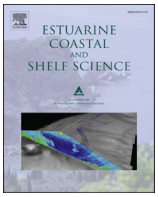
Estuarine, Coastal and Shelf Science 145 (2014) 80–95

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

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



Influence of microscale turbulence on the phytoplankton of a temperate coastal embayment, Western Australia

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ARTICLE INFO

Article history:
Received 26 March 2014
Accepted 23 April 2014
Available online 2 May 2014

Keywords:
turbulence
dinoflagellate
cell chain diatoms
nitrogen limitation
Batchelor scale
Kolmogorov scale

ABSTRACT

We investigated the influence of microscale turbulence on the large phytoplankton of a coastal embayment in south-western Australia. Microstructure, physical and fluorometric depth-profiling field measurements and water sampling for nutrient, chlorophyll-a analyses and counting of the large size fraction of phytoplankton (microphytoplankton) were conducted in late-winter and late-spring of 2012. In both seasons we observed dominance of diatoms, low numbers of dinoflagellates, low nutrient concentrations, nitrogen limitation, clear waters and high turbulence intensities. In late-winter, total nitrogen, chlorophyll-a and diatom cell concentrations were higher than in late-spring, but dinoflagellates abundance did not change substantially. This indicated that the chain-forming diatom life-forms that dominated (*Leptocylindrus*, *Chaetoceros* and *Skeletonema*) were able to utilize the increased pulses of nitrogen in late-winter. The prevailing turbulence intensities observed, associated with the wind speed, were such that the Batchelor scale was smaller than the length of the diatom chains (100–300 μm), implying that these diatoms could experience microscale nutrient gradients. By contrast, the Kolmogorov velocity scales overwhelmed the motility abilities of the dinoflagellates observed, which in turn gain only little benefit from self propulsion at high turbulence. It is suggested that, nutrient storage allows diatoms surviving calm periods of low nutrient availability and formation of siliceous cell chains provide diatoms an advantage in accessing nutrients in turbulent coastal ecosystems.

1. Introduction

The availability of nutrients and light, physical properties of the water and the dynamics of the small scale fluid motion influence phytoplankton communities (Reynolds, 2006). In the seminal work “the paradox of the plankton”, Hutchinson (1961) posed the question of how is it possible for several species of phytoplankton to coexist in fairly isotropic aquatic environments? It is now accepted that co-occurring phytoplankton species show adaptations to specific ecological niches that result from environmental heterogeneity, differential demand for limiting resources and complex ecological interactions (Litchman et al., 2010; Naselli-Flores and Rossetti, 2010). Substantial evidence demonstrates that the microenvironment experienced by phytoplankton and other microorganisms is far from homogeneous (Stocker, 2012). Recently, there has been increasing interest in linking the adaptations, or functional traits, of phytoplankton life-forms to their habitat preferences (Litchman et al., 2010). Understanding these links is essential for modelling and prediction of the phytoplankton community, occurrence of blooms and trophic state of ecosystems (Smayda and Reynolds, 2003; Reynolds, 2012; Trolle et al., 2012; Edwards et al., 2013).

Margalef (1978) showed that, among the large phytoplankton, diatoms dominate in the north-west coast of Spain during spring, when the water column was turbulent, not stratified and nutrient concentrations were relatively high, whereas dinoflagellates dominated over summer when the water column was weakly stratified and nutrient concentrations in the surface layer had been lowered by the diatom growth in spring. This seasonal pattern has also been observed in several other coastal regions, for example the western English Channel, the North Sea, Georges Bank off the Massachusetts coast (Smayda and Reynolds, 2001; Simpson and Sharples, 2012), the fjord coastline of Norway and other European seas and, more commonly, in upwelling systems (Smayda and Trainer, 2010). Furthermore, diatoms generally thrive in turbulent coastal environments where strong tidal and wind mixing prevail (Reynolds, 2006).

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http://dx.doi.org/10.1016/j.ecss.2014.04.018
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In the surface layer of lakes and the ocean, turbulence intensity, ε, measured as the rate of dissipation of turbulent kinetic energy (TKE), varies in the range 10^{-9}–10^{-4} m^2 s^{-3} due to wind stress stirring (Imberger, 1985; Imberger and Patterson, 1990). Phytoplankton cell size typically varies between less than 2×10^{-6} m (= 2 μm) to around 2×10^{-4} m (= 200 μm), although some species are known to grow, up to millimetres, by forming chains, filaments, coenobia and colonies (Reynolds, 2006). By comparison, the scale of the smallest velocity fluctuations, the Kolmogorov length microscale $L_K = (\nu^3\ \varepsilon^{-1})^{1/4}$, where ν is the kinematic viscosity of the water, ranges from 3.2×10^{-4} m to 5.6×10^{-3} m for the above range of TKE dissipation. Nutrient concentration gradients occur down to the Batchelor length microscale, $L_B = (\nu\ k_D^2\ \varepsilon^{-1})^{1/4}$, where k_D is the diffusivity coefficient of the molecule considered (Taylor and Stocker, 2012). For bio-available dissolved inorganic nitrogen (DIN) and the above range of TKE dissipation, L_B ranges from 1.4×10^{-5} m to 2.5×10^{-4} m. This implies that phytoplankton life-forms that grow more than L_B can experience these microscale nutrient gradients and access microscale nutrient maxima associated with turbulent microenvironment resources heterogeneity (Capblancq and Catalan, 1994; Peters and Marrasé, 2000). On the other hand, phytoplankton life-forms able to *swim*, propelled by flagella, at swimming velocity (V_m) greater than the Kolmogorov velocity microscale, $V_K = (\nu\ \varepsilon)^{1/4}$, can cross the nutrient gradients and also access microscale nutrient maxima (Guasto et al., 2012). For the above range of TKE dissipations, V_K ranges from 1.8×10^{-4} to 3.2×10^{-3} m s^{-1}. This may be compared to V_m of 10^{-5}–10^{-3} m s^{-1} for marine dinoflagellates (Reynolds, 2006; Smayda, 2010).

The success of diatoms in coastal environments has been related to their functional traits, including: 1. higher growth rates than other large phytoplankton taxa, i.e. dinoflagellates, especially when nutrient pulses occur in nutrient limited environments (Smayda and Trainer, 2010); 2. relative large size and siliceous armour that protect them from grazers (Hallegraeff et al., 2010) and increases stiffness (Young et al., 2012); 3. rapid nutrient uptake under turbulent conditions and the ability to store nutrients in vacuoles (Tozzi et al., 2004; Reynolds, 2006); and 4. photo adaptation capability that allows them to tolerate high and low light intensities corresponding to different depths of the mixed layer (Estrada and Berdalet, 1997; Simpson and Sharples, 2012). Collectively, these attributes give diatoms a general advantage in a turbulent, fluctuating light intensity, low nutrient environments subject to nutrients pulses, such as the turbulent surface layer of some oligotrophic coastal seas. Long celled diatoms have higher surface-to-volume ratios than spherical life-forms (Litchman et al., 2010) and often form chains that, due to the fluid small-scale shear, rotate describing Jeffery orbits and affect nutrient transport (Guasto et al., 2012). These chains, presumably, allow diatoms to access microscale peak nutrient concentrations occurring under strong turbulent conditions (Pahlow et al., 1997; Musielak et al., 2009). In this contribution we present values of the turbulent Batchelor length scale, estimated from measurements taken in the coastal embayment of Cockburn Sound, south-western Australia, to validate the hypothesis that chain-forming diatoms are advantaged relative to dinoflagellates when their length exceeds the Batchelor length scale and nutrient gradients occur.

The manuscript is organized as follows. First, we present the characteristics of the microphytoplankton taxa commonly found in the study site, followed by a description of physical, chemical and phytoplankton observations from two fieldwork campaigns. The occurrence of phytoplankton life-forms is then related to the combined influence of nutrient availability and the microscales associated with turbulence. Finally, we briefly discuss the implications at the broader ecosystem scale and for coupled hydrodynamic-ecological models.

2. Materials and methods

2.1. Study site

2.1.1. Description

Cockburn Sound (32°12′S, 115°43′E) is a semi-enclosed embayment located on the south-western Australian coast, 20 km south of Perth (Fig. 1). The Western Australian (WA) coast is characterized by low nutrient concentrations, low phytoplankton biomass (oligotrophic) and lack of large-scale upwelling due to the atypical pole-ward Leeuwin current (Pearce et al., 2006). Alongshore coastal currents, driven by the prevailing southerly winds in the area, dominate year-round, with highest velocities in summer; in winter, more variable conditions are observed leading also to a more energetic onshore-offshore exchange (Pearce et al., 2006; Zaker et al., 2007). Chains of islands and submerged limestone reefs, aligned parallel to the shoreline between 3 and 10 km from the coast, reflect and dampen the approaching surface waves and the Indian ocean swell (Zaker et al., 2007). The tidal regime is mainly diurnal and has a small range (<1 m). The weak river flow from the Swan River discharges at Fremantle and occasionally enters from the north into Cockburn Sound (Robson et al., 2008). Treated effluents from the local wastewater treatment plants, the Kwinana Industrial area and the Perth Seawater Desalination Plant, discharge through coastal outlets, near the Sepia Depression and directly into Cockburn Sound at the locations indicated in Fig. 1. The wastewater effluent forms a buoyant plume, relatively rich in nutrients (Lord et al., 2000), whereas the desalination effluent forms a negatively buoyant hyper-saline underflow (Marti et al., 2011). Other industrial effluents are also discharged directly into Cockburn Sound, but their discharge has been considerably lessened in recent decades due to environmental legislation (DEPWA et al., 1996). In general, the shallow waters of the Perth coastal margin are well mixed, clear and have low levels of nutrients and phytoplankton biomass (Johannes et al., 1994; DEPWA et al., 1996; Thompson and Waite, 2003; Pearce et al., 2006); with ratios of nitrogen to phosphorous (N:P) and nitrogen to silicon (N:Si) below the Redfield-ratio, indicating N limitation for phytoplankton growth year-round (Lord et al., 2000; Lourey et al., 2006; Thompson et al., 2011). Seasonal variations of nutrient and phytoplankton concentration have been reported for the study area, with higher levels occurring in autumn and winter when sources of N and other nutrients including exchange with offshore waters, groundwater discharges, superficial runoff, and nutrient release from the sediments are all most active (Johannes et al., 1994; Loveless et al., 2008; Greenwood, 2010; Machado and Imberger, 2014).

2.1.2. Phytoplankton

Routine historical monitoring by (DEPWA et al., 1996) showed that diatoms (Bacillariophyceae) were the most abundant phytoplankton group in the Perth coastal margin, including Cockburn Sound. Also frequently present were dinoflagellates (Dinophyceae) and Prasinophyceae. Further, Cryptomonadales (Cryptophyceae) were regularly observed, but rarely in large abundance, as they tend to be brackish-freshwater species. Silicoflagellates (Dictyochophyceae) dominated the winter assemblage in Cockburn Sound during the early 1990s; this observation was attributed to the high levels of dissolved heavy metals present at that time. Cyanobacteria, in particular *Trichodesmium* (=*Oscillatoria*) have been reported to be occasionally abundant, mainly during summer, both in the near shore and offshore regions (DEPWA et al., 1996; Thompson and Waite, 2003). In addition to being the most abundant group, diatoms were found to be more diverse, with around 200 taxa listed, including several chain-forming species, in comparison with around 45 taxa of dinoflagellates (DEPWA et al., 1996). Thompson and Waite (2003) reported diatoms dominance in the area, 43–61% by cell