



Phytoplankton community structure is influenced by seabird guano enrichment in the Southern Ocean



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ABSTRACT

Phytoplankton biomass, productivity and community structure are strongly influenced by differences in nutrient concentrations among oceanographic water masses. Changes in community composition, particularly in the distribution of cell sizes, can result in dramatic changes in the energetics of pelagic food webs and ecosystem function in terms of biogeochemical cycling and carbon sequestration. Here we examine responses of natural phytoplankton communities from four major water masses in the Southern Ocean to enrichment from seabird guano, a concentrated source of bioactive metals (Mn, Fe, Co, Ni, Cu, Zn) and macronutrients (N, P), in a series of incubation experiments. Phytoplankton communities from sub-tropical water, modified sub-tropical water from the Snares Island wake, sub-Antarctic water and Antarctic water from the Ross Sea, each showed dramatic changes in community structure following additions of seabird guano. We observed particularly high growth of prymnesiophytes in response to the guano-derived nutrients within sub-Antarctic and sub-tropical frontal zones, resulting in communities dominated by larger cell sizes than in control incubations. Community changes within treatments enriched with guano were distinct, and in most cases more extensive, than those observed for treatments with additions of macronutrients (N, P) or iron (Fe) alone. These results provide the first empirical evidence that seabird guano enrichment can drive significant changes in the structure and composition of natural phytoplankton communities. Our findings have important implications for understanding the consequences of accumulation of bioactive metals and macronutrients within food webs and the role of seabirds as nutrient vectors within the Southern Ocean ecosystem.

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1. Introduction

Pelagic food webs vary in composition and complexity from relatively simple ‘wasp-waisted’ systems where most of the productivity is channeled through a few species to complex networks with multiple recycling loops (Legendre and Rassoulzadegan, 1996). In these systems nutrients and organic matter egested and excreted from primary and secondary consumers are recycled within the microbial loop resulting in bioaccumulation within the pelagic food web and high concentrations of limiting nutrients delivered to the top trophic levels (e.g. Roman and McCarthy, 2010). One such pathway is the bioaccumulation of limiting nutrients in

the food webs supporting prey species of seabirds, egested in high concentration as guano. For example the concentration of limiting bioactive metals (e.g. Fe, Co, Zn) in seabird guano can be magnified by millions of times compared to background concentrations in the particulate pool of the Southern Ocean (Wing et al., 2014, 2016). As a result many apex species such as marine mammals, seabirds and large fish can act as important nutrient vectors in ocean ecosystems (Nicol et al., 2010; Ratnarajah et al., 2016) by receiving and redistributing essential nutrients that stimulate productivity of phytoplankton at the base of the food web (Shatova et al., 2016). Consequentially nutrient accumulation within, and direct enrichment from seabird guano may also have an influence on the composition of the underlying phytoplankton community near coastal regions where seabirds aggregate to breed.

Phytoplankton distributions in the Southern Ocean are strikingly heterogeneous (Ehnert and McRoy, 2007; Iida and Odate,

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2014). Spatial discrepancies in phytoplankton biomass and productivity are strongly influenced by differences in nutrient concentrations among oceanographic zones. For example, in terms of proxies for biomass, approximately 80% of the Southern Ocean's total area has Chl *a* concentrations less than $0.5 \mu\text{g L}^{-1}$ (Fukuchi, 1980; Moore and Abbott, 2000). Relatively high Chl *a* concentrations exceeding $1 \mu\text{g L}^{-1}$ have only been recorded near islands (Blain et al., 2007), major oceanographic fronts (Moore and Abbott, 2000) and in the vicinity of retreating sea ice in Antarctica ($2\text{--}10 \mu\text{g L}^{-1}$, Sedwick et al. (2002)). Elevated Chl *a* in these regions can be largely explained by the enhanced availability of iron (Boyd et al., 2000). Thus variability in standing stock biomass is largely confined to coastal margins and islands.

Phytoplankton community composition and size structure are also strongly influenced by availability of limiting nutrients in the mixed layer of the ocean at coastal margins (Verity and Smetacek, 1996; Marañón, 2015). In the case of phytoplankton with cell diameter smaller than $5 \mu\text{m}$, population growth rates of the primary grazers, mostly unicellular protists including ciliates, are relatively fast, allowing populations of grazers to control spread of bloom events. Nevertheless in low nutrient environments small-celled species remain more successful due to their larger surface-volume ratio and corresponding efficiency of nutrient uptake (Chisholm et al., 1992). Consequently, communities made up of small-celled species generally support high nutrient retention in the euphotic zone (Legendre and Rassoulzadegan, 1996). A change to nutrient-replete conditions can result in increases in abundance of large-celled species within a mixed assemblage (Marañón, 2009). This shift occurs because the lower surface to volume ratio of large phytoplankton species is supported under high nutrient conditions and population growth rates are typically faster than population responses of their primary grazers, euphausiids and copepods (Marañón, 2009). Phytoplankton communities dominated by large-celled species or chain-forming diatoms can form heavy aggregates with other organic materials to produce marine snow, resulting in high sinking velocities and an efficient mechanism of organic matter and nutrient export out of the upper mixed layer into the deep ocean. The resulting enhanced export of organic material has major implications for CO_2 uptake and subsequent carbon sequestration in the ocean (Tilman et al., 1982; Tortell et al., 2008). Thus, functional ecology of phytoplankton is closely linked to size, mediated by nutrient availability, with direct implications for dynamics of the oceanic food web and biogeochemical cycling.

Autotrophic biomass in some aquatic environments has been observed to increase in response to local nutrient enrichment from seabird guano (Bosman et al., 1986; Wootton, 1991). For example investigators have found significant effects of seabird guano on the structure of macroalgal and epiphytic algae communities within intertidal and estuarine systems (Bosman et al., 1986; Powell et al., 1991; Wootton, 1991; Gagnon et al., 2013). Kolb et al. (2010) demonstrated that density and N and P content of epiphytic algae as well as invertebrate abundance and size increased in the coastal zone around islands supporting seabird breeding colonies. Further Izaguirre et al. (2003) demonstrated that phytoplankton assemblages in guano-enriched Antarctic lakes had significantly higher densities of phytoplankton, higher fluctuations in biomass and more diverse phytoplankton communities dominated by chlorophytes compared to oligotrophic lakes which had consistently low phytoplankton density and dominance of nanoflagellates and chrysophytes.

Similarly, nutrient enrichment from excretion by fish has been demonstrated to significantly affect phytoplankton community composition towards the dominance of species with high P requirements, such as green algae, blue-green algae and dinoflagellates (Vanni and Layne, 1997). Further, an experimental

study by Smith et al. (2013) demonstrated an increase in biomass of three common Southern Ocean phytoplankton species to the nutrients derived from whale feces. Each of these studies highlights the potential for egested and excreted material from the higher trophic levels in a food web to provide essential nutrients for phytoplankton growth. They raise the important question: How do recycled nutrients from seabirds influence community composition and structure of phytoplankton in the Southern Ocean?

Because of the central role that phytoplankton community composition and structure play in ecosystem functioning, we investigated how phytoplankton communities respond to enrichment by seabird guano in four distinct water masses in the Southern Ocean: offshore sub-Antarctic water (SA), island wake water of the sub-Antarctic Snares Islands (IW), open waters of the sub-tropical frontal zone (STFZ), and Antarctic water from the Ross Sea (RS), each with different baseline nutrient conditions. Using an experimental approach samples of the natural phytoplankton community in each of the water masses were enriched with seabird guano and the phytoplankton community responses were measured in terms of changes in composition and structure. Further, in sub-tropical and sub-Antarctic water masses the responses of phytoplankton community structure to nutrient enrichment by seabird guano were compared to changes in the community for samples enriched with macronutrients (N, P) and inorganic sources of iron (Fe) alone. The results have important implications for understanding how high concentrations of bioactive metals and macronutrients accumulated in the food webs supporting seabirds potentially affect the structure of phytoplankton communities across the Southern Ocean.

2. Materials and methods

The current manuscript follows up on work published in Shatova et al. (2016) that presented the results of the same incubation experiments but in relation to effects of guano on phytoplankton biomass and associated changes in macronutrient concentrations. The primary aim of the current manuscript was to investigate the complex interactions occurring in phytoplankton communities following the additions of seabird guano, and to elucidate the potential impact on the associated marine food web. The thorough and detailed description of the methods engaged to conduct the incubation experiments, as well as biomass and macronutrient measurements are presented in Shatova et al. (2016). Here we present a brief description of major steps of the process. Similarly, throughout the manuscript we refer to the biomass and macronutrient data reported in Shatova et al. (2016) as it provides essential supporting evidence for the results presented in the current manuscript.

Guano-enrichment incubation experiments were performed with water collected in the open waters of the STFZ in February 2012 and February 2013 (experiments are further referred to as ST1 and ST2 correspondingly) and in the island wake waters of the Snares Islands (also located in the STFZ, and further referred to as IW), in the offshore sub-Antarctic waters east from the Otago Peninsula in April 2013 (SA2) and April 2014 (SA1) and in the Ross Sea in October 2013 (RS). Locations of incubation experiments are schematically presented on Fig. 1. Water samples were collected into 10 L collapsible LDPE containers using trace metal clean techniques described below. After collection samples were transferred to an incubator and kept under a 14:10 h light:dark cycle and at controlled temperatures close to *in situ*. The light was provided by full-spectrum Aquarelle lamps (Phillips TLD36W/89; the spectrum data may be viewed at <http://www.mv.helsinki.fi/aphalo/photobio/pdf/spectra/TLD36W89.pdf>).

Each of the water masses included in the experiments had

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