Estuarine, Coastal and Shelf Science 91 (2011) 110–120

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Microzooplankton feeding impact in a coastal upwelling system on the NW Iberian margin: The Ría de Vigo

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ARTICLE INFO

Article history:
Received 8 April 2010
Accepted 14 October 2010
Available online 28 October 2010

Keywords:
microzooplankton
microbial food web
dilution technique
microscopic enumeration
coastal upwelling systems
Ría de Vigo

ABSTRACT

The dilution technique, combined with identification and enumeration of pico-, nano- and microplankton by microscopy, was used to estimate microzooplankton impact on the microbial community in surface waters of a coastal embayment on the NW Iberian upwelling system. Microzooplankton were important consumers of autotrophic and heterotrophic plankton in this system, feeding up to 93% of standing stock and more than 100% of production of several groups. Heterotrophic bacteria and heterotrophic picoflagellates experienced the highest and constant impact, with 75–84% of their standing stocks and 85–102% of their production being channelled through the microbial food web. Pico- and nano-phytoplankton were also consumed, although maximum grazing occurred on diatoms during upwelling events, coinciding with highest primary production. Predation on pico-nano-heterotrophs was especially relevant under downwelling conditions, when consumption of total carbon and particularly autotrophic carbon was considerably lower than during upwelling. The results suggest that the existence of a multivorous food web, extending from the microbial loop to the herbivorous food web, could be a major feature in this coastal upwelling system. The microbial loop, which occurs as a permanent background in the system, would contribute to sustain the microbial food web during downwelling, whereas the herbivorous food web could coexist with a microbial food web based on large diatoms during upwelling. The multivorous food web would partially divert diatoms from sinking and hence favour the retention of organic matter in the water column. This could enhance the energy transfer to higher pelagic trophic levels in coastal upwelling systems.

1. Introduction

The role of heterotrophic nano- and micro-plankton (hereafter microzooplankton) is widely recognised across marine systems, exerting a fundamental ecological function recycling nutrients and transferring matter and energy from the small-sized organisms to large consumers (Calbet and Landry, 2004). Nonetheless, in coastal upwelling systems, the function of microzooplankton has classically been mistreated (Ryther, 1969). Typically, it has been accepted that short food chains prevail in these productive areas, with large phytoplankton directly passing to zooplankton and then to larger animals. However, microzooplankton are abundant in upwelling regions, and evidence of their importance continuously increases (Painting et al., 1992; Neuer and Cowles, 1994; García-Pámanes and Lara-Lara, 2001; Vargas and González, 2004). Thus, it is well known that microzooplankton not only feed on small phytoplankton, they also impact on communities dominated by large phytoplankton (Calbet, 2008), often abundant in coastal upwelling areas. Particularly, heterotrophic dinoflagellates are now considered as major herbivores of large and chain-forming diatoms (Sherr and Sherr, 2007). Microzooplankton also consume heterotrophic plankton, such as bacteria and other phagotrophic organisms (Azam et al., 1983; Rassoulzadegan and Sheldon, 1986; Jeong, 1999), and so modulate biogeochemical fluxes through complex interactions within the microbial food web.

Short food chains, owing to the few steps involved, are more efficient than microbial food webs transferring energy to higher trophic levels. Nonetheless, a significant amount of material can be removed from the photic layer, via rapid sinking of large diatoms and/or faecal material from large metazoans (Turner, 2002), in areas or moments with predominance of short food chains. Consequently, the co-occurrence of the two trophic ways or the existence of a "multivorous food web" (Legendre and Rassoulzadegan, 1995), in which microzooplankton are a key player, could contribute to reduce

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doi:10.1016/j.ecss.2010.10.012

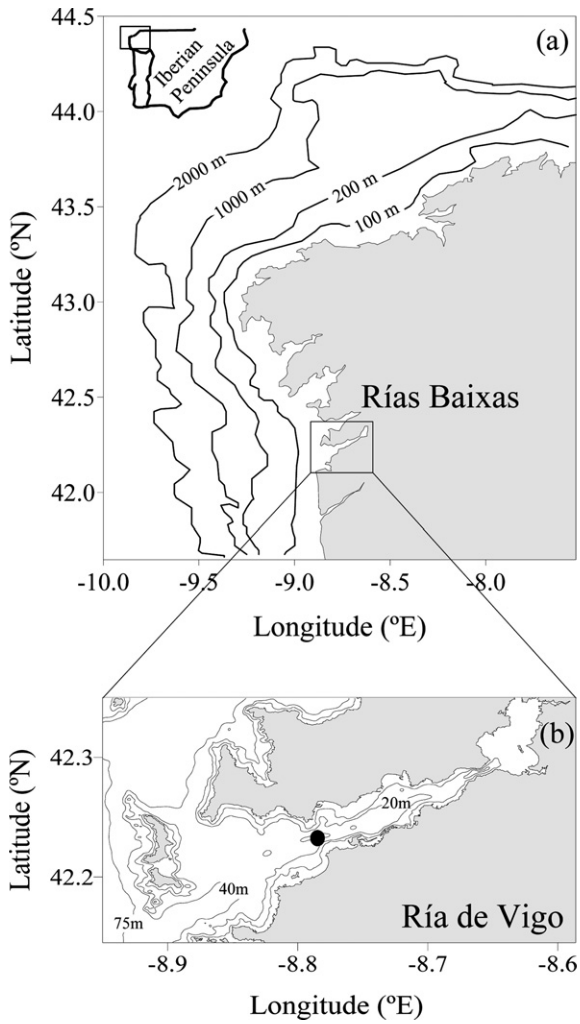

Fig. 1. (a) NW Iberian margin showing the location of the four Rías Baixas. (b) Map of the Ría de Vigo showing the position of the sampled station.

carbon losses from the photic layer while still retaining enough efficiency in the energy transfer to high pelagic trophic levels. Knowledge of the role that microzooplankton play in coastal upwelling systems is hence fundamental to advance in our understanding of carbon fluxes in these highly productive oceanic areas.

Reports on the importance of microzooplankton in the Iberian upwelling are scarce. Although some studies, through indirect approaches, suggest that microzooplankton activity must be important in this upwelling area (Figueiras and Ríos, 1993; Bode and Varela, 1994; Bode et al., 2004), microzooplankton grazing activity was only determined in shelf and oceanic waters (Fileman and Burkill, 2001). On the contrary, microzooplankton activity in the highly productive coastal bays known as Rías Baixas (Fig. 1a) has never been determined. In the Rías Baixas, coastal upwelling, induced by northerly winds, introduces subsurface nutrient-rich water through the bottom from spring to autumn. During the rest of the year, the dominant southerly winds cause downwelling (Fraga, 1981). Relaxation and even opposite events can however occur within each season, in response to short-time variations in the wind regime driven by small fluctuations in the large-scale climatology of the North Atlantic. Plankton composition in these systems is typical of temperate coastal regions, but it is also influenced by the hydrographic variability imposed by upwelling-downwelling events (Figueiras et al., 2002). Thus, large diatoms are abundant in spring, whereas the plankton community in summer is composed of heterotrophic and autotrophic organisms, with autotrophy (diatoms) dominating during upwelling events and heterotrophy (dinoflagellates and ciliates) attaining greater importance during relaxations. Large pigmented dinoflagellates, sometimes forming harmful blooms, are common in autumn, while small flagellates dominate in winter. Pico- and nano-phytoplankton are present in the system all through the year, though their contribution to the phytoplankton community is higher in winter, because peaks of autotrophic biomass during upwelling are caused by diatoms (Figueiras et al., 2002; Arbones et al., 2008). Therefore, biogeochemical fluxes in this coastal upwelling system could be affected by the high variability in plankton composition and size structure.

The aim of this work was to quantify for the first time in the coastal upwelling system of the Ría de Vigo (the southernmost of the Rías Baixas, Fig. 1b), the feeding impact of microzooplankton on the several autotrophic and heterotrophic plankton groups ($\leq$200 μm) during different hydrographic conditions. It was achieved by performing dilution experiments (Landry and Hassett, 1982) associated with identification and enumeration of plankton components by microscopy.

2. Materials and methods

2.1. Sampling and experimental set up

Sampling took place at dawn in a station located in the main channel at the central part of the Ría de Vigo (Fig. 1b) in February, April, July and September 2002 on board of the R/V *Mytilus*.

For the hydrographic survey, the station was sampled four times each month (see Fig. 2). Salinity and temperature were recorded with an SBE 9/11 CTD probe attached to a rosette sampler. Water samples were collected in plastic bottles ($\sim$75 ml) from the CTD up casts to determine nitrate concentrations in the water column. These samples were kept refrigerated until their analysis in the laboratory within 2 h of their collection.

Mortality and growth rates of autotrophic and heterotrophic plankton $\leq$200 μm at the surface layer were estimated using the dilution technique (Landry and Hassett, 1982) on two days during each sampling month (see Fig. 2). All experimental containers, bottles, filters and tubing were soaked in 10% HCl and rinsed with Milli-Q water before each experiment. Surface water was collected from 2 dips of a 30 l Niskin bottle. Water from the first dip was gravity filtered through a 0.2 μm Gelman Suporcap to a polycarbonate container and water from the second dip was directly and gently transferred to another polycarbonate container. Both containers were kept in the dark while being transported to the laboratory within 2 h of their collection.

At the laboratory, the filtered water from the first dip and the unfiltered seawater obtained from the second dip were gently combined into carboys to obtain dilution levels of $\sim$10, 20, 40, 60, 80 and 100% of unfiltered seawater. The exact dilution levels were checked from chlorophyll *a* (chl *a*) concentrations determined in triplicate samples (see below). Two clear polycarbonate bottles of 2.3 l were completely filled from each dilution level and incubated for 24 h at simulated *in situ* light and temperature conditions in an incubator placed in the laboratory's terrace. Temperature was controlled by flowing seawater directly pumped from the sea, whereas a grey mesh was placed on top of the incubator to allow the passage of $\sim$60% of incident irradiance. This is a light level similar to that found in the surface layer of the Ría de Vigo.

Nutrient addition, often performed in this type of experiments, can however affect phytoplankton growth negatively (Lessard and Murrell, 1998; Worden and Binder, 2003). Additionally, changes in the feeding behaviour of microzooplankton within the dilution series have also been reported (Worden and Binder, 2003). Because