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Nitrogen uptake of phytoplankton assemblages under contrasting upwelling and downwelling conditions: The Ría de Vigo, NW Iberia

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ABSTRACT

Regenerated production (including organic nitrogen) is shown here to be important in the Ría de Vigo (Galicia, NW Iberia) in supporting both harmful algal bloom communities during the downwelling season, but also (to a lesser extent) diatom communities during stratified periods of weak to moderate upwelling. The Galician Rías, situated in the Iberian upwelling system, are regularly affected by blooms of toxic dinoflagellates, which pose serious threats to the local mussel farming industry. These tend to occur towards the end of summer, during the transition from upwelling to downwelling favourable seasons, when cold bottom shelf waters in the rías are replaced by warm surface shelf waters. Nitrate, ammonium and urea uptake rates were measured in the Ría de Vigo during a downwelling event in September 2006 and during an upwelling event in June 2007. In September the ría was well mixed, with a downwelling front observed towards the middle of the ría and relatively high nutrient concentrations (1.0–2.6 μmol L^{-1} nitrate; 1.0–5.6 μmol L^{-1} ammonium; 0.1–0.8 μmol L^{-1} phosphate; 2.0–9.0 μmol L^{-1} silicic acid) were present throughout the water column. Ammonium represented more than 80% of the nitrogenous nutrients, and the phytoplankton assemblage was dominated by dinoflagellates and small flagellates. In June the water column was stratified, with nutrient-rich, upwelled water below the thermocline and warm, nutrient-depleted water in the surface. At this time, nitrate represented more than 80% of the nitrogenous nutrients, and a mixed diatom assemblage was present. Primary phytoplankton production during both events was mainly sustained by regenerated nitrogen, with ammonium uptake rates of 0.035–0.063 μmol N L^{-1} h^{-1} in September and 0.078–0.188 μmol N L^{-1} h^{-1} in June. Although *f*-ratios were generally low (<0.2) in both June and September, a maximum of 0.61 was reached in June due to higher nitrate uptake (0.225 μmol N L^{-1} h^{-1}). Total nitrogen uptake was also higher during the upwelling event (0.153–0.366 in June and 0.053–0.096 μmol N L^{-1} h^{-1} in September). Nitrogen uptake kinetics demonstrated a strong preference for ammonium and urea over nitrate in June.

1. Introduction

Nitrogen is generally recognised as being the nutrient limiting primary production in coastal marine ecosystems (Dugdale, 1967; Ryther and Dunstan, 1971; Howarth and Marino, 2006). Furthermore, nitrogen inputs to coastal waters are increasingly thought to be implicated in the reported global increase in Harmful Algal Blooms (HABs) (Anderson et al., 2002), in particular due to the increase in dissolved organic nitrogen (Glibert et al., 2006). Nitrogen uptake measurements provide valuable information on the relative contributions of new and regenerated forms of nitrogen to primary production. Such measurements are particularly important for understanding the ecology of HABs, especially in upwelling systems, which are characterised by large fluctuations in nitrate (NO_3^-) concentrations. A number of nitrogen uptake measurements have been made in the California and Benguela upwelling systems (Dugdale et al., 1990, 2006; Probyn, 1992; Seeyave et al., 2009). In the Iberian upwelling system some previous measurements of nitrogen uptake and regeneration have been reported in shelf waters (Slawyk et al., 1997; Joint et al., 2001; Bode et al., 2004a,b, 2005) and a few reported in the rias (Varela et al., 2003; Bode et al., 2005).

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Published *f*-ratios have been calculated either from direct measurements using ^{15}N (but most of these have not included urea), or estimated from the NO_3^- flux into the euphotic zone caused by upwelling (Álvarez-Salgado et al., 2002), or based on satellite-derived primary production estimates (Arístegui et al., 2009). The relatively low seasonally averaged ratios (0.20–0.33) derived from the latter study were attributed to low continental nutrient inputs, low nutrient concentrations in the source water, low average coastal winds and the importance of heterotrophy and therefore nutrient regeneration (Arístegui et al., 2006).

The Rías Baixas of Galicia are large coastal indentations situated on the north-west coast of the Iberian Peninsula, within the Iberian upwelling system (Fig. 1). They are the largest producer of mussels worldwide, representing 40% of European production and 15% of world production, with a first sale value of 80 million US dollars (Labarta et al., 2004). The regular occurrence of HABs in the rías is therefore a major concern for the industry (Fraga, 1989), with total losses to the shellfish industry attributed to these toxic outbreaks estimated at 10–20 M€ per year (Hoagland and Scatasta, 2006).

Upwelling occurs from approximately March to September when northerly winds prevail, whereas the rest of the year is characterised by southerly winds and downwelling (Fraga, 1981). Short-term changes in wind direction generally drive upwelling/relaxation cycles of 1–2 weeks (Blanton et al., 1987), which in turn drive the subtidal circulation in the rías. During upwelling, positive estuarine circulation forces upwelled water from the shelf into the rías along the bottom while surface water flows out of the rías. During downwelling, surface water flowing into the rías converges with water flowing out and forms a downwelling front, with the outflow occurring at depth (Figueiras et al., 1994). During upwelling, the injection of nutrients into the rías stimulates phytoplankton growth and the resulting biomass is then exported out of the ría, where it may sink and become remineralised, and can later be re-injected into the rías along with the upwelled nutrients (Álvarez-Salgado et al., 1993). This "secondary remineralisation" allows the rías to support very high rates of primary production, particularly towards the end of the upwelling season (Álvarez-Salgado et al., 1997).

The abundance of diatoms is positively correlated to upwelling (Figueiras and Rios, 1993), and HABs tend to occur during downwelling events in late summer-early autumn (Fraga et al., 1988; Figueiras et al., 1994). The horizontal distribution of diatoms and dinoflagellates also reflects the intensity of upwelling or stratification along the rías, with diatoms dominating towards the interior, where upwelling is strongest, whereas dinoflagellates tend to occur in the outer, more stratified parts of the rías (Tilstone et al., 1994). The apparent increase in blooms of certain HAB species in the last 4 decades has been attributed to enhanced eutrophication of the rías as a result of increased sewage discharges, expansion of the mussel farms and increases in forest fires (Wyatt and Reguera, 1989), as well as a decrease in the duration and average intensity of the upwelling season (Álvarez-Salgado et al., 2008).

No consensus has yet been reached regarding the mechanisms leading to HAB development in the rías (Pitcher et al., 2010). Some studies have supported the hypothesis of advection of offshore populations into the rías (Fraga et al., 1993; Sordo et al., 2000), whereas others have suggested *in situ* HAB development (Fraga et al., 1990; Figueiras and Pazos, 1991a; Pazos et al., 1995; Figueiras et al., 1998). In any case, downwelling is thought to favour motile species such as *Gymnodinium catenatum*, which can maintain themselves in the surface layer (Fraga et al., 1988; Figueiras et al., 1994; Fermin et al., 1996). HABs can also develop during weak to moderate upwelling, which raises the nutricline without being sufficiently intense to mix the entire water column (Figueiras and Rios, 1993). In this situation, dinoflagellates can undertake diel vertical migrations that allow them to exploit the high nutrient concentrations at the nutricline during the night and photosynthesise during the day in the surface layer (Figueiras and Fraga, 1990; Fraga et al., 1992, 1999). Using a box model, Ríos et al. (1995) suggested that diatom growth was sustained by nitrate during the upwelling season, whereas autumn dinoflagellate populations relied on ammonium as their main source of nitrogen.

This study aimed to characterise the nitrogen nutrition of phytoplankton assemblages during upwelling and downwelling conditions in the Ría de Vigo, using the ^{15}N stable isotope tracer technique. This provided valuable information on the nutrient biogeochemistry of the ría and also on the nitrogen sources that are utilised by HAB communities in these embayments.

2. Materials and methods

2.1. Sampling

Sampling was carried out on-board the *R/V Mytilus*, as part of the Galician programme CRIA (Circulation in a RIA). CRIA consisted of two parts, CRIA I targeting the downwelling, "HAB season" (26–30 September 2006) and CRIA II targeting the upwelling, "diatom" season (25–28 June 2007). Spatial surveys of temperature, salinity, chlorophyll-a (hereafter chl-a) fluorescence and turbidity were carried out using a lightweight towed undulating vehicle, MiniBAT

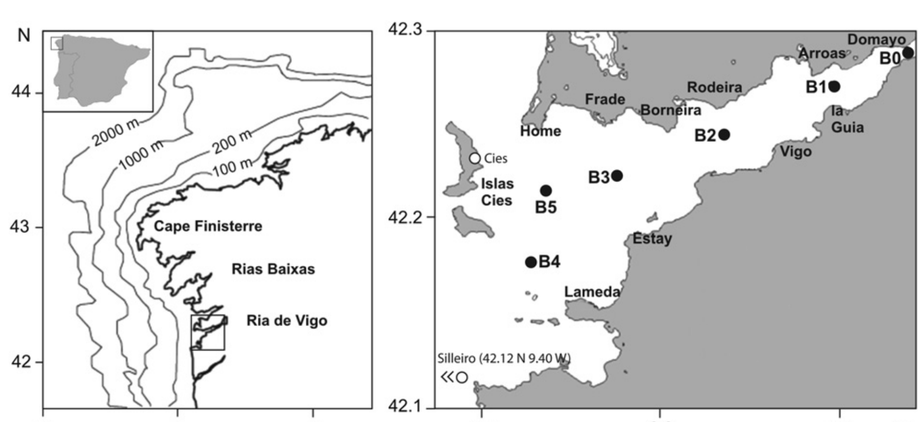

Fig. 1. Map of NW Spain showing the four Rías Baixas (left-hand panel) and detailed map of the Ría de Vigo (right-hand panel) showing the CTD stations B0–B5 (closed circles) and the meteorological stations (open circles).