Journal of Marine Systems 148 (2015) 14–25

Contents lists available at ScienceDirect

Journal of Marine Systems

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

Phytoplankton succession explains size-partitioning of new production following upwelling-induced blooms

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ARTICLE INFO

Article history:
Received 1 October 2014
Received in revised form 23 January 2015
Accepted 30 January 2015
Available online 7 February 2015

Keywords:
Phytoplankton
Cell size
Community succession
New production
Coastal upwelling
Nitrate uptake
Biogeochemical model

ABSTRACT

Large and chain-forming diatoms typically dominate the phytoplankton biomass after initiation of coastal upwelling. The ability of these diatoms to accelerate and maintain elevated nitrate uptake rates has been proposed to explain the dominance of diatoms over all other phytoplankton groups. Moreover, the observed delay in biomass accumulation following nitrate supply after initiation of upwelling events has been hypothesised to result from changes in the diatom community structure or from physiological acclimation. To investigate these mechanisms, we used both numerical modelling and experimental incubations that reproduced the characteristic succession from small to large species in phytoplankton community composition and size structure. Using the Tracers Of Phytoplankton with Allometric Zooplankton (TOPAZ) ecosystem model as a framework, we find that variations in functional group-specific traits must be taken into account, through adjustments of group-dependent maximum production rates (P_{Cmax}, s^{-1}), in order to accurately reproduce the observed patterns and timescales of size-partitioned new production in a non-steady state environment. Representation of neither nutrient acclimation, nor diatom diversity in the model was necessary as long as lower than theoretical maximum production rates were implemented. We conclude that this physiological feature, P_{Cmax}, is critical in representing the early, relatively higher specific nitrate uptake rate of large diatoms, and explains the differential success of small and large phytoplankton communities in response to nitrate supply during upwelling.

1. Introduction

A disproportionate fraction of global primary production (10–30%) and carbon sequestration (40–85%) – relative to their ocean area (5–19%) – occurs on continental shelves, especially in areas of coastal upwelling (Dunne et al., 2007; Longhurst et al., 1995; Muller-Karger et al., 2005). Wind-driven upwelling of nutrient rich water into the euphotic zone along western continental margins drives the development of phytoplankton blooms, which are often dominated by large and chain-forming diatoms (Estrada and Blasco, 1985; Kudela et al., 2008). Because of their relatively large size and biomineral content, these bloom-forming diatoms efficiently transfer newly produced biomass to higher trophic levels and to the deep ocean and seafloor, where carbon sequestration occurs (Stock and Dunne, 2010; Thunell et al., 2007). Because of this interconnection between phytoplankton community composition and biogeochemical cycles, numerical models used to understand elemental cycles in the context of climate change can be improved by incorporating explicit representation of microbial community structure.

Hydrodynamic turbulence, and hence the light and nutrient regime, exerts strong controls on the phytoplankton assemblage (Margalef, 1978). Some phytoplankton species, notably larger diatoms, are especially adept at exploiting the higher nutrient conditions that characterise upwelling events compared to other, often smaller phytoplankton species, whose growth rates saturate at lower nutrient and light levels (Barber and Hiscock, 2006; Finkel, 2001; Key et al., 2010; Litchman et al., 2007). Field and modelling studies have shown that as the total phytoplankton biomass increases, the biomass of larger phytoplankton increases relatively more than that of the smaller species. Across the resource concentration gradient, this means that disproportionally more biomass is added to the larger phytoplankton at higher resource concentrations (Goericke, 2011; Irigoien et al., 2004; Li, 2002; Poulin and Franks, 2010).

Phytoplankton cell size is often used as a key functional characteristic. Size distribution of phytoplankton communities can be modelled without invoking grazing control via bottom-up control of phytoplankton growth through maximum growth rates that increase with cell size (Irwin et al., 2006). However, this approach contradicts observed allometric relationships, which find decreasing maximum growth

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http://dx.doi.org/10.1016/j.jmarsys.2015.01.009
0924-7963/

rates with increasing cell size (Edwards et al., 2012), but see Marañón et al. (2013). To resolve this contradiction, it has been proposed that further phylogenetic constraints be included in models. For example, maximum potential growth rates can be assigned to broad taxonomic groups to impose controls on phytoplankton community structure (e.g., diatoms vs. green algae cf. Litchman et al. (2010)).

The differentiation between growth traits of functional groups in current generation global models is still poorly constrained (Finkel et al., 2010). Coastal ecosystem models using at least two, often size-based, functional phytoplankton groups have been used to improve our understanding of patterns of primary production (Goebel et al., 2010; Klein, 2002; Li et al., 2010; Moloney et al., 1991). The dynamic nature of coastal ecosystems creates transient environmental conditions to which individual phytoplankton cells rapidly adjust in terms of resource allocation to nutrient uptake and cell growth (Morel, 1987). Some of the earlier coastal ecosystem models invoked physiological mechanisms, such as acclimation to changing light and/or nutrient conditions, or ecological succession to explain the apparent acceleration of nitrate uptake rate by the whole phytoplankton community following an upwelling event (Dugdale et al., 1990; Wilkerson and Dugdale, 1987; Zimmerman et al., 1987), but see Garside (1991). In addition, many instances of acclimation of nitrate uptake or assimilation and the uncoupling of nutrient uptake and cell growth have been documented experimentally (Collos, 1986; Collos et al., 2005; Jochem et al., 2000; Smith et al., 1992). However, it has not been possible to quantitatively link these ecophysiological processes to the observed timing and partitioning of new production into different phytoplankton size and taxonomic groups following an upwelling event.

This study had two main objectives: First, to further evaluate the phytoplankton community composition and succession in a previously described mesocosm experiment (Fawcett and Ward, 2011) and second, to determine which ecophysiological processes in phytoplankton communities regulate the observed patterns in the timing and size-partitioning of new production following the initiation of an upwelling event. The mesocosm experiment simulated growth conditions after coastal upwelling initiation and measured production and nutrient uptake into three size fractions (small (P^S) = 0.7–5 μm; medium (P^M) = 5–20 μm; large (P^L) = >20 μm) during the subsequent development of a phytoplankton bloom. We hypothesised that, to explain the observed patterns in new production and shifts in community composition, i) the phytoplankton size groups had different intrinsic maximum production rates, and that the timing of new production in such a transient environment could be explained alternatively by ii) the physiologically-limited ability of phytoplankton groups to acclimate to the improved nutrient conditions, or iii) by allowing for greater resolution in taxonomic and subsequently physiological diversity. To test those hypotheses we calibrated the ecosystem model "Tracers Of Phytoplankton and Allometric Zooplankton" (TOPAZ) (Dunne et al., 2005, 2013) using a coastal upwelling species assemblage, and used it as a framework for evaluating the results of the mesocosm experiment.

2. Methods

2.1. Field experiment overview

Phytoplankton blooms were initiated by simulating coastal post-upwelling conditions in three 200 l mesocosms (hereafter, B1, B2, B3) as reported by Fawcett and Ward (2011). Briefly, water was collected during the upwelling season in central Monterey Bay, California (36.85°N, 121.97°W; bottom depth = 250 m) from 70 m depth, where the nitrate concentration ($[NO_3]$) was sufficiently high (~20 μmol l^{-1}) to initiate a bloom. The mesocosms were inoculated with 2 l of surface water and incubated for 8 days at the light and temperature conditions of surface water. The water in the mesocosms was mixed three times each day to minimise particle settling. The initial ammonium (NH_4) and NO_3 concentrations in the mesocosms were typical of seawater upwelled from 70 m depth in Monterey Bay. See Fawcett and Ward (2011) for nutrient concentration data and mass balance validation.

Ambient uptake rates of NH_4 and NO_3 by the P^S, P^M and P^L size fractions were determined daily starting on the second day using isotopic tracer (^{15}N) incubations (3 h) of 1.5 l subsamples from the mesocosms and size-fractionation of particulate nitrogen (PN) by filtration. PN and ^{15}N content were measured using an elemental analyser coupled to a Europa Scientific 20/20 mass spectrometer, as described in Fawcett and Ward (2011) and in the supplementary methods section. The uptake rates (ρ_i, μmol l^{-1} h^{-1}) were calculated according to the equation of Dugdale and Goering (1967). Specific rates of uptake of NH_4 (V_{NH4}) and NO_3 (V_{NO_3}) were calculated by normalising ρ_i to [PN] and averaging over the length of the photoperiod during the experiment (13.9 ± 0.1 h, based on continuous measurements of photosynthetic active radiation (PAR) performed by the Moss Landing Marine Laboratories Weather Station; http://weathernew.mlml.calstate.edu).

The relative specific uptake rates of NO_3 (N^i) in each PN size fraction (P^i) were calculated by normalising the specific nutrient uptake rate in a particular size fraction (V_{Ni}^{Pi}) to the combined specific uptake in all size fractions, according to:

$$RelV_{Ni}^{Pi} = V_{Ni}^{Pi} / \left(\sum_{i=1}^{n} \rho_{Ni}^{Pi} / \sum_{i=1}^{n} [PN]^{Pi} \right). \quad (1)$$

The equivalent model-derived relative specific uptake rates were calculated, using daily-averaged values, as:

$$RelV_{Ni}^{Pi} = Juptake_{Ni}^{Pi} / [PN]^{Pi} / \left(\sum_{i=1}^{n} Juptake_{Ni}^{Pi} / \sum_{i=1}^{n} [PN]^{Pi} \right). \quad (2)$$

Total and size-fractionated f-ratios were then calculated according to the formulation of Eppley and Peterson (1979):

$$f^{Pi} = V_{NO_3}^{Pi} / \left(V_{NH_4}^{Pi} + V_{NO_3}^{Pi} \right). \quad (3)$$

2.2. Plankton community composition

Plankton cells were identified and counted in preserved samples (1% paraformaldehyde) using light microscopy (Garrison et al., 2005). Smaller cells (<5 μm) were classified as autotrophic or heterotrophic flagellates based on the presence or absence of a chloroplast; picocyanobacterial cells were not counted. At least 270 smaller cells and 730 larger cells were counted each day by microscopy, yielding a minimum counting accuracy of 50% at the 95% confidence level for the species that became most abundant throughout the experiment. Larger cells were identified to the species level, except for ciliates, which were classified as *Strombidinium* sp., Oligotrichous, Tintinnid or aloricate (Hasle and Syvertsen, 1997; Steidinger and Tangen, 1997; Throndsen, 1997). Biovolumes were estimated using cellular geometrical shapes and average cellular dimensions (Olenina et al., 2006), and biovolume was then converted to carbon using the relationships of Menden-Deuer and Lessard (2000).

Growth rates of the plankton species or groups that were most abundant at the start or end of the experiment were estimated using an exponential growth model where net specific growth rate (μ, day^{-1}) equals the slope of the linear regression of the natural logarithm of cell abundance with time (Wood et al., 2005). Differences between mesocosms in the net growth rates and initial summed abundance of the main small or large phytoplankton species or groups were determined by analysis of covariance (ANCOVA) and *post hoc* Tukey's honest significant difference (HSD) test.