Journal of Marine Systems xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Journal of Marine Systems

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

Mesoscale variability in intact and ghost colonies of *Phaeocystis antarctica* in the Ross Sea: Distribution and abundance

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ARTICLE INFO

Article history:
Received 31 December 2015
Received in revised form 8 April 2016
Accepted 30 May 2016
Available online xxxx

Keywords:
Phaeocystis
mesoscale
Ross Sea, Antarctica
ghost colonies
carbon

ABSTRACT

Phaeocystis, a genus with a cosmopolitan distribution and a polymorphic life cycle, was observed during summer in the Ross Sea, Antarctica, where large blooms of this haptophyte regularly occur. The mesoscale vertical and horizontal distributions of colonies of *Phaeocystis antarctica* were assessed using a towed Video Plankton Recorder (VPR). The mean size of colonies was 1.20 mm, and mean abundances within the three VPR surveys were 4.86, 1.96, and 11.5 mL^{-1}. In addition to the typical spherical, transparent colonies, the VPR quantified an optically dissimilar form of colony that had a distinctive translucent appearance. It also measured the abundance of collapsed colonies, similar to those observed previously from cultures and mesocosms, which we called "ghost colonies". The translucent colonial form had a different distribution than the more common colonial form, and at times was more abundant. Relative to intact colonies, the ghost colonies occurred less frequently, with mean abundances in the three surveys being 0.01, 0.08, and 0.0004 mL^{-1}. Ghost colonies generally were found below the euphotic zone, where they often were in greater abundance than intact colonies. However, the relationship of ghost colonies to intact *P. antarctica* colonies was not direct or consistent, suggesting that the formation of ghost colonies from living colonies and their appearance within the water column were not tightly coupled. Given their relative scarcity and low carbon content, it is unlikely that ghost colonies contribute substantially to vertical flux; however, it is possible that we did not sample periods of major flux events, and as a result minimized the importance of ghost colonies to vertical flux. They do, however, represent a poorly documented feature of polar haptophyte life cycles.

1. Introduction

The genus *Phaeocystis* is found throughout the world's oceans, occurring in the Arctic, Antarctic, upwelling areas, the North Atlantic, and tropical and temperate coastal systems (Lancelot et al., 1998; Schoemann et al., 2005). Some of the species have polymorphic life cycles that include flagellated, solitary cells and spherical colonies, which are comprised of non-flagellated cells embedded in an organic envelope. The colonies are filled with seawater internally, are normally spherical during active growth, and range in diameter from 50 μm to 3 cm. They can form extremely dense blooms in a variety of regions, and are considered to be harmful algal blooms based on their indirect, negative effects to local systems (Schoemann et al., 2005; Blauw et al., 2010; Smith et al., 2014b). The mucopolysaccharide envelope around the colonies is relatively tough (Hamm et al., 1999), and in many regions it can represent a substantial contribution to the total particulate organic carbon (POC) pool.

P. antarctica is a dominant species in the Ross Sea and other Southern Ocean regions (Smith et al., 2014a). In the Ross Sea it typically blooms widely in austral spring and attains maximal biomass in mid- to late December, whereupon its biomass is rapidly reduced in the euphotic zone within days or weeks (Smith et al., 2011). However, significant *P. antarctica* biomass can be found throughout the entire growing season at certain locations (Smith and Jones, 2015). Its appearance in spring is thought to result from its ability to photosynthesize and grow at relatively low photon flux densities (Kropuenske et al., 2009), which are characteristic of spring in the Ross Sea due to relatively deep mixed layer depths and ice cover, both of which restrict irradiance availability. After *Phaeocystis* reaches its biomass maximum, it is thought to sink as intact colonies and/or aggregates (Asper and Smith,

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http://dx.doi.org/10.1016/j.jmarsys.2016.05.007
0924-7963/

1999, 2003), but also to liberate cells from the envelope into the water column where they develop flagella. Single cells are small (~ 5 μm; Mathot et al., 2000) and can be preyed upon by microheterotrophs such as dinoflagellates or ciliates. It has been suggested that events of *P. antarctica* sinking in spring are important fluxes to depth and to the sediments (DiTullio et al., 2000), although such events have never been detected by time-series sediment traps. In contrast, Riegstad and Wassmann (2007) proposed that most of the organic matter generated by *Phaeocystis* is remineralized within the water column, especially when contrasted to diatomaceous POC, and that little *Phaeocystis*-derived organic matter was sequestered for long time periods. Verity et al. (1988) also observed forms of colonies that were largely devoid of cells, and called these "ghost colonies". They hypothesized that ghost colonies formed when the individual cells of sinking, senescent (nitrogen limited) colonies were liberated from the mucous envelope, and that the mucoid material sank to depth. Ghost colonies, however, are exceedingly difficult to observe using discrete water samples, given their unknown vertical distribution, translucent appearance, potentially rapid sinking rates and fragile nature. Therefore, their occurrence, distribution and dynamics have never been adequately described.

In recent years the Video Plankton Recorder (VPR) has been developed to observe and quantify the distribution of plankton in the ocean's surface layer (Davis et al., 1996, 2005). Specific forms can be analyzed by pattern recognition algorithms, which automatically identify selected taxa of interest. The advantage of the VPR is that it can sample the upper layer of the ocean at small scales (both vertically and horizontally), allowing the descriptions of plankton distributions within mesoscale and sub-mesoscale features (e.g., Davis and McGillicuddy, 2006; McGillicuddy et al., 2007), as well as jets, eddies and ephemeral plankton patches (Davis et al., 1996).

We deployed a VPR within the ice-free waters of the Ross Sea during austral summer 2012 to assess the mesoscale distributions of plankton and their relationship to iron inputs and water mass structure (McGillicuddy et al., 2015). Summer is a period where *P. antarctica* contributions to biomass are normally decreasing, and diatom contributions increasing (Smith et al., 2014a), although substantial spatial variability in this pattern has been observed (Arrigo et al., 1999; Smith et al., 2013). The summer growth of diatoms likely results from their ability to grow at lower iron concentrations under high light, as well as elevated carbon:chlorophyll ratios (Kaufman et al., 2014). We hypothesized that *P. antarctica* distributions were correlated with iron fluxes and irradiance levels, and hence would be influenced by mesoscale features throughout the continental shelf and contribute to the substantial spatial variability. As part of our observations, we detected and quantified the distribution and abundance of *P. antarctica* ghost colonies; this report describes the vertical and horizontal distribution of these colonies, their relationship to intact colonies and potential significance in the Ross Sea.

2. Materials and methods

We conducted VPR tows and sampled the water column as part of the PRISM (Processes Regulating Iron Supply at the Mesoscale) project. Sampling occurred from January 9 through February 6, 2012 from the *R.V.I.B. N.B. Palmer* Cruise NBP12–01. Water samples were collected using a rosette system with 24 10-L Niskin bottles fitted with Teflon-coated external closures. A SeaBird 911+ CTD system, WetLabs fluorometer, BioSpherical quantum sensor, and SeaTech transmissometer were also mounted on the rosette. Samples were collected for discrete chlorophyll *a* analysis (JGOFS, 1996) and particulate organic carbon and nitrogen (Gardner et al., 2000).

A Video Plankton Recorder (Mark II) was towed behind the ship at 10 knots to assess the plankton composition as well as the small-scale hydrographic structure. The VPR was fitted with sensors to measure depth, temperature, salinity, chlorophyll fluorescence and optical backscattering, as well as a digital video camera and strobe, which collected 30 image frames per second. Resolution of the camera system was ca. 10 μm, allowing plankton of ca. 50 μm and larger to be visualized. Individual regions of interest (ROIs) were extracted from each image frame by firmware that detects objects within the field of view, and the ROIs were stored on a computer. Density was calculated from standard

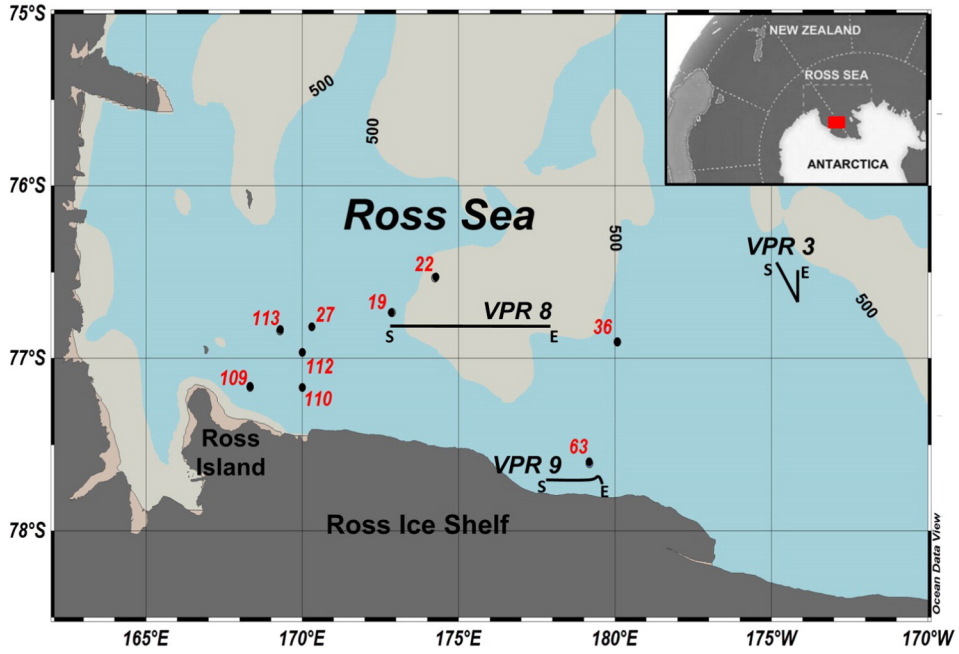

Fig. 1. Map of the Video Plankton Recorder surveys reported in this analysis. Also included are locations of stations used to calibrate the fluorescence and optical backscattering data. The 500 m depth contour is shown, and the red square in the inset is the PRISM sample area. S and E indicate the locations of the start and end of the VPR surveys. Note that only a portion of the VPR8 survey is reported on here.

Please cite this article as: Smith, W.O., et al., Mesoscale variability in intact and ghost colonies of *Phaeocystis antarctica* in the Ross Sea: Distribution and abundance, J. Mar. Syst. (2016), http://dx.doi.org/10.1016/j.jmarsys.2016.05.007