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Hydrodynamic conditions associated with the formation, maintenance and dissipation of a phytoplankton thin layer in a coastal upwelling system

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ABSTRACT

During May–June 2005, a 17-d cruise was carried out in Ría de Pontevedra (Galician Rías Baixas) to study the physical–biological interactions that may lead to subsurface aggregations of phytoplankton organisms in thin layers (TLs). Physical processes governed the initiation and development, maintenance, and decline of a diatom (toxin producing *Pseudo-nitzschia* spp. and *Chaetoceros socialis*) TL during an upwelling relaxation-upwelling–downwelling sequence. Differences in shear profiles appeared to lead to the formation of a TL during upwelling events. These results reveal that the coupling between maximum values of shear and buoyancy frequency can shape a subsurface chlorophyll maximum (SCM) into a TL. The effect of shear upon phytoplankton patches, which has been predicted on the basis of theoretical studies, has been corroborated in this study in which the vertical distribution of an observed TL was controlled by physical processes.

Understanding both local fine-scale circulation patterns and regional physical processes will improve our knowledge of the spatial and temporal occurrence of these layers. Results here bring new understanding in TL dynamics at coastal upwelling sites and provide information about the physical processes involved in TL development, which can be used to predict their occurrence and understand their ecological implications.

1. Introduction

Spatial heterogeneity or "patchiness" in plankton distributions is one of the oldest oceanographic observations reported. A phytoplankton patch is defined as a water mass containing a concentration of cells which is several times the background concentration (Bainbridge, 1957). Thin layers (TLs) of plankton are coherent and conspicuous heterogeneities in the vertical distribution of marine organisms. These structures were first detected by Strickland (1968) and sampled in detail by Derenbach et al. (1979). In the last two decades, advances in instrumentation and sampling techniques (Donaghay et al., 1992; Gentien et al., 1995; Franks and Jaffe, 2001) have confirmed that phytoplankton TLs occur in a variety of conditions in marine waters (Vilicic et al., 1989; Bjørnsen and Nielsen, 1991; Donaghay et al., 1992; Gentien et al., 1995). These fine structures appear frequently in the water column and can persist for days (Dekshenieks et al., 2001). They range in vertical dimension from centimetres to a few metres, and have been observed to extend horizontally for kilometres (Dekshenieks et al., 2001; Rines et al., 2002).

Significant progress has been made in describing the spatial and temporal scales of TLs and their variability relative to oceanographic forcing in some regions (McManus et al., 2003, Lunven et al., 2005); several empirical studies have revealed strong statistical relationships between plankton TLs and the physical structure of the water column (Dekshenieks et al., 2001). Surveys in East Sound (WA, US) and Monterey Bay (CA, US) have shown that stratification, shear, and regional water mass variability all influence the development and evolution of TLs (McManus et al., 2003; Ryan et al., 2008); TLs have also been found associated with episodic environmental events, such as upwelling–downwelling cycles (Ryan et al., 2008; Velo-Suárez et al., 2008). Although there have been significant advances in this field, there is still a lack of information about the processes involved in TL development, advection and maintenance; this topic is being dealt with by the GEOHAB core research project of "HABs in Stratified Systems" (GEOHAB, 2008).

A key question is whether TLs are a passive response of the plankton promoted by physical processes or are developed from active aggregation of the organisms that constitute them. To address this question, several theoretical approaches have been used to explain TL generating mechanisms. Franks (1992)

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examined the importance of buoyancy forces to maintain the position of phytoplankton organisms along a particular isopycnal. Later, the same author (Franks, 1995) proposed a shear-driven mechanism for layer formation based on the interaction between internal waves and phytoplankton patches. Gallager et al. (2004) and Genin et al. (2005) invoked the swimming behaviour of some dinoflagellates and zooplankton to explain TL development and maintenance. Stacey et al. (2007) discussed the effects of turbulent dissipation combined with three TL-convergence mechanisms: straining (vertical shear of the horizontal current), motility and buoyancy. Recently developed models on TL formation point towards vertically sheared horizontal currents as the main factor involved in their development (Birch et al., 2008). Durham et al. (2009) has also proposed the coupled action of phytoplankton motility and horizontal shear as a TL formation mechanism (gyrotactic trapping).

TLs are a significant source of small-scale vertical heterogeneity in the marine environment. Development of phytoplankton TLs influences coastal ocean ecological processes in many ways. They may provide a mechanism for the long-term maintenance and sudden expression of harmful algae blooms (HABs). The onset of a bloom can remain undetected since HAB populations may be concentrated in a discrete TL that can easily be missed by conventional sampling methods used in monitoring programmes (Bjørnsen and Nielsen, 1991; McManus et al., 2008; Velo-Suárez et al., 2008). These structures not only affect optical and acoustical signatures in the sea but also have a significant influence on the dynamics of marine ecosystems. Nowadays, models have thus far been restricted by insufficient ability to gauge the interactions between the biology of algal taxa and underlying physical processes. Therefore, it is critical to improve our ability to understand the spatio-temporal dynamics of these structures in coastal environments at the appropriate scales.

During spring 2005, a two-week multidisciplinary cruise was conducted to describe the fine-scale physical and biological structure of the water column and to explore the occurrence of TLs of harmful microalgae in Ría de Pontevedra (Galicia, northwest Spain). Studies were carried out on board R/V *Mytilus* from 31 May to 14 June 2005. The phytoplankton assemblages and the physical–biological interactions in Ría de Pontevedra during the study are described in an earlier publication (Velo-Suárez et al., 2008). Here we focus on the fine-scale optical and physical structure of the water column and its relation with the distribution of microplankton at a fixed sampling station during the cruise. The onset, maintenance and dispersion of a TL in an upwelling prevalent period followed by upwelling relaxation conditions in the Ría are described. In this work, thin phytoplankton layers were identified from chlorophyll fluorescence data measured by sensors on the high resolution profilers, using the criteria detailed in Dekshenieks et al. (2001): 'For a structure to be considered a thin layer, the chlorophyll profile has to meet 3 criteria: (1) The feature has to be ≤ 5 m thick; this is below the scale routinely sampled with bottles and nets on most oceanographic cruises. Layer thickness is measured where the optical signal was at half maximum intensity. (2) The optical signal has to be present in 2 or more sequential profiles. (3) The optical signal has to be at least 3 times greater than background. These criteria are conservative and effectively eliminate ephemeral features' (Dekshenieks et al., 2001).

2. Materials and methods

2.1. The study area

Ría de Pontevedra is a flooded tectonic valley located on the NW coast of the Iberian Peninsula (Fig. 1). This Ría has a surface of

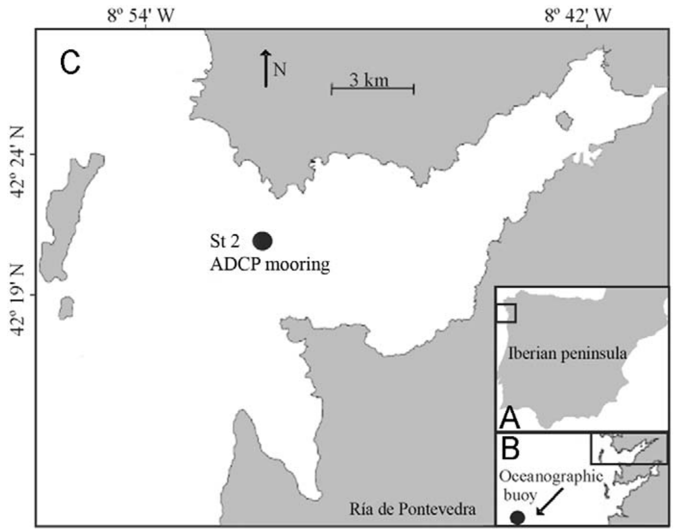

Fig. 1. (A) The Galician Rías Baixas (NW Iberian Peninsula). (B) The Ría de Pontevedra in relation to the Rías Baixas and the location of the Sea watch buoy of Puertos del Estado (www.puertos.es) off Cabo Silleiro and (C) Map of the study area showing location of the station and the ADCP mooring (sta 2).

141 km^2, a mean depth of 31 m and a volume of 3.5 km^3. Hydrodynamics of the Ría is mainly driven by freshwater inputs and the wind regime (Prego et al., 2001). Tidal forcing appears to be a minor factor since wind speeds higher than 4 m s^{-1} reverse surface currents against the tide (De Castro et al., 2000). The Lérez River (Fig. 1) provides the main freshwater input; its monthly discharge rate ranges from 2 to 80 m^3 s^{-1} and closely follows rain patterns (Gómez-Gesteira et al., 2001).

Northerly winds promote upwelling of cold, salty and nutrient-rich Eastern North Atlantic Central Water (ENACW) from spring to early autumn (March to October). Upwelling forces a two-layer density-induced positive circulation, characterized by the outflow of surface water and the compensating inflow of upwelled waters at the bottom (Wooster et al., 1976). In autumn and winter (October to March) southerly winds are predominant in the area and the circulation reverses. Shelf water enters the Ría at the surface and there is a compensating outflow at the bottom (Prego et al., 2001). Changes in wind forcing lead to rapid changes (<24 h; Sousa, 1995) in the oceanographic conditions of the Ría, which in turn force significant changes in plankton distribution and ecology (Tilstone et al., 2000; 2003).

2.2. Sampling overview

Fine-scale profiles of biological and physical structure were simultaneously measured at a fixed 45 m deep station (st. 2), located in the navigation channel (42° 21.38′N, 8° 50.07′W), during the whole survey (Fig. 1). Its position makes it suitable for evaluating and averaging of the main processes that take place in the system due to changes in external forcing factors (Nogueira et al., 1997).

Daily measurements were carried out during the cruise with the high-resolution IFREMER particle size analyser profiler (IPSAP), which includes an SBE 25 CTD Probe (Sea-Bird Electronics, Washington, USA), a fluorescence sensor (Seapoint Sensors, Inc., Exeter, New Hampshire, USA), and a particle size analyser (CILAS, Orléans, France). The sensor for photosynthetically active radiation (PAR) measurements was a LICOR Spherical SPQA. The IPSAP profiler provides a synchronized set of data in real time (Gentien et al., 1995; Kononen et al., 2003; Velo-Suárez et al., 2008); it allows real time data acquisition at 5 Hz of standard