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Plankton community diversity from bacteria to copepods in bloom and non-bloom conditions in the Celtic Sea in spring

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ABSTRACT

The plankton community composition comprising heterotrophic bacteria, pro-/eukaryotes, heterotrophic nanoflagellates, microzooplankton and mesozooplankton was assessed during the spring bloom and at non-bloom stations in the English Channel and Celtic Sea between 6 and 12 April 2002. Non-bloom sites were characterised by a dominance of pro-/eukaryotic phytoplankton <20 μm, higher abundance of heterotrophic nanoflagellates, microzooplankton standing stocks ranging between 60 and 380 mg C m^{-2}, lower mesozooplankton diversity and copepod abundance of between 760 and 2600 ind m^{-3}. Within the bloom, the phytoplankton community was typically dominated by larger cells with low abundance of pro-/eukaryotes. Heterotrophic nanoflagellate cell bio-volume decreased leading to a reduction in biomass whereas microzooplankton biomass increased (360–1500 mg C m^{-2}) due to an increase in cell bio-volume and copepod abundance ranged between 1400 and 3800 ind m^{-3}. Mesozooplankton diversity increased with an increase in productivity. Relationships between the plankton community and environmental data were examined using multivariate statistics and these highlighted significant differences in the abiotic variables, the pro-/eukaryotic phytoplankton communities, heterotrophic nanoflagellate, microzooplankton and total zooplankton communities between the bloom and non-bloom sites. The variables which best described variation in the microzooplankton community were temperature and silicate. The spatial variation in zooplankton diversity was best explained by temperature. This study provides an insight into the changes that occur between trophic levels within the plankton in response to the spring bloom in this area.

1. Introduction

Zooplankton ranging in size from small nanoflagellates (>2 μm) through to larger crustaceans (<2000 μm) play an important role in the pelagic food web through their interactions with higher and lower trophic levels within the water column. In temperate regions, diatoms generally dominate spring bloom phytoplankton assemblages and zooplankton populations are thought to increase in response to the diatom-dominated spring bloom. The traditional view is that during spring blooms, mesozooplankton, often dominated by large copepods, play a key role in the transfer of phytoplankton carbon to higher, and commercially important, trophic levels (larvae and juvenile fish) without high loss of energy during the transfer (Cushing, 1989). Smaller copepods, on the other hand, are capable of exploiting components of the microbial food web (Turner, 2004). It is now well established, however, that the microzooplankton form a significant proportion of the total zooplankton abundance and biomass in both coastal and oceanic environments and play an important role in carbon and energy flow through pelagic ecosystems (Calbet and Landry, 2004). Thus the interactions within the food web and its trophic structure are highly dynamic and more complex than once thought (Azam et al., 1983). The abundance and community composition of each of the different components of the zooplankton community is regulated by the availability of food resources and predation. Microzooplankton tend to be the major grazers of phytoplankton in marine ecosystems (Calbet and Landry 2004; Calbet 2008) and can also act as a link between pico- and nano-sized particles and the mesozooplankton which would otherwise be unavailable to mesozooplankton due to their smaller size (e.g. Sherr and Sherr, 1988; Stoecker and Cappuzzo, 1990). Microzooplankton can also be significant bacterivores (e.g. Sherr and Sherr, 1994; Strom, 2000) and can comprise a significant proportion of the mesozooplankton diet (in particular copepods) (Calbet and Saiz, 2005; Campbell et al., 2009). Nanozooplankton are important components of the

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microbial food web because of their role as consumers of bacteria and picoplankton (e.g. Mc Manus and Fuhrman, 1988; Caron et al., 1991; Sanders et al., 1992; Zubkov and Tarran, 2008). A recent study has shown that nano- and picophytoplankton smaller than 5 μm are also significant consumers of bacteria in the temperate Atlantic Ocean (Zubkov and Tarran, 2008).

In order to understand the relative importance of the zooplankton in the functioning of the aquatic food web it is important to consider all components of the community. Changes in zooplankton community structure in response to environmental variables have been examined in mesozooplankton communities, in particular copepods (e.g. Woodd-Walker et al., 2002; Thor et al., 2005; Vidjak et al., 2006) and microzooplankton, specifically the ciliated protozoa, (James and Hall, 1995). Only a few studies have looked at the community structure of the whole zooplankton assemblage from 2 to 2000 μm (Stelfox et al., 1999) and further related this to abiotic variables (Pedersen et al., 2005; Rollwagen-Bollens et al., 2006; Isari et al., 2007).

From previous phytoplankton bloom studies in the Celtic Sea it is known that during the winter the phytoplankton community is dominated by small nanoflagellates and eukaryotic picoplankton and these are replaced by larger phytoplankton when the water column stratifies (Joint et al., 1986). A typical spring bloom in the region is generally dominated by large diatoms, specifically *Nitzschia*, *Thalassionema* and *Chaetoceros*, although dinoflagellates and nanoflagellates are also present (Rees et al., 1999). The biomass of mesozooplankton is thought to be generally low in the Celtic Sea area during April/May (Joint et al., 2001). While it was previously thought that copepods are the main grazers of phytoplankton in the Celtic Sea (Joint and Williams, 1985), the microzooplankton can consume between 30 and 65% of the phytoplankton daily during summer months (Burkill et al., 1987). Further work has demonstrated that grazing by the microzooplankton is, in fact, higher than that of the mesozooplankton in the spring and summer months (Joint et al., 2001). Large copepod species are not thought to be the major grazers of the spring bloom in the western Irish Sea, smaller species which often dominate copepod populations are more important (Gowen et al., 1999) and these could typically favour microzooplankton as food (Castellani et al., 2008; Campbell et al., 2009).

The overall objectives of this study were (1) to provide a quantitative description of the picoplankton, nanoplankton, microzooplankton and mesozooplankton communities found at non-bloom and bloom stations during April in the Celtic Sea; and (2) to determine how the structure of the zooplankton community is affected by potential food resource availability (pro-/eukaryotic phytoplankton and chlorophyll-*a*) and environmental variables during the spring bloom compared to non-bloom situations. Concurrent investigations of mesozooplankton grazing and the decline of the spring bloom have already been published (Fileman et al., 2007; Llewellyn et al., 2008) and will be used to help draw conclusions about food web structure in the discussion (Section 4).

2. Methods

2.1. Sampling sites

Sampling was carried out onboard RRS *Discovery* (cruise D 261) at 4 stations located along a transect from the English Channel to the Great Sole Bank area of the western Celtic Sea (Fig. 1). This included a non-bloom coastal station (Stn 1), 2 further stations representing non-bloom conditions on the shelf (Stn 4) and offshelf (Stn 6) and a bloom station (Stn 7) situated on the Great Sole Bank at 49°37′N and 10°20′W (Table 1). The bloom station was tracked using a drifting buoy for a period of 7 days between 6 and 12 April 2002. Samples for pro-/eukaryotic phytoplankton <20 μm, heterotrophic nanoplankton, micro- and mesozooplankton communities were collected at each station and on a daily basis from 6 to 11 April at the bloom station. No sampling was carried out on day 2 at the bloom station because of stormy conditions. The wind from the storm which occurred on day 2 may have caused the marker buoy to drift with respect to the water column although the physical properties of the water indicate that this study was conducted in a similar body of water and that sampling on days 3–7 was still within the spring bloom.

2.2. Sampling protocol

To determine the vertical structure of the plankton community (pro-/eukaryotic phytoplankton <20 μm, heterotrophic nanoplankton and microzooplankton) water samples were collected from 3 to 6 depths within the euphotic zone using 20 L Niskin bottles attached to a Seabird CTD rosette system.

2.2.1. Pro- and eukaryotic phytoplankton

Seawater samples were collected in clean 125 ml polycarbonate bottles and stored in the dark at 4 °C until analysed (within 1 h). A 2 ml sub-sample was used for immediate analysis by flow cytometry to characterise and enumerate *Synechococcus* sp. (SYN), picoeukaryotes (PEUK), cryptophytes (CRYPTO), coccolithophores (COCCO) and other nanophytoplankton (NEUK) based on their light scattering and fluorescence properties. For enumeration of heterotrophic bacteria, 1.8 ml seawater was preserved with filtered formaldehyde (1% final concentration) in 2 ml cryovials, stored in

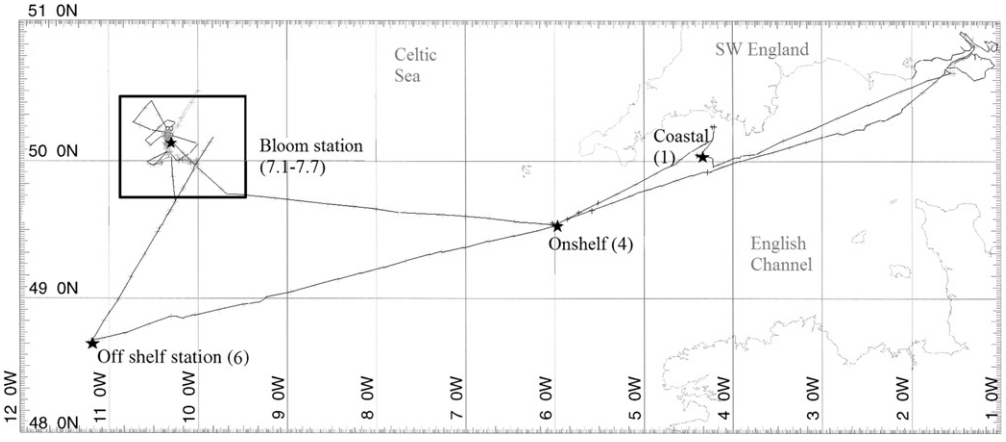

Fig. 1. Map of the study area showing station locations in the English Channel and western Celtic Sea. Sampling was conducted from 3 to 11 April 2002.

Table 1
Sample station information, euphotic depth, average euphotic temperature and size fractionated chlorophyll measurements.

Station no.	1	4	6	7.1	7.2	7.3	7.5	7.7
Site	Coastal	Shelf	Offshelf	Shelf	Shelf	Shelf	Shelf	Shelf
Condition	Non-bloom	Non-bloom	Non-bloom	Bloom	Bloom	Bloom	Bloom	Bloom
Sampling date	3/4/02	4/4/02	5/4/02	6/4/02	8/4/02	9/4/02	10/4/02	11/4/02
Euphotic depth (m)	30	30	55	40	40	40	35	35
Temp °C	10.7	10.7	12.0	11.2	11.3	11.4	11.5	11.5
% Chl <5 μm	66	66	69	32	7	3	4	5
% Chl >5 μm	34	34	31	68	93	97	96	95

a refrigerator for 24 h and then frozen at -20 °C. Prior to analysis, the bacteria samples were defrosted at room temperature, 500 μl of sample were mixed with 5 μl SYBR Green (10^{-4}) of commercial concentration) plus 45 μl potassium citrate (300 mM) and left to stain for 1 h in the dark at room temperature. Cells were counted using a Becton Dikinson FACSort™ flow cytometer equipped with an air-cooled laser providing blue light at 488 nm following the method of Tarran et al. (2006). Abundance of SYN was converted to carbon using a conversion factor of 0.35 pg C μm^{-3} (Tarran et al., 2001); PEUK, NEUK and CRYPTO were converted to carbon using a conversion factor of 0.22 pg C μm^3 (Booth, 1988) and by applying this to cell volumes calculated from median cell diameter measurements (Tarran et al., 2006). COCCO cell numbers were converted to C biomass using a higher C conversion factor of 0.285 pg C m^{-3} due to higher C associated with coccolithophores and median cell diameter measurements (Tarran et al., 2006). Bacteria abundance was converted to carbon using a conversion factor of 19 fg C $cell^{-1}$ (Zubkov et al., 1998).

2.2.2. Heterotrophic nanoflagellates

Water samples (30–80 ml) were fixed with glutaraldehyde (1% final conc.) and concentrated to ca. 10 ml onto 25 mm, 0.8 μm pore-sized black polycarbonate filters. The samples were stained with DAPI (final conc. 0.5 μg ml^{-1}) for 5 min and then stained with Proflavine (final conc. 0.5 μg ml^{-1}) and collected onto the filter. Filters were mounted onto glass slides covered with a coverslip and frozen at -20 °C. All slides were examined under ×1200 magnification with an epifluorescence microscope. Autotrophic flagellates were distinguished from heterotrophic forms on the basis of red autofluorescence from chlorophyll-*a* using appropriate filter sets. Heterotrophic flagellates in 50 fields of view (equivalent to >200 cells) were counted and sized using a semi-automated image analysis system with Image Pro Plus software v 5.0. Flagellate cell volumes, calculated assuming their shape to be ellipsoid or semi-ellipsoid, were converted to C biomass using a C:volume conversion factor of 220 fg C μm^{-3} (Borsheim and Bratbak, 1987).

2.2.3. Microzooplankton

Water samples (250 ml), were fixed with acid Lugol's solution (2% final conc). Fixed samples were stored cool and in the dark until they were analysed by inverted microscopy. Sub-samples of up to 50 ml were concentrated by sedimentation and examined at ×200 magnification using an Olympus IMT-2 inverted microscope (Utermöhl, 1958) and all protozoan microzooplankton were counted. Microzooplankton included all ciliates together with heterotrophic dinoflagellates greater than 20 μm in length. The latter were distinguished from autotrophic dinoflagellates by reference to known heterotrophic species reported by Lessard and Swift (1986) and Lebour (1925). By contrast, all ciliates apart from the common phototrophic ciliate *Myrionecta rubra*, were assumed to be heterotrophic. Cells were sized using×300 magnification. Each organism was categorised according to size and taxonomic group: *M. rubra*, heterotrophic dinoflagellates (>20 μm), three size classes of aloricate 'choreo-oligotrich' ciliates i.e. aloricate ciliates belonging to the subclasses Choreotrichia and Oligotrichia (Lynn and Small, 2000) (<1×10^3 μm^3, 1×10^3–30×10^3 μm^3 and >30×10^3 μm^3), tintinnid ciliates, other ciliates and sarcodines. The volume of each protozoan cell was calculated from cell area, measured using Plankton Visual Analyser software (AZTI – www.azti.es), assuming an ellipsoid or a semi-ellipsoid shape. The carbon content of each protozoan cell was then determined using the carbon to volume conversion equations of Putt and Stoecker (1989) for ciliates and Menden-Deuer and Lessard (2000) for heterotrophic dinoflagellates. Sarcodines were only found at stations 1 and 4 and their abundance was very low, therefore they have not been included in this dataset. Metazoan microzooplankton were not counted therefore the term microzooplankton used here refers only to the protozoan component.

2.2.4. Mesozooplankton

Duplicate vertical hauls were made at each station, pre-dawn, from approx.100 m depth (excluding station 1, where water depth constrained sampling to 50 m depth) to the surface using a 200 μm mesh WP-2 net. The samples were stored in 5% buffered formalin prior to analysis where they were split, sorted and counted into major taxonomic groups or to species level. Zooplankton abundance was recorded as individuals per m^{-3}. Shannon diversity index, H′ and Pielou's evenness, J, were calculated for each station.

2.2.5. Community data analyses

Multivariate community data analyses, using PRIMER software (version 6) (Clarke and Warwick, 1994), were used to describe differences in the variation/structure of the nano- micro- and mesozooplankton communities and to relate these differences to changes in the environment. Community data were square root transformed to reduce the influence of abundant species and subjected to Hierarchical Cluster analysis to group stations based on the Bray–Curtis similarity index. Non-metric multi-dimensional scaling (MDS) was also performed to configure the data in two-dimensional space allowing relationships between groups to be assessed. As MDS ordinations and Cluster analysis techniques are complementary to each other, the cluster analysis data was superimposed onto the MDS ordinations to view the data in combination. Significant differences between assemblage composition under non-bloom and bloom conditions were investigated using a one-way analysis of similarity (ANOSIM, Clarke and Green, 1988). The main species contributing to any dissimilarity between assemblage groups were assessed using SIMPER (similarity percentages, Clarke, 1993). The BIOENV procedure (Clarke and Ainsworth, 1993) was used to investigate which environmental variables best explained the observed community assemblage composition.

3. Results

3.1. Background information

At non-bloom stations nitrate and silicate concentrations were relatively high ranging between 4 and 7 μM in the euphotic zone

(Dixon et al., 2006). The phytoplankton community was dominated by cells in the 0.2–5.0 μm size fraction (Table 1) and primary production was greater in this size fraction, although total primary productivity was generally low compared to measurements made by Joint et al. (1986) suggesting that sampling was carried out during winter mixed pre-bloom conditions (Dixon et al., 2006). Chlorophyll-*a* concentrations were <1 μg Chl l^{-1} (Dixon et al., 2006).

At the bloom stations, silicate and nitrate concentrations were lower than at non-bloom stations and there was a decrease in the silicate:nitrate ratio (Dixon et al., 2006). Average temperature in the euphotic zone increased from 11.2 (±0.006) °C to 11.5 (±0.04) °C (Table 1). The >5 μm fraction dominated the phytoplankton, initially accounting for 68% of the total chlorophyll, and pigment analysis revealed that in the initial stages, the community comprised a relatively even mixture of prasinophytes, prymnesiophytes, cryptophytes and diatoms (Llewellyn et al., 2008). Chlorophyll-*a* concentration in the euphotic zone reached >5 μg Chl l^{-1} at the peak of the bloom on 10 April (Llewellyn et al., 2008) and at this time, the >5 μm fraction comprised 92% of the phytoplankton population of which diatoms were the dominant component (88 mg C m^{-3} at 33% light depth, Dixon et al., 2006). This coincided with maximum carbon and nitrogen uptake rates (Andy Rees, pers comm., [Plymouth Marine Laboratory]). The diatom community at this time was dominated by *Chaetoceros debilis*, *Dactyliosolen fragilissimus* and *Guinardia striata* (Dixon et al., 2006).

3.2. Pro- and eukaryote community

Within the pro-/eukaryotic phytoplankton community (<20 μm), nanoeukaryotes (NEUK) dominated at non-bloom stations with standing stocks of between 500 and 600 mg C m^{-2} (Fig. 2 a). Standing stocks of cryptophytes (CRYPTO) and coccolithophores (COCCO) were highest at the coastal non-bloom station and lowest during the bloom. Standing stocks of *Synechococcus* spp. (SYN) were generally low, particularly at the bloom station and were highest at the offshore non-bloom station. Standing stocks of COCCO, NEUK and CRYPTO were all lower at the bloom station than at non-bloom stations. Standing stocks of PEUK remained relatively low but highest concentrations were encountered on day 1 at the bloom station.

3.3. Zooplankton community

3.3.1. Heterotrophic nanoflagellates

The average abundance of heterotrophic nanoflagellates (HNAN) within the euphotic zone was highest at the coastal non-bloom station 1 (3671 ± 798 cells ml^{-1}) and lowest at the bloom stations (484 ± 182 to 649 ± 152 cells ml^{-1}) (Table 2). HNAN biomass ranged from 1 to 15 mg C m^{-3} and showed a similar trend to abundance, being highest at the coastal station and lowest during the bloom.

Average HNAN cell bio-volume varied from approx. 8 to 27 μm^3 and there was a significant difference between mean cell volume at non-bloom (23 ± 4) versus bloom stations (14 ± 7) with larger cells being present at non-bloom stations (student *t*-test $p < 0.005$). At the bloom station, average cell bio-volume decreased significantly ($p < 0.005$) from 21 μm^3 on day 1 to 8 μm^3 on day 7. This coincided with a 4-fold increase in the mean cell volume of protozoan cell bio-volume (6×10^3 μm^3 at non-bloom sites; $>24 \times 10^3$ μm^3 in the bloom (range 8×10^3 to 48×10^3 μm^3)) (Table 3).

HNAN standing stocks were highest at coastal station E1 (458 mg C m^{-2}), lower at the other non-bloom stations (mean 158 ± 26 mg C m^{-2}) and lowest at the bloom stations decreasing from 108 to 34 mg C m^{-2} (average 65 ± 29 mg C m^{-2}) (Fig. 2b).

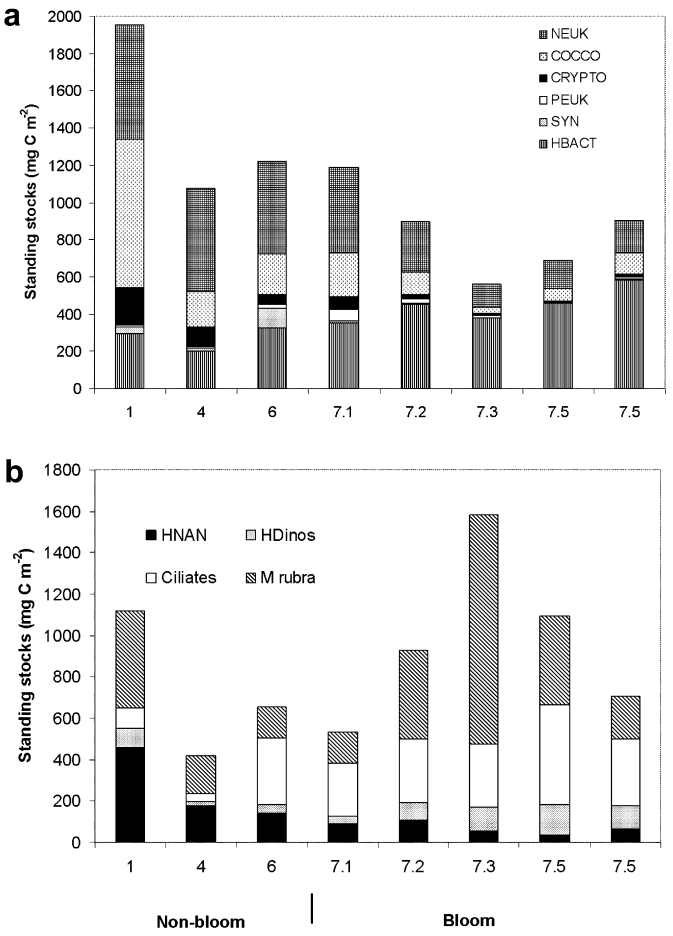

Fig. 2. Standing stocks of (a) the pro-/eukaryote community: heterotrophic bacteria (HBACT), Synechococcus (SYN), picoeukaryotes (PEUK), cryptophytes (CRYPTO), coccolithophores (COCCO) and nanoeukaryotes (NEUK) (b) the nano- and microzooplankton community: heterotrophic nanoflagellates (HNAN) ciliates, heterotrophic dinoflagellates and *Myrionecta rubra* at non-bloom and bloom stations.

3.3.2. Microzooplankton

The average microzooplankton abundance within the euphotic zone at non-bloom stations ranged from 2000 to 10,000 cells l^{-1} (Table 2) which is similar to the bloom stations, with cell concentrations ranging between 8000 and 11,000 cells l^{-1}. However, microzooplankton biomass was significantly lower at non-bloom stations (63–375 mg C m^{-2}) compared to the bloom stations (355–1477 mg C m^{-2}) (Fig. 2b). This difference can be attributed to differences in cell size between non-bloom and bloom stations. In particular, at the offshelf non-bloom station, more than 80% of the total microzooplankton abundance (>7900 cells l^{-1}) consisted of small aloricate choreo-oligotrich ciliates with an average bio-volume of $<4.9 \times 10^3$ μm^3 and half of these had a bio-volume of $<1 \times 10^3$ μm^3 (Fig. 3a). Large heterotrophic dinoflagellates with cell bio-volumes $>10 \times 10^3$ μm^3 comprised less than 15% of the total heterotrophic dinoflagellate abundance and less than 4% of the total microzooplankton abundance at non-bloom stations (Fig. 3b). At the bloom stations small choreo-oligotrich ciliates comprised <4% of the total ciliate abundance whereas the contribution of larger ciliates (mostly *Myrionecta rubra* and a large *Strombidium* sp.) to total abundance increased. This was most pronounced on day 3 of the bloom station when over 50% of the total ciliate abundance was due to cells $>5 \times 10^3$ μm^3 and 45% of these had cell bio-volumes $>10 \times 10^3$ μm^3. Similarly, heterotrophic dinoflagellates increased in size at the bloom station and by day 4, large

Table 2
Average concentrations of heterotrophic nanoflagellates (HNAN) and microzooplankton (MZP) in the euphotic zone. Standard deviation given in brackets, $n = 3$.

	Non-Bloom			Bloom				
	1	4	6	7.1	7.2	7.3	7.5	7.7
Abundance cells l^{-1}								
HNAN	3671 (798)	1038 (461)	972 (676)	567 (261)	649 (152)	484 (182)	598 (350)	626 (–)
MZP	6953 (1047)	2480 (329)	10420 (1499)	9013 (2363)	10960 (682)	7827 (2754)	10213 (2981)	9210 (2643)
Myrionecta rubra	1040 (198)	473 (83)	500 (198)	2333 (1620)	2067 (439)	2747 (1617)	2560 (1772)	1360 (721)
Choreo-oligotrich ciliates	3573 (339)	1200 (151)	8540 (820)	5440 (624)	6387 (323)	2987 (821)	5507 (1552)	5800 (2261)
Heterotrophic dinoflagellates	2087 (424)	567 (155)	1060 (707)	1120 (423)	1987 (129)	1840 (342)	1880 (485)	1780 (239)

heterotrophic dinoflagellates ($>10 \times 10^3$ μm^3) comprised 45% of the total heterotrophic dinoflagellate abundance (Fig. 3b). However, due to the lower abundance of heterotrophic dinoflagellates relative to ciliates, this only equated to 12% of total microzooplankton abundance. The average microzooplankton cell bio-volume was 6×10^3 μm^3 at non-bloom stations whereas at the bloom station microzooplankton cell bio-volume increased from 8×10^3 μm^3 on day 1 to $>48 \times 10^3$ μm^3 on day 4 (average $24 \times 10^3 \pm 15 \times 10^3$ μm^3) (Table 3).

Microzooplankton standing stocks ranged between 63 and 375 mg C m^{-2} at non-bloom stations and between 355 and 1477 mg C m^{-2} at bloom stations (Fig. 2b). *Myrionecta rubra* comprised between 2 and 8% of the total microzooplankton standing stock at non-bloom stations but comprised a much greater proportion of the total microzooplankton community at bloom stations (18–71%). Heterotrophic dinoflagellates comprised between 8 and 19% of the standing stock at the bloom station. Microzooplankton standing stocks, excluding *M. rubra*, increased steadily from 290 to 630 mg C m^{-2} over the first 4 days at the bloom station (Fig. 2b).

Mixotrophic choreo-oligotrichs were commonly encountered in the samples at both non-bloom and bloom stations. The proportion of known mixotrophic ciliates in the microzooplankton community (i.e. *Myrionecta rubra*, *Tontonia* spp., *Laboea strobila*, *Strombidium conicum*, *Strombidium vestitum* and *Strombidium reticulatum*) was almost twice as high at bloom stations; on average these mixotrophic ciliates comprised 24 ± 6% of total microzooplankton abundance at non-bloom stations and 44 ± 7% during the bloom.

Aloricate choreo-oligotrich ciliates dominated the microzooplankton biomass at all stations. These were mostly of the genera *Strombidium* and *Stobilidium*. Differences were observed between the average size of this community at non-bloom and bloom stations. At bloom stations aloricate choreo-oligotrichs were, on one occasion more than 4 times larger than the non-bloom average and were overall almost 3 times larger. Small ciliates of <30 μm in length primarily of the genus *Strombidium* dominated at non-bloom stations. Bloom stations were dominated by ciliates >30 μm in length. Heterotrophic dinoflagellates were dominated at all stations by *Gyrodinium* spp. and *Protoperidinium* spp. increased in abundance (up to 500 cells l^{-1}) around days 3 and 4 at the bloom station. Tintinnids (*Stenosomella* sp., and *Salpingella* spp.) were found in concentrations of up to 500 cells l^{-1} at the coastal station but concentrations were generally very low or they were absent at all other stations.

3.3.3. Mesozooplankton

A total of 41 mesozooplankton taxa were identified (15 non-crustaceans, 26 crustaceans) including 20 copepod taxa (Table 4). The mesozooplankton community was dominated by copepods which comprised 72–89% of the total abundance at non-bloom stations and 58–88% at bloom stations. Non-crustacean zooplankton abundance ranged between 240 and 340 ind m^{-3} at non-bloom stations and 550 and >1400 ind m^{-3} at the bloom station. Copepod abundance ranged between 764 and 2562 ind m^{-3} at non-bloom stations and between 1392 and 3750 ind m^{-3} during the bloom.

The species composition of non-crustacean zooplankton differed considerably at non-bloom stations, polychaete larvae dominated the coastal station, *Oikopleura* spp. dominated on the shelf and a combination of *Oikopleura* spp., siphonophores and foraminifera were present at the offshelf station. At the bloom stations the non-crustacean community was more uniform comprising mostly *Oikopleura* spp. and Echinoderm larvae.

Table 3
Mean cell size (μm^3) of heterotrophic nanoflagellates (HNAN) and microzooplankton (MZP). % variation in brackets.

Station	Mean cell size (μm^3)	
	HNAN	MZP
1	20.4	6.6×10^3
2	27.4	6.2×10^3
3	19.6	5.5×10^3
4	21.4	8.3×10^3
6	21.3	16.5×10^3
7	12.3	48.7×10^3
8	8.8	30.2×10^3
9	7.9	19.5×10^3
Bloom average	14 (30%)	24.6×10^3 (2%)
Non-bloom average	22 (29%)	6.1×10^3 (9%)

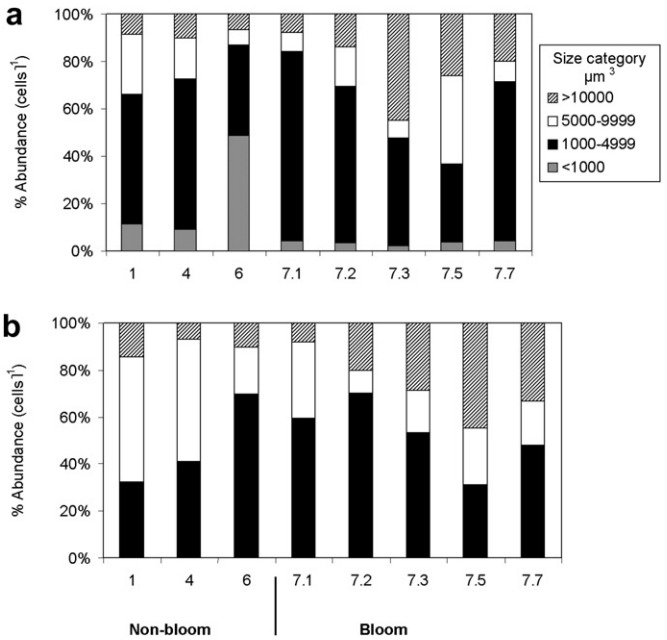

Fig. 3. Size frequency of the microzooplankton community at non-bloom and bloom stations (a) ciliates (b) heterotrophic dinoflagellates.

Table 4
Mesozooplankton community abundance (N m^{-3}) and diversity.

Station		Non-bloom			Bloom				
		1	4	6	7.1	7.2	7.3	7.5	7.7
Non-crustaceans									
Cnidaria	Arachnactis larvae	0	0	0	11	0	0	0	0
	Hydromedusae	8	0	56	0	0	0	5	5
	Siphonophores	5	3	24	0	65	11	38	65
Polychaeta	Polychaete larvae	275	3	0	0	22	22	16	27
	Tomopteris spp.	0	0	0	0	0	0	5	0
Chaetognatha		5	0	9	0	0	22	27	27
Mollusca	Gastropod larvae	0	3	0	11	0	0	0	0
	Lamellibranch larvae	0	3	0	0	0	0	0	5
	Limacina spp.	3	0	2	44	5	11	0	5
	Ostracod	0	0	9	0	0	0	0	0
Echinodermata	Echinoderm larvae	0	0	2	132	307	189	97	458
	Auricularia larvae	0	0	0	0	38	49	92	75
Urochordata	Doliolida	0	0	7	0	0	5	0	0
Appendicularia	*Oikopleura* spp.	16	323	60	275	420	625	264	717
Chordata	Fish eggs	8	3	5	0	22	11	0	0
	Fish larvae	19	0	0	0	5	0	5	16
Crustaceans									
Cladocera	*Evadne* spp.	0	0	5	0	0	0	0	0
	Hyperiida	0	0	0	22	5	0	0	0
	Mysidacea	0	0	0	0	0	0	0	5
Euphausiacea	Euphausiid calyptopis	3	27	0	0	5	0	5	0
	Euphausiid adult	0	0	0	11	0	0	5	0
Decapoda	Decapod larvae	16	16	0	99	5	5	16	5
Copepoda		1391	2562	764	3750	1880	1749	1392	1965
	Metridia lucens	0	5	12	11	5	16	0	5
	Acartia clausii	3	0	3	110	49	11	0	0
	Candacia armata	0	19	0	0	11	0	22	5
	Unidentified Centropages	5	8	0	11	5	11	0	16
	Centropages typicus	0	0	0	0	0	0	0	5
	Temora longicornis	11	0	0	0	0	0	0	0
	Calanus helgolandicus	19	496	17	121	162	162	280	167
	Unknown copepod	0	0	10	44	0	0	0	11
Unidentified Para/pseudo/cteno/clauso		0	0	158	0	0	0	0	0
	Clausocalanus spp.	0	0	117	367	58	125	30	261
	Ctenocalanus spp.	0	0	11	0	132	181	0	0
	Paracalanus parvus	797	1175	23	975	390	349	396	431
	Pseudocalanus elongatus	444	805	233	637	309	269	152	244
	Eucalanus spp.	0	3	15	11	32	0	11	22
	Euchaeta hebes	3	0	0	0	43	16	16	16
Cyclopoida	*Oithona* spp.	94	43	142	1419	647	604	453	755
Poecilostomatoida	*Oncaea* spp.	5	8	17	0	38	5	5	27
	Corycaeus anglicus	8	0	3	0	0	0	0	0
Harpacticoida	Unidentified harpactacoid	0	0	2	0	0	0	0	0
	Euterpina acutifrons	0	0	0	44	0	0	0	0
	Clytemnestra spp.	3	0	0	0	0	0	0	0
Copepod eggs and nauplii		19	92	5	264	280	291	299	771
	Species Richness	24	20	27	24	29	25	26	28
	Shannon index H′	1.7	1.7	2.5	2.3	2.5	2.4	2.4	2.3
	Evenness J	0.5	0.6	0.8	0.7	0.8	0.8	0.7	0.7

Crustacean zooplankton present at non-bloom stations comprised predominantly *Paracalanus parvus* and *Pseudocalanus elongatus* (78–90%) at station 4 (on the shelf) and *P. elongatus*, *Clausocalanus* spp. and *Oithona* spp. (81%) at station 6 (offshelf). The composition of the crustacean community remained similar at the bloom stations dominated by *P. parvus*, *P. elongatus*, *Clausocalanus* spp. and *Oithona* spp. (87–91%) but abundance of copepod nauplii was higher than that found at non-bloom stations and increased significantly throughout the duration of the bloom station (Table 4).

The mesozooplankton communities at non-bloom stations 1 (coastal) and 4 (shelf) both had a lower Shannon diversity index H′ (average H′ = 1.7) than non-bloom station 6 (offshelf) (average H′ = 2.5) and the bloom stations (average H′ = 2.4). Changes to Pielou's evenness were similar to those of H′ with an average value at bloom stations of 0.7 and 0.6 at non-bloom stations 1 and 4 (Table 4). With the exception of station 6 which was situated offshelf, mesozooplankton diversity increased with increase in primary productivity ($p = <0.05$).

3.4. Data analysis

Linear regression analysis of plankton abundance (Pro-/eukaryotes, HNAN, microzooplankton) data and environmental data (temperature, nitrate concentration, chlorophyll-*a*) resulted in a number of significant positive correlations (Table 5). The abundance of HNAN was correlated with SYN and CRYPTO but not with HBACT or PEUK. Microzooplankton abundance was significantly correlated to temperature and PEUK abundance. Further significant correlations resulted from regression analysis of aloricate choreo-oligotrich abundance with chlorophyll-*a*, PEUK and HBACT (only choreo-oligotrichs $< 10 \times 10^3$ μm^3) and large heterotrophic dinoflagellates ($>30 \times 10^3$ μm^3) with nitrate and chlorophyll-*a*. There was also a significant negative correlation between heterotrophic dinoflagellates and CRYPTO (Table 5). The RELATE statistic was used to determine whether there was a relationship between microzooplankton abundance and the pro-/eukaryote community. The observed value of ρ exceeded that found in 95% of the simulations

Table 5
Linear regression analysis of heterotrophic nanoflagellates (HNAN), microzooplankton (MZP), heterotrophic dinoflagellates (HDinos) and Choreo-oligotrich standing stocks versus environmental variables (temperature, nitrate and Chl-*a*) and pro-/eukaryote groups. SYN = Synechococcus; CRYPTO = cryptophytes; PEUK = picoeukaryotes; NEUK = nanoeukaryotes; HBACT = heterotrophic bacteria. Significance levels: - = not significant; * $p = <0.05$; ** $p = <0.01$; *** $p = <0.005$; **** $p = <0.001$.

	N	Temp °C	Nitrate	Chl-*a*	SYN	CRYPTO	PEUK	NEUK	HBACT
HNAN	32	–	–	–	****	***	–	–	–
MZP	22	**	–	–	–	–	****[b]	–	*
HDinos	22	–	**[a]	***[a]	–	*** -ve	–	–	–
Choreo-oligotrichs	22	–	–	*[a]	–	–	****[b]	–	****[c]

[a] Cells with volume $>30 \times 10^3$ μm^3 only.
[b] Excluding data from #7.1.
[c] Cells with volumes $1-10 \times 10^3$ μm^3 only.

therefore there was a significant relationship between the variation in microzooplankton abundance and that of the pro-/eukaryotes ($\rho = 0.72$, $p = 0.002$).

Differences in the environmental variables (temperature, nutrients, Chl-*a*, primary production) which distinguish non-bloom from bloom stations are illustrated with a multi-dimensional scaling (MDS) ordination of the data (Fig. 4a). The results from Hierarchical Cluster analysis (a technique that can be used to distinguish sites with differing community structure) were superimposed onto the MDS ordination to demonstrate the percentage similarities between clusters. The data show 2 distinct clusters: non-bloom stations 1 and 4 cluster closely together although the offshelf non-bloom station 6 can still be described by similar environmental variables. Bloom stations 7.2, 7.3 and 7.7 cluster very closely together with stations 7.1 and 7.5, although less similar, still clustering within the same environmental dataset.

The MDS ordination of pro- and eukaryotic phytoplankton, showed a similar pattern to the environmental data with stations 7.2–7.7 and 1–4 being 80% similar except for the divergence from the other stations of stations 6 and 7.1 to form a third cluster which was 70% similar (Fig. 4b). Both stations 6 and 7.1 had the highest concentrations of SYN and PEUK respectively. MDS ordinations of square root transformed microzooplankton abundance, combined with Hierarchical Cluster analysis, resulted in less distinct clustering than that found for environmental variables and pro-/eukaryotes. There was no clustering of non-bloom stations but there was a cluster of the bloom stations at 50% similarity (Fig. 4 c). Cluster analysis of total zooplankton abundance data clearly identified 3 stations at the 60% similarity level – stations 7.2–7.7 being 75% similar but station 7.1 being 60% similar forming a cluster of the bloom stations (Fig. 4d). Stations 1 and 4 both onshelf non-bloom stations were 60% similar and station 6 the offshelf non-bloom station was most dissimilar.

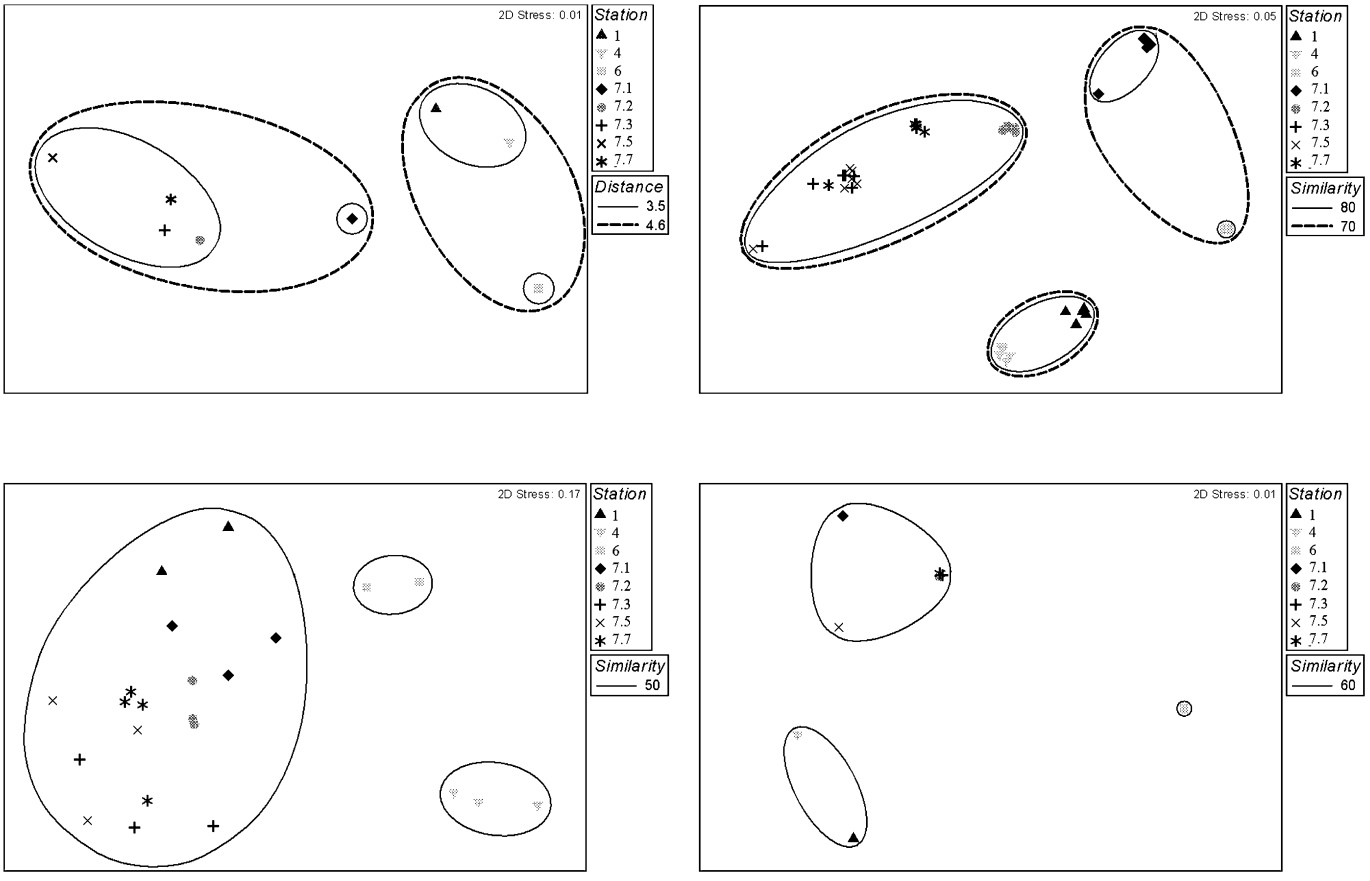

Fig. 4. Multi-dimensional scaling plots with superimposed clusters from Heirarchical analysis of (a) normalised environmental data (temp, nutrients, Chl-*a*, primary production), (b) square root transformed pro-/eukaryote abundance data, (c) square root transformed microzooplankton community abundance data, and (d) square root transformed mesozooplankton community abundance data. Stress < 0.05 gives excellent representation of the data in two dimensional space; Stress < 0.2 indicates a potentially useful 2 dimensional picture (Clarke and Warwick, 1994).

ANOSIM showed significant differences between environmental variables at bloom and non-bloom stations and between pro-/eukaryotic phytoplankton, microzooplankton and total zooplankton communities at bloom and non-bloom stations (Table 6). SIMPER analysis, used to assess the main species contributing to any dissimilarity between assemblages, suggested that the average similarity in terms of zooplankton species abundance between non-bloom stations was 70% which was mainly due to *Paracalanus parvus* and *Pseudocalanus elongatus* (65% of the total cumulative similarity). For the bloom stations, the average similarity was 75% with *Oithona* spp., *P. parvus*, Copepod nauplii and *P. elongatus* contributing 67% of the total cumulative similarity. The average difference (dissimilarity) in zooplankton species abundance between non-bloom and bloom stations was 42%. Of this, *Oithona* spp, Copepod nauplii, *Clausocalanus* spp. and *P. parvus* accounted for 50% of the dissimilarity between non-bloom and bloom stations.

In order to examine relationships between community and environmental data we used the BIOENV procedure. Significant correlations were found between total micro- and mesozooplankton abundance and environmental variables (Table 7). The overall influencing environmental parameter that best explained the mesozooplankton assemblage pattern was temperature and for microzooplankton it was temperature and silicate. However, within the bloom stations, the variables that best described the mesozooplankton similarity matrix were nitrite and primary production and for the microzooplankton it was silicate.

Table 6
Results of one-way ANOSIM analysis to test for significant differences between assemblage composition between non-bloom and bloom stations.

Pairwise tests	Statistic	*P* value
Environmental variables		
Non-bloom v Bloom	0.85	0.02
Pro-/eukaryotes		
Non-Bloom[a] v 6 & 7.1	0.87	0.001
Non-Bloom[a] v Bloom[b]	0.93	0.001
6 & 7.1 v Bloom[b]	0.90	0.001
Microzooplankton abundance		
Non-bloom v Bloom	0.72	0.001
Microzooplankton bio-volume		
Non-bloom v Bloom	0.78	0.001
Choreo-oligotrich bio-volume		
Non-bloom v Bloom	0.50	0.004
Mesozooplankton		
Non-bloom[a] v Bloom	0.98	0.05

[a] Stations 1 and 4 only.
[b] Stations 7.2–7.7 only.

Table 7
Results from BIOENV analysis of micro- and mesozooplankton populations and environmental variables. PP = primary production; Temp = temperature °C.

	Environmental variable(s)	Sample statistic	*P* value
All stations			
Mesozooplankton	Temperature	0.82	<0.004
Microzooplankton	Silicate, Temp	0.86	<0.002
Bloom stations only			
Mesozooplankton	Nitrite, PP	0.95	<0.03
Microzooplankton	Silicate	0.87	<0.04

4. Discussion

This study has provided a quantitative description of the plankton communities found at non-bloom and bloom stations during April in the English Channel and Celtic Sea. It highlights significant differences between the environmental variables, the phytoplankton community, the pro-/eukaryotic communities, microzooplankton and zooplankton communities at bloom and non-bloom stations and has provided an insight into changes which occur between trophic levels in response to the spring bloom in this area.

4.1. Comparison of different sites from non-bloom to bloom

There were contrasting differences in chlorophyll-*a* biomass and the structure of the phytoplankton community between stations with low and high productivity (non-bloom and bloom stations). At non-bloom stations chlorophyll-*a* concentration and primary productivity were low (Dixon et al., 2006) the majority of the phytoplankton were small in size (<20 μm) comprising predominantly pro-/eukaryotes. During the bloom, nitrate and silicate levels were reduced, chlorophyll-*a* concentrations and primary productivity increased and the phytoplankton was dominated by larger cells specifically chain-forming diatoms (Dixon et al., 2006). These differences can be directly attributable to changes in environmental variables (nutrients, temperature and light), but biological factors such as herbivory and predation can also be important in structuring phytoplankton assemblages (e.g. Widdicombe et al., 2002).

Heterotrophic nanoflagellates are thought to represent a major trophic link in the microbial loop as dominant consumers of prokaryotes in marine surface waters (Strom, 2000) and in temperate regions they usually reach maximum abundances in spring due to increased food supply (Boenigk and Arndt, 2002). Their abundance may be regulated by availability of food resources (bacteria and picoeukaryotes) and (or) predation by ciliates (Weisse, 1991) and copepods (Stoecker and Cappuzzo, 1990). Despite the higher primary productivity within the bloom, the standing stocks of heterotrophic nanoflagellates at bloom stations were significantly lower than at non-bloom stations and this is reflected in the availability of suitably sized food (HBACT, CRYPTO, SYN, COCCO) for this size fraction.

Microzooplankton are known to feed on a variety of food sources, including bacteria, pico- and nanophytoplankton and nanoflagellates (Capriulo, 1990; Caron et al., 1991, Pierce and Turner, 1992) and diatoms (Sherr and Sherr, 2007). The abundance and composition of microzooplankton communities will depend on food size and the abundance of different food sources. The significant correlations between microzooplankton and PEUK (at all stations except 7.1), and specifically aloricate choreo-oligotrichs with PEUK and HBACT (Table 5), indicate a possible trophic relationship between these populations during this study. Such correlations have also been reported in other coastal ecosystems (e.g. James and Hall, 1995; Setala and Kivi, 2003). Microzooplankton biomass increased with increase in primary production, however, this was not associated with an increase in protozoan abundance, but to an increase in the size of microzooplankton. Such an increase in larger protozoa with increased productivity and phytoplankton size has been observed in other studies (Arndt et al., 2000; Auer and Arndt, 2001; Strom et al., 2007; Aberle et al., 2007).

Despite the differences in productivity and phytoplankton community structure between non-bloom and bloom stations, the copepod species that numerically dominated the mesozooplankton community were similar, but their abundance varied between stations. These were mostly the small copepods *Paracalanus parvus*, *Pseudocalanus elongatus*, *Clausocalanus* spp. and *Oithona* spp. Copepod eggs and nauplii, were only abundant at the bloom station. Small copepods such as *Oithona* spp. and *Pseudocalanus* typically dominate in nearshore shallow waters (e.g. Nielsen and Sabatini, 1996; Gowen et al., 1998) with larger species becoming more dominant in deeper oceanic areas (Turner, 2004). While small

species may dominate the abundance, larger species present in lower numbers may dominate the biomass. Although the low size-dependent growth rates characteristic of larger species could render them relatively unimportant in terms of production (Hirst and Lampitt, 1998). Whilst we do not have biomass data from this study, the larger calanoid species, *Calanus helgolandicus* was clearly more abundant during the bloom station than at non-bloom sites (abundance 17–496 ind m^{-3}) and may have contributed significantly to total zooplankton biomass. These abundance data are within the range of maximum monthly abundances for *C. helgolandicus* of 147–779 for station L4 in the English Channel (Irigoien and Harris, 2003). However, studies in the nearby western Irish Sea and North Sea spring blooms concluded that large copepods were not the major grazers of the spring bloom in these regions and that smaller copepod species were more important (Nielsen and Richardson, 1989; Gowen et al., 1999).

Copepods are known predators on larval stages of appendicularians (Gorsky and Fenaux, 1998; Lopez-Urrutia et al., 2003) however, even though copepod abundance was high at all but station 6 (offshore, non-bloom station), appendicularian abundance (*Oikopleura* spp.) increased at the bloom stations in this study. Abundance was within the range reported for station L4 in the Western English Channel (www.pml.ac.uk/westernchannelobservatory) (2002 maximum 298 ind m^{-3}). This could be because of increased bacterial food supply as appendicularians are known to feed on bacterioplankton (Zubkov and Lopez-Urrutia, 2003) and/or reduced copepod predation on appendicularians due to higher phytoplankton concentrations encountered during the bloom (Lopez-Urrutia et al., 2003).

The abundance and composition of the nano- micro- and mesozooplankton populations studied showed distinct distribution patterns relating to environmental conditions and food resources. This is supported by multivariate analysis of the environmental variables (temperature, nitrate, silicate, nitrite, primary production) which, using an MDS ordination and Cluster analysis, clearly showed that the sample stations fell into two significantly different clusters (non-bloom and bloom stations) (Fig. 4a). One of the aims of this study was to determine whether some of these abiotic variables could explain the spatial variation in community abundance and composition (Table 7) and this will be discussed further in Section 4.2.

4.2. Bloom progression

The significant drop in abundance of SYN and PEUK which occurred within the pro-/eukaryotic phytoplankton communities after day 1 at the bloom station and the subsequent shift in the community to larger phytoplankton led to significant changes within higher trophic levels as the bloom progressed. Whilst HNAN abundance can be regulated by the availability of food resources and is often highly correlated with a source of nutrition (see Table 1 in Sanders et al., 1992), they are also subject to top-down control by ciliates (Weisse, 1991), dinoflagellates (Kuparinen and Bjørnsen, 1992), copepods (Stoecker and Cappuzzo, 1990; Gasparini and Castel, 1997), rotifers (Dolan and Gallegos, 1991) and cladocerans (Güde, 1989). At the bloom station, there was a general reduction in HNAN standing stocks. This significant decrease in HNAN biomass which occurred between 8 and 10 April corresponded with a significant decrease in HNAN cell size. Combined with the fact that there was a corresponding increase in the size of aloricate ciliates, which have been reported to prey upon nano-sized particles (e.g. Kivi and Setälä, 1995), the data imply that there was a degree of predatory control of HNAN populations, particularly of the larger-sized cells by the microzooplankton during the bloom. Further evidence of this is provided by flow cytometric data from microzooplankton grazing experiments which showed significant grazing of nanoeukaryotes by the microzooplankton and this was highest on 10 April, station 7.5 (unpubl. data) coinciding with the maximum abundance of large aloricate choreo-oligotrichs ($>10 \times 10^3$ μm^3). Other studies have also shown that ciliates are responsible for the top-down control of HNAN (e.g. Weisse, 1991; Weisse and Scheffel-Möser, 1991). The size of HNAN cells reported in this study (10–34 μm^3) is within the range reported in the literature (e.g. Stoecker et al., 1994; Tanaka and Rassoulzadegan, 2002). HNAN abundances of between 3000 and 7000 cells ml^{-1} and biomass in the range of 1 and 15 mg C m^{-3} are within the range reported for the North Atlantic spring bloom (Stoecker et al., 1994), but are higher than reported for non-bloom coastal (Table 4 in Sanders et al., 2000) and estuarine waters (Dolan and Coats, 1990; Rollwagen-Bollens et al., 2006).

Bacterial abundance did not appear to be strongly coupled with HNAN abundance, a finding which is in agreement with Gasol and Vaque (1993) who concluded that HNAN do not always control bacterial abundance. While we found no significant relationship between HNAN and bacteria, there was a significant relationship between HNAN and *Synechococcus* spp., and cryptophytes confirming the importance of these groups in the diet of HNAN (Table 5). In some coastal marine systems, small aloricate ciliates have been documented as primary grazers of heterotrophic bacteria (Sherr and Sherr, 1987). However, in this study, a strong correlation between heterotrophic bacterial abundance and diatoms coinciding with low abundance of small ciliates, suggests that top-down control of the bacterial population was unlikely particularly towards the end of the bloom when release of dissolved organic matter from algal cells increased in response to poor nutrient conditions and viral lysis (Llewellyn et al., 2008).

It is widely accepted that microzooplankton exert tight grazing control over phytoplankton consuming between 60 and 70% of total primary productivity in the oceans (Calbet and Landry, 2004). However, microzooplankton are unlikely to be able to prevent the initiation of phytoplankton blooms (Sherr and Sherr, 2009). While microzooplankton are capable of grazing on large chain-forming diatoms (e.g. Olsen and Strom, 2002) and large pelagic ciliates have been shown to be significant grazers of diatom blooms (Aberle et al., 2007), microzooplankton have been shown to consume small cells (<20 μm) more readily than larger cells (Strom et al., 2007) and the impact of microzooplankton grazing in diatom blooms can sometimes be low to negligible (Gifford et al., 1995) particularly if the community is dominated by ciliates as found in this study, rather than by large heterotrophic dinoflagellates (Sherr and Sherr, 2007). Nevertheless, microzooplankton standing stocks increased significantly at the bloom station, doubling from days 1–3 and again from days 3–4. Standing stocks reached a peak of almost 1500 mg C m^{-2} at a time when phytoplankton biomass was in excess of 100 mg C m^{-3} (Dixon et al., 2006) and there was no evidence of saturation of microzooplankton biomass in relation to the increased phytoplankton biomass such as that described by Irigoien et al. (2005). This could imply that microzooplankton growth was not limited by predation by mesozooplankton. Increase in microzooplankton biomass at the bloom stations was due to an increase in microzooplankton cell size rather than an accumulation of cells and was clearly related to increasing chlorophyll-*a* concentration in particular the >5 μm size fraction ($p = <0.05$). Standing stocks of microzooplankton were within the ranges reported in the literature e.g. during a bloom of the coccolithophore *Emiliania huxleyi* (905–2498 mg C m^{-2} – Fileman et al., 2002) and for an iron induced phytoplankton bloom (648–1140 mg C m^{-2} Henjes et al., 2007) and were higher than determined during the development of the spring bloom in the North Atlantic (430–638 mg C m^{-2} – Fileman and Leakey, 2005).

There was a notable change in the size structure of the ciliate community, whereby larger ciliates dominated at the peak of the spring bloom. Whilst this could result from a change in species composition from ciliates that graze on pico- and nanoplankton to ciliates that graze larger sized cells such as diatoms (e.g. Aberle et al., 2007) it could also be caused by relaxation of grazing pressure by large copepods on these ciliates under diatom bloom conditions (Kiørboe, 1997). Fileman et al. (2007), in a concurrent study, found that at the bloom stations, some copepods gained most of their dietary carbon from phytoplankton ingestion. This is also shown by the high levels of chlorophyll transformation products measured at the peak of the bloom which indicated zooplankton grazing pressure on the diatom bloom (Walker and Keely, 2004). The change in the ciliate community observed during this study at the bloom stations was partly due to an increase in abundance of a large *Strombidium* species similar to *Strombidium conicum* which has been shown to feed on diatoms and nanoflagellates (Montagnes et al., 1988a) and an increase in abundance of *Myrionecta rubra*, a phototrophic ciliate known to feed on cryptophyte algae (Johnson and Stoecker, 2005).

Such an increase in large ciliates with increased productivity is not uncommon and has been documented for temperate nearshore waters (Tamigneaux et al., 1997), the northern Baltic Sea (Setälä and Kivi, 2003; Johansson et al., 2004), the Gulf of Maine (Montagnes et al., 1988b), the North Atlantic (Fileman and Leakey, 2005) and freshwater lakes (Arndt et al., 2000; Auer and Arndt, 2001). Further studies have shown that copepods of the family Oithonidae can play a central role in structuring the size composition and biomass of the microzooplankton (Tamigneaux et al., 1997). Our estimates of *Oithona* spp. abundance are within the ranges, but lower than the maximum abundances reported in the literature (Nakamura and Turner, 1997; Porri et al., 2007). In the present study, abundance of *Oithona* spp. at the bloom stations ranged from 453 to 1419 ind m^{-3} although these abundance estimates are likely to be underestimated because of the use of a 200 μm mesh size (Gallienne and Robins, 2001), with which up to half the copepod biomass can be missed in temperate waters (Hopcroft et al., 2001).

Copepods are able to influence community structure through preferential grazing. High abundance of small copepod species feeding on smaller particles will have a strong top down effect on smaller food fractions and phytoplankton availability (Kiørboe and Nielsen, 1994). *Oithona* spp., the most abundant copepod species found at the bloom stations, is a small omnivorous copepod with an ability to change diet with season and food availability (Atkinson, 1998). It is reported to have high predation rates on ciliated protozoa, (including *Myrionecta rubra*) in particular those in the 20–30 μm size range, and flagellates (Castellani et al., 2005). Whilst experimental studies demonstrated that *Calanus helgolandicus* and *Para-pseudocalanus* spp. gained the majority of their carbon from phytoplankton ingestion at the bloom stations (Fileman et al., 2007), *Oithona* spp. are likely to be more important predators of nanoflagellate and microzooplankton populations during the bloom. However, with concentrations of <2 ind l^{-1} similar to that encountered by Nakamura and Turner (1997), the feeding impact on the microzooplankton was likely to be minimal, although Turner (1994) showed that when the abundance of *Oithona* was much higher (50 ind l^{-1}), the feeding impact on ciliates >20 μm and dinoflagellates was substantial. This study has showed that as *Oithona* spp. abundance increased at the bloom station, the abundance of ciliates $>10 \times 10^3$ μm^3 decreased ($r^2 = 0.72$; $p = 0.1$) although feeding efficiency on *M. rubra* (the most abundant ciliate within the $>10 \times 10^3$ μm^3 size category) may have been low due to low capture efficiency of this fast-swimming ciliate (Castellani et al., 2005).

Mesozooplankton diversity (Shannon-Wiener index) fell within the ranges reported in the literature (e.g. Valdes and Moral, 1998) and was positively correlated with chlorophyll concentration. Mesozooplankton diversity tends to be higher when food availability is high and there is low competition for food resources. The presence of higher food availability at the bloom stations would reduce the inter-specific competition for food and lead to larger numbers of species (Giller, 1984). Changes in species diversity such as these are generally caused by differences in environmental variables such as temperature and nutrient concentrations, resulting in low or high productivity (e.g. Woodd-Walker et al., 2002; Vallet and Dauvin, 2004; Brucet et al., 2006; Badosa et al., 2007). In this study, results from the BIOENV analysis revealed that mesozooplankton community distribution was mainly determined by temperature, this is not surprising since both ingestion rate (Kiørboe et al., 1982) and the rate of population development (Durbin and Durbin, 1992) are temperature dependent. However, within the bloom stations mesozooplankton distribution was correlated with nitrite concentration and primary production. Other studies have reported zooplankton community distribution to be related to temperature in coastal and shelf waters (Vidjak et al., 2006; Zuo et al., 2006). Increases in western Irish Sea copepod abundance during the spring bloom were found to be related to temperature and increased phytoplankton standing stock (Gowen et al., 1999). Whilst an extensive study of copepods in the Atlantic concluded that copepod diversity was influenced primarily by primary production and that any correlations with temperature are simply an association (Woodd-Walker et al., 2002), further studies on a global scale have shown that temperature best explains large-scale variation in copepod diversity (Rombouts et al., 2009·2010).

4.3. Summary

Our analysis of the in situ plankton community structure in this study, combined with information from other published datasets collected while sampling the same system (Dixon et al., 2006; Fileman et al., 2007; Llewellyn et al., 2008), has shown that the functioning of the food web varied with trophic condition and plankton community structure. During non-bloom conditions, when small phytoplankton cells predominated, microzooplankton were favoured as a food resource by mesozooplankton (Fileman et al., 2007), resulting in the channelling of more energy through the microbial food web before transfer to higher trophic levels. At the diatom bloom stations, it is known that copepods gained most of their carbon from ingestion of phytoplankton even though *Myrionecta rubra* (a preferred food for copepods at the non-bloom stations) was very abundant (Fileman et al., 2007). This demonstrates a direct link between the mesozooplankton and the phytoplankton during the bloom which could have resulted in reduced top down control of microzooplankton populations (particularly *M. rubra*). The shift in ciliate size structure is also likely to have been due to an increase in larger diatom-ingesting ciliates such as *Strombidium conicum*. Such changes in the ciliate community size structure subsequently influenced the size structure of the heterotrophic nanoflagellate population which reduced significantly in size during the bloom station. The subsequent increase in bacterial biomass observed at the end of the bloom station was most likely to be due to release of DOM from algal cells under nutrient deplete conditions (Llewellyn et al., 2008) rather than a reduction in top-down control from the nano- or microzooplankton.

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