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Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend

MARK A. MOLINE*, HERVÉ CLAUSTRE†, THOMAS K. FRAZER‡, OSCAR SCHOFIELD§ and MARIA VERNET¶

**Department of Biological Sciences, California Polytechnic State University, San Luis Obispo, CA 93407, USA, †Observatoire Océanologique de Villefranche (CNRS-INSU), Laboratoire de Physique et Chimie Marines 06238, Villefranche-sur-mer, France, ‡Department of Fisheries and Aquatic Sciences, University of Florida, Gainesville, FL 32653, USA, §Coastal Ocean Observation Laboratory, Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, NJ 08903, USA, ¶Marine Research Division, Scripps Institute of Oceanography, University of California, San Diego, La Jolla, CA 92093, USA*

Abstract

In the nearshore coastal waters along the Antarctic Peninsula, a recurrent shift in phytoplankton community structure, from diatoms to cryptophytes, has been documented. The shift was observed in consecutive years (1991–1996) during the austral summer and was correlated in time and space with glacial melt-water runoff and reduced surface water salinities. Elevated temperatures along the Peninsula will increase the extent of coastal melt-water zones and the seasonal prevalence of cryptophytes. This is significant because a change from diatoms to cryptophytes represents a marked shift in the size distribution of the phytoplankton community, which will, in turn, impact the zooplankton assemblage. Cryptophytes, because of their small size, are not grazed efficiently by Antarctic krill, a keystone species in the food web. An increase in the abundance and relative proportion of cryptophytes in coastal waters along the Peninsula will likely cause a shift in the spatial distribution of krill and may allow also for the rapid asexual proliferation of carbon poor gelatinous zooplankton, salps in particular. This scenario may account for the reported increase in the frequency of occurrence and abundance of large swarms of salps within the region. Salps are not a preferred food source for organisms that occupy higher trophic levels in the food web, specifically penguins and seals, and thus negative feedbacks to the ecology of these consumers can be anticipated as a consequence of shifts in phytoplankton community composition.

Keywords: Antarctica, climate, cryptophytes, krill, phytoplankton, salps

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Introduction

Mean air temperatures along the Antarctic Peninsula have increased significantly (2–3 °C) over the past 50 years (King, 1994; Smith, 1994; Stark, 1994). This regional change in air temperature has long-term consequences for sea ice and ice shelf dynamics (Vaughan & Doake, 1996; Smith & Stammerjohn, 2001), as well as glacial melting (Ashley *et al*., 1994; Dierssen *et al*., 2002), and is likely to impact the structure and function of coastal food webs. For example, ice edge dynamics strongly influence overall phytoplankton productivity (Prézelin *et al*., 2000), which, in turn, fuels higher trophic levels in a relatively short food web where Antarctic Krill, *Euphausia superba*, is a keystone species. Most higher-level consumers depend either, directly or indirectly on this pelagic species as a food source (Laws, 1985).

Although krill are often abundant along the Antarctic Peninsula, their distributional patterns are highly variable in space and time (see Ross *et al*., 1996). *Salpa thompsoni*, another important plankton grazer in the vicinity of the Antarctic Peninsula (Nishikawa *et al*., 1995; Loeb *et al*., 1997), exhibits similar broad-scale spatial and temporal variation in abundance and distribution (Ross *et al*., 1996). Both species (i.e. *E. superba* and *S. thompsonii*) are capable of forming large aggregations, although they seldom co-occur in space (Nishikawa *et al*., 1995; Loeb *et al*., 1997; Kawaguchi

Correspondence: Mark A. Moline, fax +1 805 756 1419, e-mail: mmoline@calpoly.edu

et al., 1998; Ross *et al.*, 1998; Hosie *et al.*, 2000). Marked decreases in krill abundance have occurred recently in the Antarctic Peninsula region and it has been suggested that the decline is the result of poor recruitment associated with alterations in winter sea-ice development (Loeb *et al.*, 1997). This observed change could be due to the decrease in the frequency of winters with extensive sea-ice development associated with the 50-year atmospheric warming trend. Alternatively, it has also been suggested that the changes in ice melting may have altered phytoplankton community composition and biomass, and may underlie the changing spatial and temporal patterns of krill and salp abundance (Hosie *et al.*, 2000, compare with Kopczynska, 1992).

As part of the Long-Term Ecological Research Program (Smith *et al.*, 1995), the waters near Palmer Station, Antarctica were sampled from 1991 to 1996, in part, to describe the temporal variability in the taxonomic composition of phytoplankton communities. Results are used here to comment on the shifts in the food web being observed in the coastal waters of the Antarctic Peninsula.

Methods

Discrete water samples were collected during austral spring and summer (1991–1996) at a site offshore of Palmer Station (64°46.45′S, 64°03.27′W) and also during a series of shipboard transects along the Antarctic Peninsula at established stations within the LTER sampling grid (Smith *et al.*, 1995, see also http://www.icess.ucsb.edu/lter/overview/overview.html). Discrete samples were collected with Niskin bottles and were analyzed for phytoplankton pigment concentrations. In-water temperature and salinity data were collected with a SBE-19 conductivity–temperature–depth sensor (Sea-Bird Electronics Inc., Bellevue, WA, USA). Daily air temperature and initiation of glacial melt-water (as measured by absence of snow cover) were made at Palmer Station during the study period as part of a long-term database collected by the US National Science Foundation. Phytoplankton pigments were determined using high-performance liquid chromatography (HPLC) on whole-water samples (Moline & Prézelin, 1996). Pigment data were used to estimate phytoplankton standing crop (chlorophyll *a*) and as chemotaxonomic markers to differentiate between algal groups using ChemTax (Mackey *et al.*, 1996, 1998). From the class-specific accessory pigments and total chlorophyll *a*, the percent contribution of each taxonomic group to the overall biomass was calculated (Everitt *et al.*, 1990; Moline & Prézelin, 1996). Pigment-based estimates were verified microscopically. The dominant phytoplankton taxonomic groups highlighted in this paper were cryptophytes ($<10\,\mu$m single-celled flagellated algae), diatoms (15–270 μm single-celled and chain-forming algae) and prymneseophytes (single-celled algae that often form colonies $>200\,\mu$m). Since phytoplankton abundances were not normally distributed, a randomization ANOVA technique (100 000 randomizations, cf. Manly, 1991) was used to verify significance levels obtained from initial single classification ANOVA approach used to evaluate significant differences between phytoplankton groupings. Least square means procedures were employed as follow-up pairwise tests when distinguishing between taxonomic groupings to add robustness to the statement that these groupings in fact occupied significantly different temperature and salinity environments.

A simple model was developed to quantify the partitioning of carbon through the Antarctic food web. Total autotrophic carbon production, measured from December to January of 1991–1994, served as the model's primary input (Table 1; Moline & Prézelin, 1996). This study also provided estimates of group-specific production rates, which was used to partition the total production into either cryptophytes or 'other phytoplankton' (the sum of diatoms and prymnesiophytes in this study). Production from cryptophytes varied annually, with one season producing up to half the total carbon. The relative fluxes from the primary carbon pool to krill and salps were dependent on the carbon in each phytoplankton assemblage and transfer efficiencies between phytoplankton and grazers. Transfer efficiencies of carbon used in the model were mean values from previous studies relating percent retention of algae by krill based on size (Table 1; McClatchie & Boyd, 1983; Meyer & El-Sayed, 1983; Boyd *et al.*, 1984; Quetin & Ross, 1985) and on feeding studies of *S. thompsoni* (Madin & Kremer, 1995), a principle tunicate in the Southern Ocean (Huntley *et al.*, 1989). Partitioning of carbon to grazers was also a function of a range of previously reported krill to salp carbon ratios (Table 1; Pakhomov *et al.*, 1994; Nishikawa *et al.*, 1995; Loeb *et al.*, 1997). Carbon from the grazers was directed either to higher trophic levels (Foxton, 1966; Gon & Heemstra, 1990; Huntley *et al.*, 1991), sedimentation or respiration (Huntley *et al.*, 1989, 1991).

Results and discussion

Despite high interannual variability in chlorophyll *a*, a consistent and repeated pattern in phytoplankton community composition and succession was observed. Diatoms-dominated spring phytoplankton populations each year. However, there was a consistent transition from diatoms to populations of cryptophytes every

Table 1 Model inputs used to calculate energy transfer throughout the Antarctic food web

Model inputs	Model values	Reference
Autotrophic carbon production ($\mathrm{g\,C\,m^{-2}}$)*	104.63 (1991–1992) 37.67 (1992–1993) 32.86 (1993–1994)	Moline & Prézelin (1996)
Cryptophyte carbon	19–53%	Moline & Prézelin (1996)
Other phytoplankton carbon	47–81%	Moline & Prézelin (1996)
Krill to salp carbon ratio	33.3, 0.0641	Loeb *et al.* (1997)
Krill to salp carbon ratio	5.65	Nishikawa *et al.* (1995)
Krill to salp carbon ratio	0.641	Pakhomov *et al.* (1994)
Carbon transfer efficiencies		
Cryptophytes to krill	10%	McClatchie & Boyd (1983), Boyd *et al.* (1984), Quetin & Ross (1985)
Cryptophytes to salps	60%	Madin & Kremer (1995)
Other phytoplankton to krill	60%	McClatchie & Boyd (1983), Meyer & El-Sayed (1983), Boyd *et al.* (1984), Quetin & Ross (1985)
Other phytoplankton to salps	60%	Madin & Kremer (1995)
Carbon to higher trophic levels from krill	32.5%	Huntley *et al.* (1991)
Carbon to higher trophic levels from salps	5%	Foxton (1966), Gon & Heemstra (1990)
Carbon to respiration from krill	34%	Huntley *et al.* (1991)
Carbon to respiration from salps	14.8%	Huntley *et al.* (1989)

Autotrophic carbon production was partitioned into a cryptophyte and ‘other’ phytoplankton pool based on measurements made from 1991 to 1994. The transfers of carbon from the primary producers to grazer pools were calculated based on grazing rates that were dependent on the size class of the algae. Carbon from primary grazers is transferred to higher trophic levels, respiration and other losses. The model incorporates both the effect of changing phytoplankton assemblage and various carbon ratios of krill to salp.

*Carbon production between December and January.

summer (Fig. 1a). The dominance of cryptophytes was coincident with the occurrence of low salinity water (Fig. 1a, b), which was associated with glacial melt-water input when air temperatures were above freezing (Fig. 1c). Cryptophyte-dominated algal biomass during melt-water events and their presence was confined to the relatively high temperature/low salinity water characteristic of the melt-water lens (Fig. 1b). While confined to surface waters, the melt-water plume often extended to depths as great as 25 m. In contrast, diatoms and prymnesiophytes dominated the phytoplankton communities in other physiochemical domains. Shipboard transects along the Antarctic Peninsula confirmed spatially the dominance of cryptophytes in low salinity nearshore waters over the broad study region (Fig. 2). The cryptophyte-dominated waters were a significant geographic feature ranging in size from 11 000 to 48 000 km^2 depending on the year and extended as far as a 100 km offshore. This dominance of cryptophytes within low salinity environments is consistent with observations from other coastal areas around the Antarctic continent (Kopczynska, 1992; McMinn & Hodgson, 1993; Kang & Lee, 1995; Arrigo *et al.*, 1998; Garibotti *et al.*, 2003) and in other ecosystems, showing physiological tolerance and even preference by cryptophytes to lower salinity waters (Prézelin & Bozcar, 1986; Lewitus & Caron, 1990; Lizotte & Priscu, 1992; Claustre *et al.*, 1997; Walsh *et al.*, 2001). The recurrent transition from diatoms to cryptophytes represents a fundamental decrease in the size class of the phytoplankton. Bloom-forming diatoms range in size from 15 to 270 μm (Kopczynska, 1992; Moline & Prézelin, 1996), while the Antarctic cryptophytes have been measured microscopically at 8 ± 2 μm (McMinn & Hodgson, 1993). This size decrease will impact the grazing efficiencies of different zooplankton species.

There has been a recent and significant decrease in krill abundance along the Antarctic Peninsula, which has been hypothesized to reflect poor recruitment associated with a decline in winter sea-ice development (Loeb *et al.*, 1997). The competing hypothesis is that spatial heterogeneity in the phytoplankton is the other major determinant for the patterns of krill and salp abundance (Kopczynska, 1992; Hosie *et al.*, 2000). Salps can efficiently graze food particles as small as 4 μm in size (Harbison & McAlister, 1979; Deibel, 1985; Harbison *et al.*, 1986; Kremer & Madin, 1992; Madin &

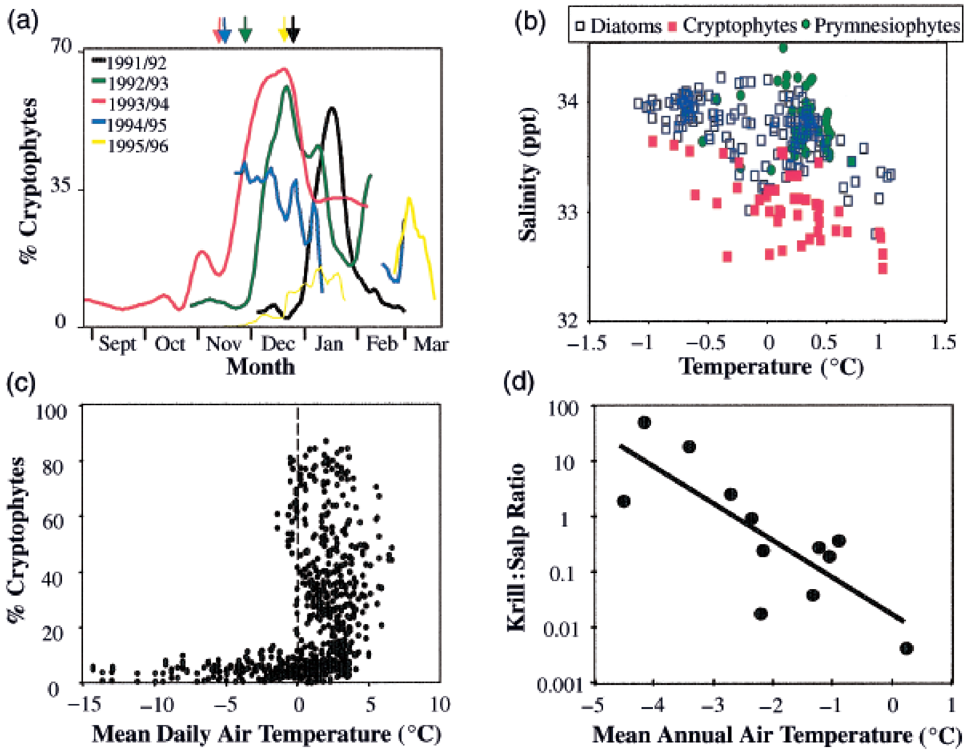

Fig. 1 (a) Seasonal changes in percent cryptophyte biomass during the spring and summer months off Palmer Station from 1991 to 1996. Arrows indicate the initiation of glacial melt-water input into the region during each year at Palmer Station. (b) Bivariate plot of temperature and salinity. Sample points indicate a >50% contribution to the total phytoplankton biomass by diatoms, cryptophytes and prymnesiophytes at Palmer Station from 1991 to 1994. When dominant, cryptophytes occupied significantly lower salinity water than either diatoms or prymnesiophytes, which were not significantly different from each other ($P < 0.001$; see Methods section for statistical approach). (c) Percent cryptophytes from (a) shown as a function of mean daily air temperature at Palmer Station for the five sampling periods ($n = 696$). (d) Relationship between mean annual air temperature (°C) measured at Palmer Station and the annual ratios of krill to salp abundance ($r^2 = 0.63$, $n = 12$). Paired krill and salp data from the Antarctic Peninsula region were taken for 12 years between 1980 and 1996 (see Table 1 in Loeb *et al.*, 1997).

Kremer, 1995), but adult krill cannot. The grazing efficiency of *E. superba* decreases significantly with particles <20 μm (Meyer & El-Sayed, 1983; Boyd *et al.*, 1984; Quetin & Ross, 1985; Weber & El-Sayed, 1985); therefore it is not surprising that grazing rates of krill on cryptophytes are negligible (Haberman *et al.*, 2003).

Salps are thought to be more efficient grazers than krill on limited phytoplankton food resources. Although environmental conditions that favor salp development are not well understood, low chlorophyll concentrations and small food particles do appear to foster salp blooms (Harbison *et al.*, 1986; Quetin *et al.*, 1996; Ross *et al.*, 1996 and references therein). Loeb *et al.* (1997) also suggests that salps are direct consumers of krill eggs and larvae (Huntley *et al.*, 1989; Nishikawa *et al.*, 1995), further intensifying the impact. However, segregated distribution patterns of salps and krill could alternatively indicate a low probability for the same food source (Kawaguchi *et al.*, 1998). In areas of high primary productivity and high phytoplankton standing crops, krill are often observed, but salps are generally not. Under these conditions, the filtering apparatus of salps can become irreversibly clogged with negative consequences for growth and survival (Nishikawa *et al.*, 1995; Quetin *et al.*, 1996; Perissinotto & Pakhomov, 1998a, b). Therefore, shifts from dense populations of large-celled diatoms to smaller less dense populations of cryptophytes are likely to favor the presence of salps over krill.

Increasing air temperatures documented along the Antarctic Peninsula will alter both ice shelf dynamics (Vaughan & Doake, 1996; Smith & Stammerjohn, 2001) and glacial melting (Ashley *et al.*, 1994; Dierssen *et al.*, 2002). If this warming trend continues, the proportion of cryptophyte biomass to total phytoplankton biomass would be expected to increase. This is ecologically significant and would negatively impact the coastal food webs in the Antarctic. A decrease in the phytoplankton size spectrum with warming would favor an increase in salps and would not favor krill (Fig.

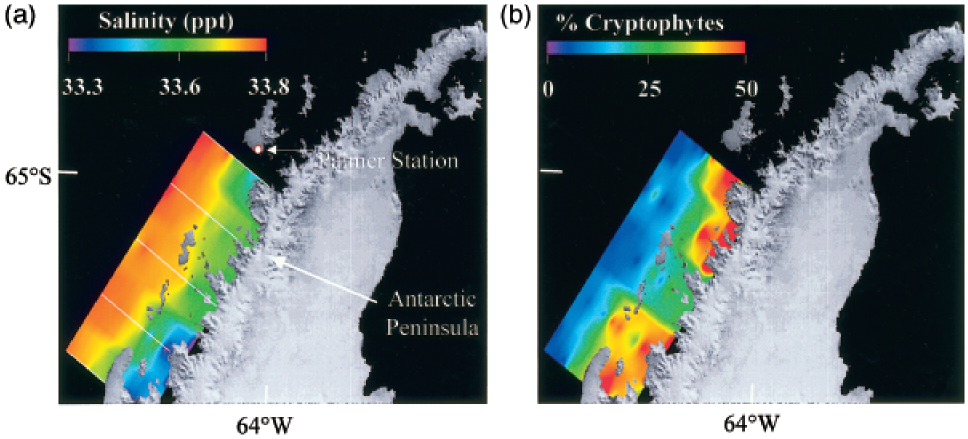

Fig. 2 (a) Surface water salinity for a survey (December 1991–January 1992) along the Antarctic Peninsula. Stations were occupied every 20 km along the historical LTER transect lines (white lines). (b) Concurrent integrated water column contribution of cryptophytes to total phytoplankton biomass.

Table 2 The impact of phytoplankton community composition on the percentage of carbon transferred to higher trophic levels, respired and exported to the benthos

	Krill-to-salp ratio		
Phytoplankton community	Low (1 : 15.6)	Medium (1 : 1)	High (33 : 1)
Cryptophytes only			
Carbon to higher trophic levels (%)	7.3	6	4.6
Carbon to benthos (%)	57.4	38.6	17.8
Respiration (%)	35.3	55.4	77.6
Other phytoplankton (%)			
Carbon to higher trophic levels (%)	7.7	9.4	11.1
Carbon to benthos (%)	58.0	43.5	27.3
Respiration (%)	34.3	47.1	61.6

Model results based on partitioning and transfer efficiencies in Table 1.

1d). This transition is supported by modeling efforts (Walsh *et al*., 2001) and could occur rapidly as salps reproduce via asexual reproduction in response to favorable environmental conditions (see Alldredge, 1984). An alteration in the grazing assemblage could, in turn, lead to changes in the carbon transfer within the system. *E. superba* is central to the Antarctic marine food web and broad-scale shifts in its spatial distribution during summer would affect higher trophic levels, including penguins, seals and whales. As an example, the krill foraging distances for land-based species such as the Adelie penguin would necessarily increase with a subsequent negative feedback to its growth and reproduction (Fraser & Trivelpiece, 1996). The impact on higher trophic levels may be especially significant, as cryptophyte dominance occurs during summer months when feeding activities are at a maximum (Laws, 1985). Recent reports suggest that historical penguin ranges and migration rates appear to be changing (Fraser & Patterson, 1997; Ainley *et al*., 2003).

We estimated the maximal and minimal efficiencies of carbon transfer through the Antarctic Peninsula food web based on krill and salp diets of either cryptophytes or 'other phytoplankton' (assumed primarily diatoms, Table 2). The table values represent a conservative percentage of carbon from primary productivity that will either be available to higher trophic levels or will be exported out of the mixed layer. The diatom-dominated waters represent the most efficient pathway for carbon transfer up the food chain. The cryptophyte-dominated waters are less efficient, taking into account not only grazing by salps, but also the inefficient grazing by krill on small cells and the subsequent loss of biomass to the following year's class and to higher trophic levels. A switch from diatoms to cryptophytes could lead to a 40–65% decrease in carbon transferred to higher trophic levels (Table 2). Similarly, the different phytoplankton assemblages result in a wide range of carbon transported to depth. Depending on the relative numbers of krill and salps, carbon transport to the benthos could fluctuate by as much as 300%.

The duration and significant geographic extent of melt-water runoff (Fig. 2) is likely to increase due to the observed 2–3 °C warming trend along the Antarctic Peninsula (King, 1994; Smith, 1994; Stark, 1994; Dierssen *et al*., 2002). We hypothesize that an increase in melt-water input will increase the spatial and temporal extent of cryptophytes. Historical data indicate an emerging presence of cryptophytes and other phytoflagellates in low salinity coastal waters (Ferreyra & Tomo, 1979; Whitaker, 1982; Krebs, 1983; Buma *et al*., 1992; Kopczynska, 1992; McMinn & Hodgson, 1993; Kang & Lee, 1995), corroborating this hypothesis. Observations (Loeb *et al*., 1997) and modeling studies (Walsh *et al*., 2001) also show changes in Antarctic zooplankton community composition, with an increase in salp abundance and concurrent variations in penguin migration patterns (Ainley *et al*., 2003). These alterations in the food web, if persistent, will ultimately impact biogeochemical cycling in Antarctic coastal waters (Walsh *et al*., 2001).

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