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Nanoplankton and picoplankton in the Western English Channel: abundance and seasonality from 2007–2013



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ABSTRACT

The nano- and picoplankton community at Station L4 in the Western English Channel was studied between 2007 and 2013 by flow cytometry to quantify abundance and investigate seasonal cycles within these communities. Nanoplankton included both photosynthetic and heterotrophic eukaryotic single-celled organisms while the picoplankton included picoeukaryote phytoplankton, Synechococcus sp. cyanobacteria and heterotrophic bacteria. A Box-Jenkins Transfer Function climatology analysis of surface data revealed that Synechococcus sp., cryptophytes, and heterotrophic flagellates had bimodal annual cycles. Nanoeukaryotes and both high and low nucleic acid-containing bacteria (HNA and LNA, respectively) groups exhibited unimodal annual cycles. Phaeocystis sp., whilst having clearly defined abundance maxima in spring was not detectable the rest of the year. Coccolithophores exhibited a weak seasonal cycle, with abundance peaks in spring and autumn. Picoeukaryotes did not exhibit a discernable seasonal cycle at the surface. Timings of maximum group abundance varied through the year. Phaeocystis sp. and heterotrophic flagellates peaked in April/May. Nanoeukaryotes and HNA bacteria peaked in June/July and had relatively high abundance throughout the summer. Synechococcus sp., cryptophytes and LNA bacteria all peaked from mid to late September. The transfer function model techniques used represent a useful means of identifying repeating annual cycles in time series data with the added ability to detect trends and harmonic terms at different time scales from months to decades.

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1. Introduction

The importance of time series in identifying, understanding and quantifying the rate of climate change cannot be over-stated. The iconic Mauna Loa Observatory in Hawaii, charting the increase in atmospheric carbon dioxide (CO₂) since 1958 has been pivotal in raising societal awareness of climate change and global warming in particular, which has been happening at a greater rate over the past 50 years than the previous 10,000 years (IPCC, 2013, 2014). Time series in the marine environment are also vitally important; for marine conservation (protecting biodiversity and marine ecosystems), marine pollution and fisheries (Frost et al., 2006).

The oceans, covering approx. 70% of the Earth's surface, are extremely important in climate change terms. They have a vast capability for buffering both fluctuations in temperature and CO₂

Abbreviations: WCO, Western Channel Observatory; HNA, high nucleic acid-containing bacteria; LNA, low nucleic acid-containing bacteria; IPCC, Intergovernmental Panel on Climate Change; ICES, International Council for the Exploration of the Sea; WGPME, Working Group on Phytoplankton and Microbial Ecology; MSFD, Marine Strategy Framework Directive; EU, European Union.

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(House et al., 2002). Within the oceans, the biota also has a major role to play in global climate. Phytoplankton, in particular are responsible for 45% of global primary production (Brewin et al., 2010 and references therein) and more than 50% of the oxygen in the atmosphere. Oceanographic time series, whether coastal or open ocean, which monitor phytoplankton, as well as other components of planktonic communities and associated hydrographic measurements and processes are, therefore extremely important for gauging climate change around the world and providing data to estimate future changes in climate and the effects on both natural and man-made environments. Without time series it would not be possible to measure things such as the Atlantic Multi-decadal Oscillation (Alheit et al., 2014; Harris et al., 2014; Edwards et al., 2013) and detect major changes such as regime shifts (deYoung et al., 2008). Documented effects of climate change in the marine environment through the use of time series include declines and increases in different phytoplankton taxa (Hinder et al., 2012; Eloire et al., 2010), latitudinal shifts in the distributions of phytoplankton and zooplankton (Harris et al., 2014) and shifts in phytoplankton phenology (Schlüter et al., 2012), which can result in trophic mismatching between phytoplankton and higher trophic levels (Atkinson et al., 2015).

International efforts are now being made to bring together spatially diverse time series, for example, phytoplankton in the North Sea/English Channel (Kraberg et al., 2012) and the North Atlantic Ocean (O'Brien et al., 2012). Scientists are working together within ICES (International Council for the Exploration of the Sea) to provide better basin-scale understanding of the effects of climate change on phytoplankton through the Working Group on Phytoplankton and Microbial Ecology (WGPME). To date, over 200 marine time series across the globe have been identified by the newly formed IGMETS (International Group for Marine Ecological Time Series), funded by the United Nations Intergovernmental Oceanographic Commission, whose primary aim is to provide, "An analysis and synthesis of global marine ecological changes as seen through biogeochemical and plankton time series".

Time series also act as a platform for shorter-term scientific studies (Dixon et al., 2014; Archer et al., 2009; Steele et al., 2015) and as a test bed for new methods (Harris, 2010 and references therein, Archer et al., 2011); the infrastructure and core measurements of the time series providing a contextual framework for the specific scientific questions being addressed. The data produced from time series are also invaluable for numerical modelling research to build an understanding of specific biological processes (Polimene et al., 2015), biogeochemistry (Ciavatta and Pastres, 2011) and physics (Siddorn et al., 2003) as well as entire ecosystems (Rose and Allen, 2013).

The Western Channel Observatory (WCO) is a long-lived observatory with temperature and salinity measurements going back as far as 1903 at station E1 (Smyth et al., 2010). The WCO is in a strategic position, at the gateway to one of the busiest shipping lanes in the world. The WCO is also being considered within the European Union (EU) Marine Strategy Framework Directive (MSFD) as a sentinel site to act as a baseline for good environmental status in order for member states of the EU to conduct "an ecosystem-based approach to the management of human activities which supports the sustainable use of marine goods and services. The over-arching goal of the Directive is to achieve 'Good Environmental Status' (GES) by 2020 across Europe's marine environment." (http://jncc.defra.gov.uk/page-5193). Other long-term marine time series include the Sir Alister Hardy Foundation for Ocean Science (SAHFOS), which commenced in 1931 and the Helgoland Roads time series which began in 1962. Both of these time series have focussed their efforts on the analysis of plankton communities of both zooplankton and phytoplankton. Plankton community structure and dynamics have been regularly sampled (weekly) at station L4, another site in the Western Channel Observatory for twenty-five years. Both zooplankton and phytoplankton abundance have been shown to have repeating seasonal patterns (Eloire et al., 2010; Highfield et al., 2010; Widdicombe et al., 2010), with some taxa exhibiting increasing or decreasing trends. Both the zooplankton and phytoplankton analyses at L4 have been carried out by microscopy, which, because it is time consuming has meant that sampling has generally been limited to a single depth or integrated sampling via vertical net hauls, with little replication. There have also been molecular studies of bacteria community structure and diversity between 2003 and 2008 (Mary et al., 2006b; Gilbert et al., 2012), but these time series were also limited to a single depth. Since 2007, weekly samples from four depths between the surface and 50 m have been analysed by flow cytometry to quantify the eukaryotic nano- and picophytoplankton and heterotrophic flagellates as well as autotrophic Synechococcus sp. cyanobacteria and heterotrophic bacteria. These groups within the plankton are numerically dominant and very important within the microbial food web and on through to higher trophic levels, as well as contributing significantly to primary production, in the case of the nano- and picophytoplankton. Their high abundance, coupled to flow cytometric analysis enables analysis of replicated samples at multiple depths, providing robust data for time series analyses.

This paper introduces the L4 time series for the smallest algae and bacteria, analysed by flow cytometry since 2007. It presents the abundance data of the different planktonic groups through the water column and undertakes a preliminary investigation into their seasonal patterns using novel time series analysis methods to study their climatologies.

2. Materials and methods

2.1. Sample site description, sample collection and preparation

Samples for phytoplankton smaller than approx. 20 µm, heterotrophic flagellates and bacteria were collected and analysed as part of the Western Channel Observatory (WCO, www.westernchannelobservatory.org.uk), long-term oceanographic and marine biodiversity time series study at station L4. L4 is situated in the Western English Channel, 7.25 nautical miles south southwest of Plymouth, England, UK (50°15.00'N, 4°13.02'W) (Fig. 1). L4 has a water column depth of approx. 53 m. It is well mixed during the winter and stratified from April to September (Smyth et al., 2010). When stratified there is often a 2 °C difference in temperature between the upper and lower layers. L4 also experiences maximum tidal ranges in excess of 5 m and currents of 0.5–0.6 m s⁻¹ at the surface (Cross et al., 2015). The surface temperature at L4 ranges from 8 °C in mid-winter to between 17-18 °C in mid-August (Fig. 2A). The seasonal cycles for the major nutrients; nitrate + nitrite, silicate and phosphate (Fig. 2B) are essentially mirror images of the seasonal cycle for temperature. Fig. 2C. illustrates the seasonal cycle for chlorophyll-a from 10 m between 2007 and 2013. Chlorophyll-a concentration is always lowest during late autumn and winter and higher during spring and summer. There is a great deal of variability from month to month and in some years a clear bimodal distribution in peak chlorophyll-a concentration is observed.

Water samples were collected weekly by the RV Plymouth Quest from 2, 10, 25 and 50 m depth using 10 L Niskin bottles mounted on a rosette sampler which also housed a Seabird 19+ CTD. Sub-samples were decanted into clean 500 mL polycarbonate bottles and placed in a cool box. Samples were returned to the laboratory, generally within 3 h and samples processed immediately. On occasions when it was not possible to process samples immediately, 2.95 mL samples were placed in cryovials containing

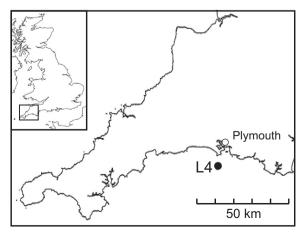


Fig. 1. Location of station L4 within the Western English Channel.

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