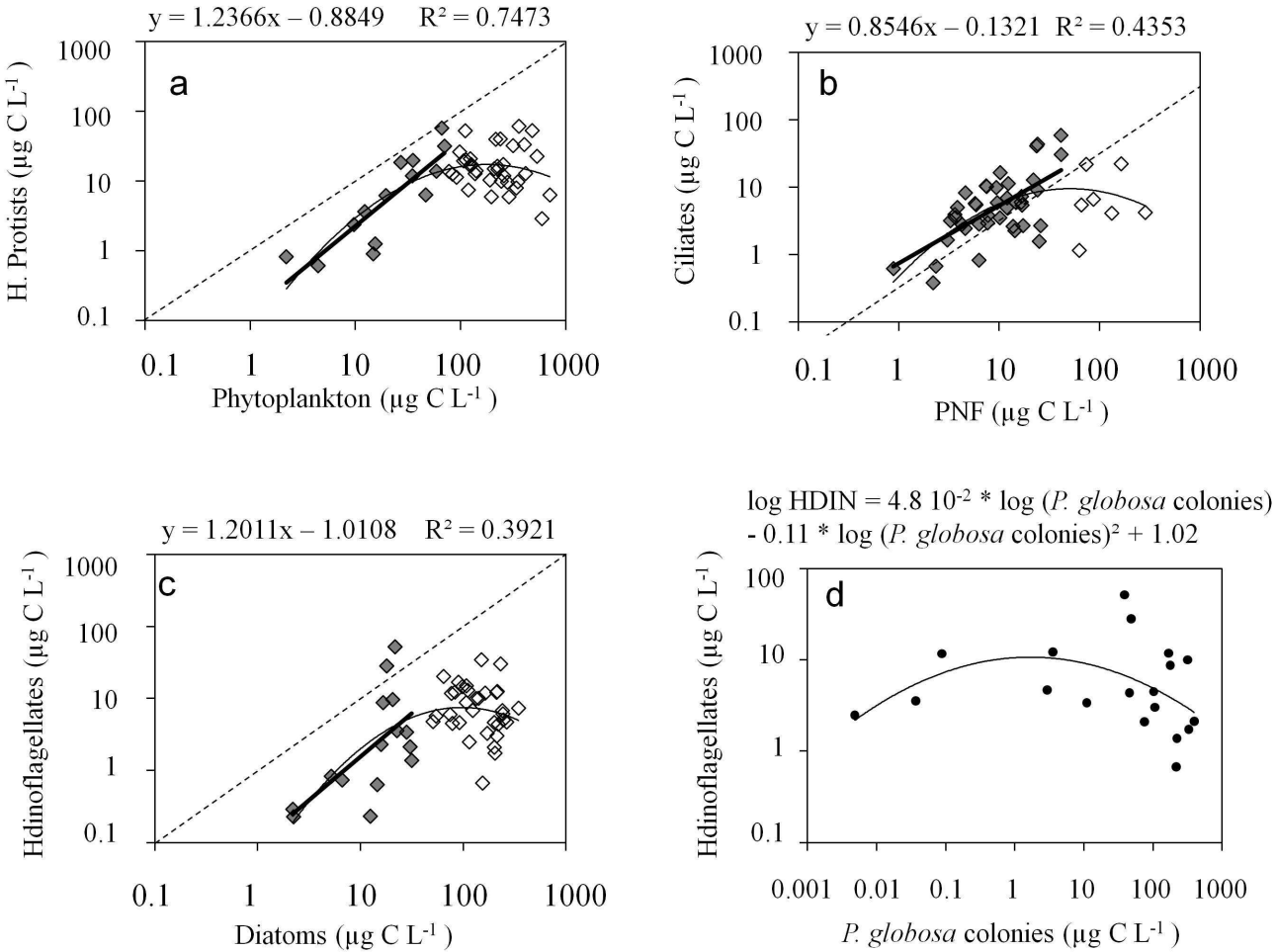


Fig. 6