

36 Changes in Phytoplankton Assemblages Along the Antarctic Peninsula and Potential Implications for the Antarctic Food Web

MARK A. MOLINE¹, HERVÉ CLAUSTRE², THOMAS K. FRAZER³, JOE GRZYMSKI⁴, OSCAR SCHOFIELD⁴ AND MARIA VERNET⁵

¹Biological Sciences Department, California Polytechnic State University, San Luis Obispo, California, 93407 USA;

²Observatoire Océanologique de Villefranche (CNRS-INSU), Laboratoire de Physique et Chimie Marines 06238, Villefranche-sur-mer, FRANCE;

³Department of Fisheries and Aquatic Sciences, University of Florida, Gainesville, Florida 32653, USA;

⁴Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, New Jersey 08903, USA;

⁵Marine Research Division, Scripps Institute of Oceanography, University of California, San Diego, California 92093, USA

e-mail: mmoline@calpoly.edu

ABSTRACT

The majority of the yearly organic carbon production in the coastal regions of the Southern Ocean occurs during summer blooms. Changes in the quantity and quality of the phytoplankton standing crop during this period will likely impact organisms that occupy higher trophic levels within the ecosystem. Here we report a recurrent shift in the dominant phytoplankton taxa during the austral summer in a coastal region along the Antarctic Peninsula. The pattern was observed each year between 1991 and 1996 despite radically different biomass concentrations and meteorological and hydrographic conditions. We show that a repeated dominance of cryptophytes (Cryptophyceae) during the austral summer was significantly related (MANOVA; $P \ll 0.001$) to decreased salinities during periods of glacial melting. The transition from a system traditionally dominated by diatoms to one dominated by cryptophytes represents a fundamental decrease in the average size of water column phytoplankton. This is reason for concern, as smaller size classes are not efficiently grazed by *Euphausia superba*. Higher proportions of cryptophyte biomass during the critical summer months may alter zooplankton assemblages and reduce carbon available to higher trophic levels by as much as 70%. Mean air temperatures along the Antarctic Peninsula have increased significantly (2-3 °C) over the past 50 years. Warmer weather will likely extend the spatial and temporal influences of glacial meltwater and may increase the importance of cryptophytes, with significant consequences for Antarctic food web dynamics and coastal biogeochemistry.

Key Words: Phytoplankton, cryptophyceae, zooplankton, Antarctic Peninsula, food webs, regional.

INTRODUCTION

Despite a rich literature describing the abundance and distribution of phytoplankton, the mechanisms governing the composition of phytoplankton assemblages are poorly understood. Though the effects of changing light/nutrient regimes on the structure of phytoplankton communities have received some attention in the region (Sommer and Stable 1986; Sommer 1986; 1988; 1991), the large spatial scale associated with the above investigations often lack a temporal component needed to resolve the kinetic aspect of phytoplankton succession (Moline

and Prézelin 1997). Despite numerous descriptive studies on phytoplankton distribution and succession in open-ocean and nearshore environments, mechanisms for the observed changes are poorly understood. The structure of phytoplankton assemblages is an important ecological consideration as it can impact the feeding efficiency of zooplankton grazers (Quetin and Ross 1985). This is particularly important in nearshore waters during the austral summer when the magnitude and rates of trophic interactions are maximal (Laws 1985).

Phytoplankton community structure also plays a key role in the cycling of nutrients. Communities dominated by diatoms have been shown to have significant impact on silica cycling in the Southern Ocean (Leynaert *et al.* 1991; Nelson *et al.* 1991; Quéguiner *et al.* 1991). The different taxonomic groups of phytoplankton also vary by size class which affects assimilation rates of nitrogen and carbon (Goeyens *et al.* 1991; Owens *et al.* 1991; Boyd and Newton 1995; Claustre *et al.* 1997). These assimilation rates will, therefore, influence the rates of particulate organic carbon and nitrogen flux to the deep ocean (Boyd and Newton 1995).

The Long-Term Ecological Research Program (LTER; Smith *et al.* 1996) was established in 1990, in part, to quantify how variability in the timing and extent of sea-ice formation influences the structure of the Antarctic food web. The initiation of this program was timely given documented environmental changes presently occurring in the Southern Ocean, including depletion of stratospheric ozone during the austral spring/summer (Farman *et al.* 1985) and a significant warming trend along the Antarctic Peninsula over the past 50 years of 2–3°C (King 1994; Stark 1994; Smith *et al.* 1996). These environmental variations may underlie the observed large-scale shifts in both zooplankton communities (Loeb *et al.* 1997) and penguin populations (Trivelpiece *et al.* 1990; Fraser *et al.* 1992). Changes in the Antarctic food web structure may be a “bottom up” response to alterations in phytoplankton biomass and/or community composition. The purpose of the present work was to utilize the LTER dataset to examine the environmental regulation of phytoplankton community composition in a nearshore coastal environment and to assess the potential impacts on higher trophic levels and consequences for biogeochemical cycling in the Southern Ocean.

MATERIALS AND METHODS

Sampling

Over the austral spring/summer period from November 1991, through February 1996, 872 discrete water samples were collected at a nearshore station off Anvers Island (64° 46.45' S, 64° 03.27' W; ~75 m in depth). Water column sampling was conducted from a Mark V Zodiac® using 5L GoFlo® bottles within 2 hours of solar noon. Samples were stored at ambient temperature in dark bottles and returned to Palmer Station for analyses. Salinity and temperature profiles were measured simultaneously using a SeaBird® CTD on a second Zodiac®, described by Smith *et al.* (1992).

Daily air temperature, snow cover and average wind speed/direction measurements were made at Palmer Station during the study period as part of a long term database collected by the U. S. National Science Foundation. Sea ice coverage was assessed by daily observations.

Phytoplankton pigmentation and assemblages

Aliquots of all whole water samples were analyzed for the algal pigments using reverse-phase HPLC procedures detailed in Moline and Prézelin (1996). To estimate the respective contribution of each taxonomic group, multiple regression analyses were performed on the concentrations of discrete samples of the taxonomic pigments against chlorophyll *a* (Chl *a*; Gieskes *et al.* 1988; Everitt *et al.* 1990; Bustillos

et al. 1995). For each sampling date, the Chl *a* associated with each taxonomic group was computed using the regression coefficients from the concentration of its representative pigment(s); alloxanthin for cryptophytes, chlorophyll *b* for chlorophytes, fucoxanthin for diatoms, and the sum of 19'-butanoyloxyfucoxanthin and 19'-hexanoyloxyfucoxanthin for nanoflagellates/prymnesiophytes (not including cryptophytes). Computed taxon-specific Chl *a* concentrations were, in turn, used to estimate the contribution of each taxonomic group to the total biomass. The predicted Chl *a* concentrations from the regression analyses agreed well with the measured concentrations over the five year study (Predicted Chl *a* = 0.99 * Measured Chl *a*, R² = 0.99), indicating the total Chl *a* could be attributed to these four taxonomic groups. Groupings from these analyses were confirmed microscopically using fresh samples collected from whole water and a Zeiss Axiophot microscope, with a combination of light and epifluorescence microscopy at 400x.

Statistical tests

Differences between mean values were determined with a single classification analysis of variance (ANOVA). Since many of the variables were not normally distributed, a randomization ANOVA technique (100,000 randomizations, *cf.* Manly 1991) was used to verify significance levels obtained from initial ANOVA results. LS Means procedures were employed as follow-up pair-wise tests when distinguishing between taxonomic groupings in Fig. 3a.

Trophic transfer model

A model was developed to quantify the partitioning of carbon through the Antarctic food web. Total autotrophic carbon production served as the model's primary input, which was partitioned into either cryptophytes or other phytoplankton groups. Input values were based on measurements made throughout December and January of 1991–1994 (Moline and Prézelin 1996). The relative fluxes from the primary carbon pool to krill, salps and other grazers (*i.e.*, copepods) were dependent on the phytoplankton assemblage and transfer efficiencies. Transfer efficiencies of carbon (cryptophytes to krill=10%, cryptophytes to salps=60%, other phytoplankton to krill=60%, and other phytoplankton to salps=60%) were mean values from previous studies relating percent retention of algae by krill based on size (MacClatchie and Boyd 1983; Meyer and El-Sayed 1983; Boyd *et al.* 1984; Quetin and Ross 1985) and on feeding studies of *Salpa thompsoni* (Madin and 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 ratios (Pakhomov *et al.*; Nishikawa *et al.*; Loeb *et al.* 1997). Carbon from the grazers was directed either to higher trophic levels, sedimentation or respiration. Transfer of carbon from krill to respiration was 34% (Huntley *et al.* 1991), from krill to higher trophic levels was 32.5% (Huntley *et al.* 1991), with the remaining fraction going to sedimentation. Transfer of carbon from salps to respiration was 14.8% (Huntley *et al.* 1989), from salps to higher trophic levels was assumed low at 5% (Foxton 1966; Gon and Heemstra 1990), with the remaining fraction going to sedimentation.

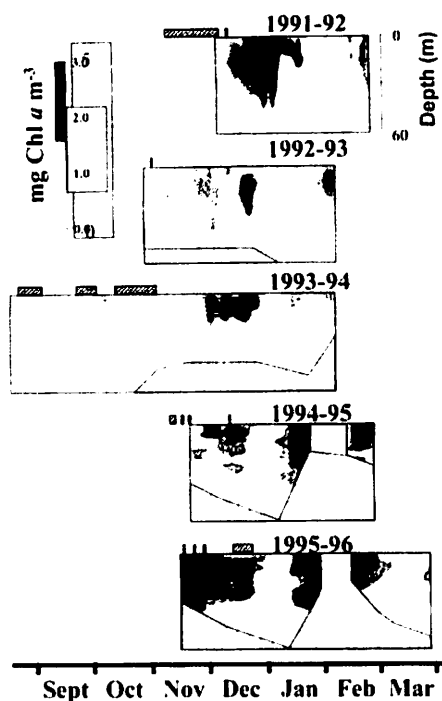


Fig. 1: Seasonal change in the depth distribution of chlorophyll *a* from 1991-1996. Contours are shown with a maximum of 5 mg m⁻³ Chl *a* for comparative purposes between years. Peak chlorophyll *a* concentrations (29.2 mg m⁻³) occurred in December 1991. The presence of significant pack ice (>50% coverage) is indicated by hatch bars. Measurements were taken at 64° 46.45'S, 64° 03.27'W.

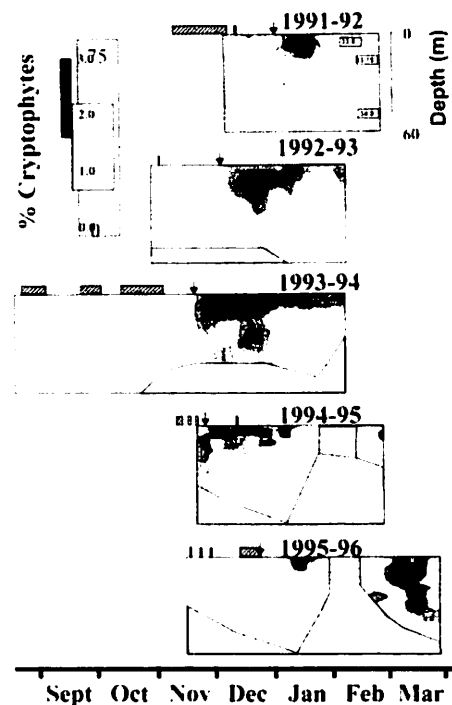


Fig. 2: Seasonal change in the depth distribution in the percent contribution of cryptophytes to the overall biomass from 1991-1996. Contours are shown with a maximum of 75% cryptophyte contribution for comparative purposes between years. The presence of significant pack ice (>50% coverage) is indicated by hatch bars. Arrows indicate the initiation of glacial meltwater input into the region. Overlaid in the 1991-1992 plate are contours of salinity at 0.25 SU intervals. Measurements were taken at 64° 46.45'S, 64° 03.27'W.

RESULTS

There was high inter-annual variability in peak phytoplankton standing stock (2.3 - 29.2 mg Chl *a* m⁻³; Fig. 1). Seasonal and annual patterns were primarily driven by water column stability influenced by local wind stress, which varied dramatically between years (Moline and Prézelin 1996). Daily average wind speeds of 12 m s⁻¹ was found to be a critical threshold for significant water column mixing. Continual winds above this threshold were correlated with periods of low biomass. During the 1992-1993 season, continual high winds resulted in low biomass throughout the season (Fig. 1). In contrast, during an extended period of daily average winds below 5 m s⁻¹ in 1991-1992, the depth of the mixed layer shallowed and a large bloom developed (Fig. 1, Moline and Prézelin 1996, 1997; Moline *et al.* 1997).

Despite high inter-annual variability in Chl *a*, a consistent and repeated pattern in the succession of the phytoplankton community was observed. In all five years of this study, diatoms dominated the late spring phytoplankton populations (Moline and Prézelin 1996), with a transition to surface populations of cryptophytes during the summer of each year (Fig. 2). The transition to cryptophytes coincided with the initiation of glacial meltwater input to the coastal waters (Fig. 2). When the percent dominance of cryptophytes and the salinity at discrete points in the water column were directly compared, there was a significant correlation (Fig. 3; $p < 0.001$). The fact that this relationship does not take the temporal dynamics into consideration indicates that the 'response' of cryptophytes to these low salinity environments occurs on time scales similar to the sampling effort (2-3 days). When comparing the response of the major taxonomic groups of the study, cryptophyte dominance was found to be significantly

dependent (MANOVA, $p < 0.001$) on the low salinity water characteristic of the meltwater lens (Fig. 4a). In contrast, diatoms and prymnesiophytes dominated the phytoplankton assemblages in other physical domains and were not significantly different from each other (Fig. 4a).

The occurrence of cryptophytes correlated also with the daily mean air temperature measured during the five-year study period (Fig. 4b). When mean air temperatures exceeded the freezing point, the percent of cryptophytes to the total biomass increased significantly from ~5% to ~15% (ANOVA; $p < 0.05$). As the mean temperature increased to 1-2° C, there was a highly significant increase in the percent cryptophytes to ~30% (ANOVA; $p < 0.001$). Overall, there was a highly significant difference between samples $> 0^{\circ}$ C and those $< 0^{\circ}$ C (ANOVA; $p < 0.001$), which supports the assertion that the relative abundance of cryptophytes changed in response to the formation of glacial meltwater.

DISCUSSION

Warming trends along the Antarctic Peninsula

Mean air temperatures along the Antarctic Peninsula have increased significantly (2-3 °C) over the past 50 years (King 1994; Stark 1994; Smith *et al.* 1996), with potential consequences for ice shelf dynamics (Vaughan and Doake 1996) and glacial melting (Ashley *et al.* 1994). The increased temperature will likely alter the spatial extent and timing of glacial meltwater runoff. Low salinity water is already a significant geographic feature of the Antarctic Peninsula during summer months,

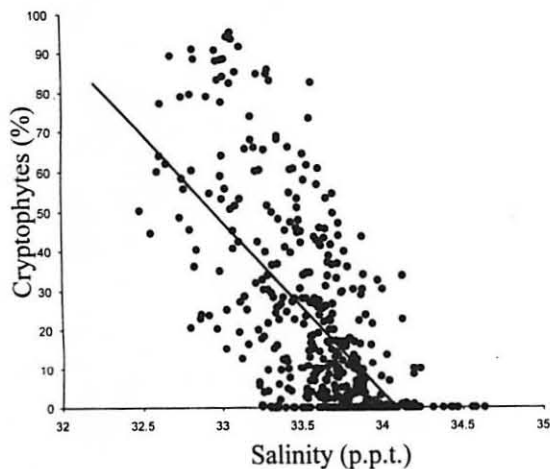


Fig. 3: Relationship between salinity and the percent contribution to the total phytoplankton biomass by cryptophytes for 454 discrete samples collected for the five field seasons of this study from 1991 - 1996.

extending 80 - 100 km offshore, well beyond the present study site (Fig. 5). Given this and the significant response of cryptophytes to meltwater input (Figs. 2-4), a significant shift in the structure of both the phytoplankton and zooplankton communities in the shelf waters of the Southern Ocean may be occurring.

Warming trends and the change in phytoplankton assemblages

Although long-term data sets of phytoplankton assemblages are scarce, a limited number of past studies combined with a large number of recent reports are suggestive of a change. A 24-year study (1970-1993) in Paradise Bay has revealed a significant reduction in the abundance of diatoms and an increase in cryptophytes and other phytoflagellates (Ferreya and Tomo 1979; Ferreya, pers. comm.). Krebs (1983) sampled at biweekly intervals from 1972-1974 in approximately the same location as the present study and found only diatoms; cell numbers were highly correlated to Chl *a* concentrations, suggestive of low abundances of other phytoplankters. More recently, a four-year study (1990-1993) near the South Shetland Islands found dramatic decreases in the abundance of diatoms and a corresponding increase in cryptophytes and other phytoflagellates (Villafañe *et al.* 1995). Although these taxonomic changes were not directly attributed to low salinity, there were associated changes in the salinity fields (Amos 1993). Cryptophytes have been found to contribute to the majority of the total biomass (over 95% in some cases) in the low salinity waters of retreating marginal ice zones in the Weddell-Scotia-Bellingshausen Confluence areas (Lancelot *et al.* 1991; Tréguer *et al.* 1991; Buma *et al.* 1992; Mura *et al.* 1995; Kang and Lee 1995; Aristegui *et al.* 1996). In the Ellis Fjord, *Cryptomonas cryphila* was dominant during the summer when there was a high input of glacial meltwater (McMinn and Hodgson 1993). Kocczynska (1992) also found a recurring dominance of phytoflagellates (primarily cryptophytes) over diatoms in Admiralty Bay, King George Island during mid-summer periods of meltwater input. Kang *et al.* (1997) found a significant relationship between cryptophytes and decreasing salinity in the same location. The occurrence of cryptophytes in low salinity environments in the Southern Ocean is consistent with observations made in temperate

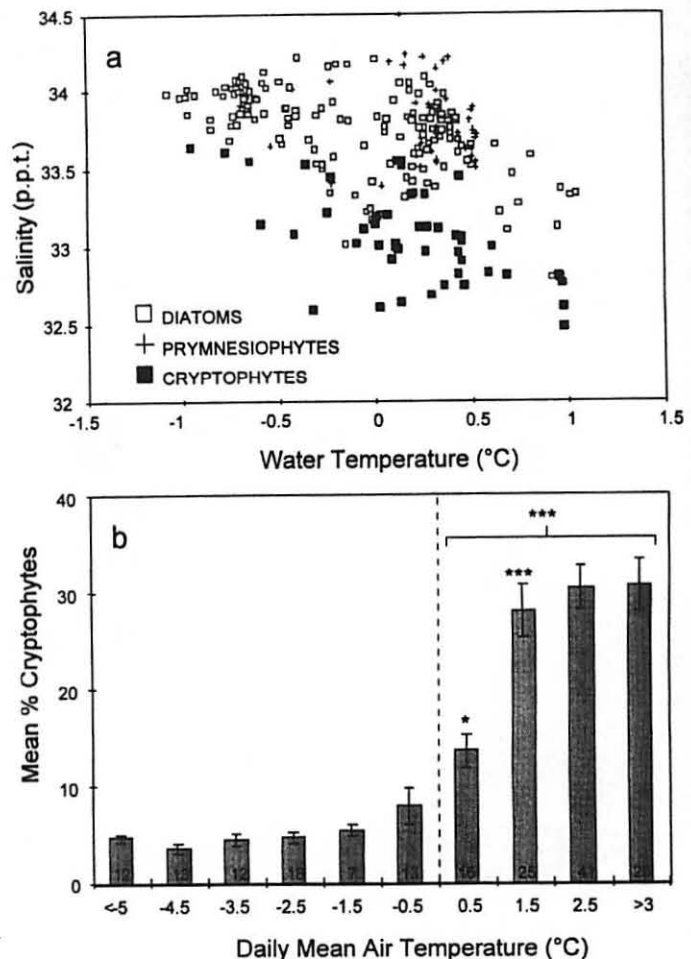


Fig. 4: a) Sample points indicate a > 50% contribution to the total water column phytoplankton biomass by diatoms (open squares), prymnesiophytes (crosses), and cryptophytes (filled squares) as a function of both temperature and salinity. Cryptophytes, when dominant, occupied significantly lower saline water than either diatoms or prymnesiophytes, which were not significantly different from each other. (b) A frequency histogram of the average percent contribution of cryptophytes to total depth-integrated biomass as a function of daily mean air temperature averaged over the study period from 1991 - 1996. Temperatures are shown in one degree bins (i.e., 0-1°C are in the 0.5°C bin). The numbers of observations for each bin are shown in the bars. Significance is indicated from left to right (*denotes $P < 0.05$; *** denotes $P < 0.001$).

regions, where cryptophytes are often associated with brackish water (Prézelin and Bozcar 1986).

Mechanisms, other than decreased salinity, have been suggested to explain phytoplankton successional events from diatoms to phytoflagellates in the Antarctic. Kocczynska (1992) found significant krill populations corresponding to low diatom and high phytoflagellate concentrations, and suggested this was a result of previous selective grazing pressure. Kocczynska (1992) and others have also shown a dominance of flagellates in areas of deep vertical mixing, while Sommer (1988) has shown these phytoplankton to exist in regions with shallow mixing depths. The effects of changing light/nutrient regimes on the structure of phytoplankton communities have received some attention (Sommer and Stale 1986; Sommer 1986; 1988; 1991), with the dominant phytoflagellate, *Phaeocystis pouchetii*, in environments characterized by low nitrogen and high silicate concentrations.

While grazing, mixing regimes and macronutrient conditions have been related to community structure, they were not found to be

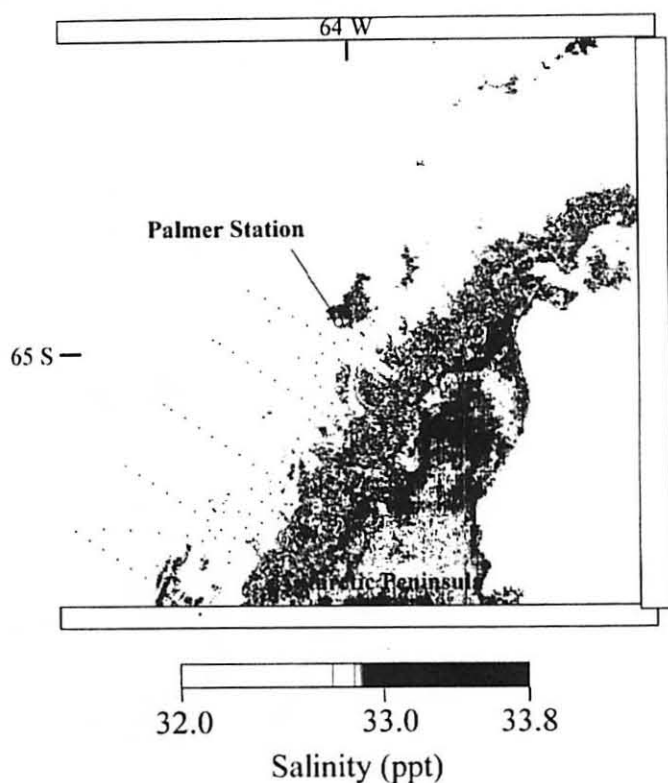


Fig. 5: Visual satellite image (DMSP-11 OLS) of the Antarctic Peninsula. Superimposed is the spatial distribution of salinity (ppt) from January, 1993. Sampling stations and the location of Palmer Station are included. (Salinity data is courtesy of the LTER database, R.C. Smith data manager).

responsible for the dominance of cryptophyte populations in this study. The abundance and types of grazers in the study area were found to vary between years (see Baker *et al.* 1996; Ross *et al.* 1996). While prymnesiophytes, in this case *P. pouchetii*, were generally found to dominate the phytoplankton biomass during high mixing regimes in late summer, similar to Kopczynska (1992), the repeated pattern of cryptophyte dominance occurred during different mixing conditions. During the 1991-92 season, cryptophyte populations were found dominant in a stable water column resulting from meltwater input and continual low wind speeds (Moline and Prézélin 1996; Moline 1998). Cryptophyte dominance also occurred the following year, however, persistent high winds maintained deep mixing the entire season (Moline and Prézélin 1996). Macronutrients measured during this study also varied within and between years and were not consistent with the occurrence of cryptophytes (Moline 1996). While not quantified here, micronutrients within the glacial meltwater may be an important factor leading to phytoplankton successional events and should be considered during future studies. Salinity was the only parameter found during this study to significantly correlate to the transition to cryptophytes within the phytoplankton community from year to year.

Implications for a change in phytoplankton assemblages

The recurrent transition from diatoms to cryptophytes in this study represents a fundamental decrease in the size class of the phytoplankton. Bloom-forming diatoms range in size from 15-270 μm (Krebs 1983; McMinn and Hodgson 1993), while cryptophytes at this study site were measured at $8 \pm 2 \mu\text{m}$ (see McMinn and Hodgson 1993; Kang

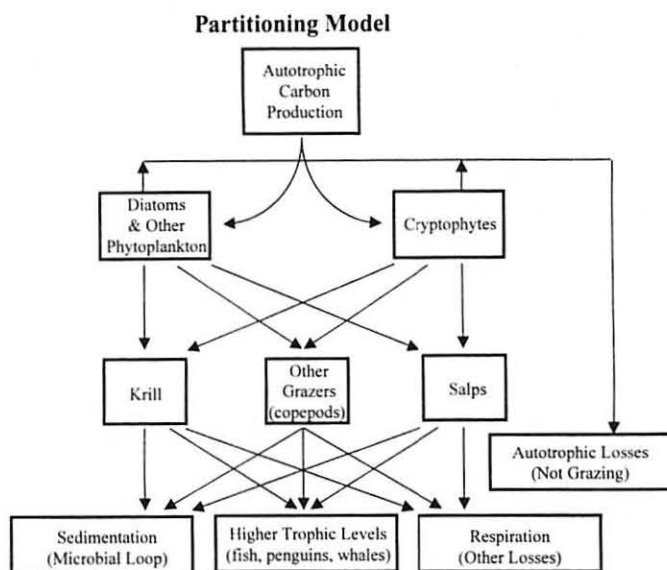


Fig. 6: Flow diagram of the model used to calculate energy transfer throughout the Antarctic food web. Autotrophic carbon production was partitioned into a cryptophyte and 'other' phytoplankton pool based on measurements made from 1991 - 1994 (Moline and Prézélin 1997). The transfer of carbon from the primary producers to grazer pools was calculated based grazing rates that were dependent on the size class of the algae. Carbon from primary grazers is transferred to sedimentation, higher trophic levels and other losses. The model incorporates both the effect of changing phytoplankton assemblage and various ratios of krill to salp biomass.

and Lee 1995). This size difference can impact the grazing efficiencies of key zooplankton species. Antarctic krill, *Euphausia superba*, for example, does not feed equally well on all sizes classes of phytoplankton; cells $< 20 \mu\text{m}$ are retained with $< 50\%$ efficiency (MacClatchie and Boyd 1983; Meyer and El-Sayed 1983; Boyd *et al.* 1984; Quetin and Ross 1985; Granéli *et al.* 1993). Moreover, recent field evidence suggests that adult krill selectively graze larger phytoplankton cells resulting in a relative increase in the abundance of smaller cells including cryptophytes (Kopczynska 1992). In contrast, salps are capable of feeding on a large range of particle sizes and have been shown to effectively graze on phytoplankton in the size range of cryptophytes (Madin and Kremer 1995).

Phytoplankton assemblages can also influence the distribution of krill (Daly and Macauley 1991; Madin and Kremer 1995; Quetin *et al.* 1996). Increased cryptophyte dominance may cause adult krill to exhibit a directed offshore movement, independent of hydrography (Kanda *et al.* 1982), to more effectively graze larger diatom populations. Krill is considered the keystone species in the Antarctic marine food web and shifts in its spatial distribution during summer will affect numerous organisms, particularly penguins and some seals/whales. As an example, the foraging distances for land-based species such as the Adélie penguin would likely increase with a negative feedback to its growth and reproduction (Fraser and Trivelpiece 1996). The impact on higher trophic levels may be especially significant, as cryptophyte dominance occurs during summer months when feeding activities and growth of most species are maximal (Laws 1985).

High concentrations of cryptophytes and the absence of krill in nearshore waters may allow for a proliferation of salps, which reproduce rapidly in response to favorable environmental conditions via asexual reproduction (see Alldredge 1984 for relevant review). In fact, *Salpa*

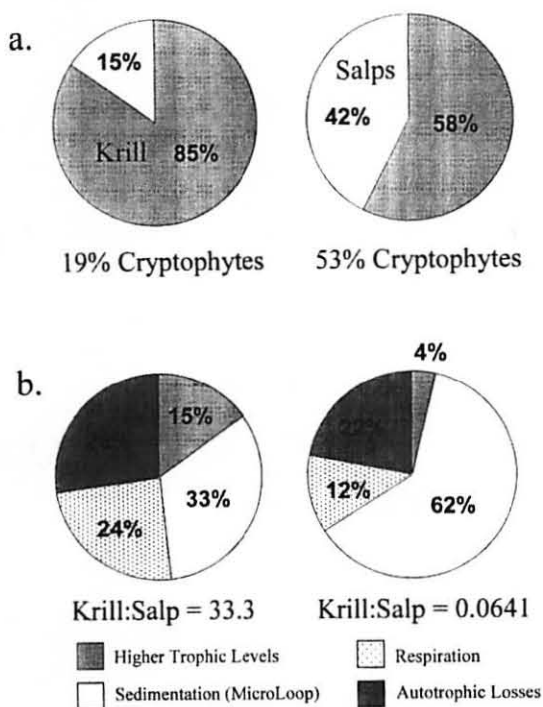


Fig. 7: Results from the model used to calculate the partitioning of energy throughout the Antarctic food web. a) The calculated flow of carbon through either krill (shaded) or salps (open) based on the percentage of cryptophyte primary production. The percent of cryptophyte primary production ranged from 19% in 1991-1992 to 53% in 1993-1994. b) The partitioning of carbon into higher trophic levels (light shade), respiration (stippled), sedimentation (microbial loop) and autotrophic losses (dark shade) was calculated based on changing krill to salp ratios. Krill to salp ratios ranging from 0.0641 to 33.3 (Loeb 1997) were used and corresponded to 19 and 53% cryptophytes, respectively.

thompsoni was abundant in coastal areas, including the Palmer basin, and less prevalent offshore during the summer months of 1993-94 (Ross *et al.* 1996), coincident with a peak occurrence of cryptophytes (Fig. 2).

A recent report documents a long-term shift in the zooplankton community near Elephant Island in response to fluctuations in sea-ice cover and changes in mean air temperature (Loeb *et al.* 1997). Colder years with extensive sea-ice development were found to favor reproduction and survival of Antarctic krill, *Euphausia superba*, while warmer years, where mean yearly air temperatures occasionally exceeded -1°C , reduced the extent of sea-ice and showed *Salpa thompsoni* was the dominant herbivore (Loeb *et al.* 1997). Other studies have also quantified this inverse distribution of krill versus salps near the Antarctic Peninsula (Huntley *et al.* 1989; Nishikawa 1995) and frontal regions (Pakhomov *et al.* 1994).

Changes in the phytoplankton assemblage documented in this study provide an alternative mechanism from Loeb *et al.* (1997) to explain these observed shifts in zooplankton communities. During warmer years, there is a potential for increased glacial melting during the summer and an increase in cryptophytes, which may favor salps over krill. Conversely, colder years will tend to decrease the abundance of cryptophytes and favor diatoms and krill. These changes in zooplankton communities and the prevalence of salps as the dominant zooplankton during the increasing number of 'warm' years is important as salps are not a significant source of carbon to vertebrate predators in the Southern Ocean and represent a terminus in carbon transfer to higher trophic levels (Foxton 1966; Gon and Heemstra 1990).

A model was developed to quantify the potential effects of changing phytoplankton size class and zooplankton assemblage on the flow of carbon through the Antarctic food web (Fig 6). Model results revealed that both a shift in the phytoplankton community composition and the relative ratio of krill to salp biomass significantly altered the amount of carbon available to higher trophic levels and increased sedimentation (Fig. 7). From 1991 to 1994, the percent of total carbon production from cryptophytes during summer months increased from 19% to 53%. The direct effect of this change in phytoplankton productivity was to decrease the amount of carbon flow through krill by 32% (Fig. 7a). Because of decreased phytoplankton size and decreased grazing efficiencies by krill, the carbon available to salps increased almost threefold. The direct effects of this increase in a krill dominated system were to decrease trophic transfer (43%) and sedimentation (41%) as a consequence of fecal production by krill. Sedimentation as a result of salp feeding activities increased fivefold. Similarly, Boyd and Newton (1995) have shown that between years of similar biomass and productivity, the changes in the community structure can alter the flux of particulate organic carbon by two fold. The increased abundance of cryptophytes would decrease the biogenic silica production in the upper water column and decrease the rate and quantity of biogenic silica accumulation in the sea-bed.

In response to a relative decrease in krill abundance, the model revealed that 75% of fixed carbon originally transferred to higher trophic levels would be redirected to the sediments (Fig. 7b). The decreased krill to salp ratio was also shown to double the carbon sedimented or available to the microbial loop. This is in part caused by decreased krill fecal pellet production and the fact that salps are not efficiently utilized as a carbon source by other predators (Foxton 1966; Gon and Heemstra 1990). These outputs should also be viewed as conservative, given that the model does not incorporate the 7:1 difference in longevity between krill and salps, respectively. Model results illustrate that the influence of cryptophytes and the change in zooplankton community has the potential of altering the structure of the food web and directing carbon away from use by top vertebrate predators of the Antarctic ecosystem, such as fishes, birds, seals and whales.

CONCLUSIONS

We postulate that continued warming along the Antarctic Peninsula will lead to an increase in the spatial extent and duration of summer glacial meltwater runoff. Lower salinity water will rapidly alter the composition of summer phytoplankton blooms from primarily diatoms to those dominated by cryptophytes. Historical data are supportive of this hypothesis and the literature suggests an emerging dominance of cryptophytes and other phytoflagellates in low salinity coastal waters. This will likely influence krill distributions and increase the reproductive success of salps in coastal waters. Our described relationship between lower salinity and cryptophyte dominance provides a mechanism explaining the results of a recent report (Loeb *et al.* 1997) which related a decrease in krill abundance (with a corresponding increase in salps) to regional warming of surface air-temperatures along the Antarctic Peninsula. If documented warming trends continue, the importance of cryptophytes will likely increase with significant consequences for Antarctic food web dynamics and coastal biogeochemistry.

ACKNOWLEDGMENTS

N. Boucher, B. Bozcar, T. Diem, T. Evens, B. Golden, P. Handley, R. Jovine, H. Matlick, T. Newberger, S. Roll, K. Seydel, K. Scheppe, J. Standish, B. Sullivan, T. Westerberry and the ASA personnel at Palmer Station are acknowledged for their assistance in data collection during the three field seasons. Special thanks to B. Prézelin for continual support. We also thank R. Bidigare and M. Ondrusek for generously providing HPLC training and pigment standards. We acknowledge support from the Office of Polar Programs, NSF (DPP 90-901127 to B. Prézelin), and the Agricultural Research Service Cooperative Agreement, USDA (58-6435-6-028 to O. Schofield). Salinity data (Fig. 5) were retrieved from the Palmer LTER data archive which is supported by the Office of Polar Programs, U. S. National Science Foundation (OPP-96-32763) (www.ices.ucsb.edu/lter; R.C. Smith, LTER data manager).

REFERENCES

- Allredge A.L. (1984). The quantitative significance of gelatinous zooplankton as pelagic consumers. In: *Flows of Energy and Materials in Marine* (ed. Fasham M.J.R.) New York, Plenum Press, pp 407-433.
- Amos A.F. (1993). AMLR program: Interannual variability in the Elephant Island surface waters in the austral summer. *Ant. J. U. S.* **28**, 201-204.
- Aristegui J., Montero M.F., Ballesteros S. and Basterretxea, van Lenning K. (1996). Planktonic primary production and microbial respiration measured by ^{14}C assimilation and dissolved oxygen changes in coastal waters of the Antarctic Peninsula during austral summer: implications for carbon flux studies. *Mar. Ecol. Prog. Ser.* **132**, 191-201.
- Ashley G.M., Smith N.D., Goss M.C. and Smith P.C. (1994). Sedimentation at a subpolar tidewater glacier, Marr Ice Piedmont, Anvers Island, Antarctic Peninsula. *Ant. J. U. S.* **29**, 94-96.
- Baker K.S., Kozłowski W.A., Vernet M., Jones J.L., Quetin L.B., Ross R.M., Smith R.C. and Fraser W.R. (1996). Palmer LTER: Annual season October 1995 through March 1996. *Ant. J. U. S.* **31**, 160-162.
- Boyd C.M., Heyraud M. and Boyd C.N. (1984). Feeding of the Antarctic krill, *Euphausia superba*. *Crustacean Biology* **4**, 123-141.
- Boyd P. and Newton P. (1995). Evidence of the potential influence of planktonic community structure on the interannual variability of particulate organic carbon flux. *Deep-Sea Res.* **42**, 619-639.
- Buma A.G.J., Gieskes W.W.C. and Thomsen H.A. (1992). Abundance of Cryptophyceae and chlorophyll-*b* containing organisms in the Weddell-Scotia Confluence area in the spring of 1988. *Polar Biol.* **12**, 43-52.
- Bustillos-Guzman J., Claustre H. and Marty J-C. (1995). Specific phytoplankton signature and their relationship to hydrographic conditions in the coastal northwestern Mediterranean Sea. *Mar. Ecol. Prog. Ser.* **124**, 247-258.
- Claustre H., Moline M.A. and Prézelin B.B. (1997). Sources of variability in the photosynthetic cross section for Antarctic coastal waters. *J. Geophys. Res.* **102**, 25,047-25,060.
- Daly K.L. and Macaulay M.C. (1991). Influence of physical and biological mesoscale dynamics on the seasonal distribution and behavior of *Euphausia superba* in the Antarctic marginal ice zone. *Mar. Ecol. Prog. Ser.* **79**, 37-66.
- Everitt D.A., Wright S.W., Volkman J.K., Thomas D.P. and Lindstrom E.J. (1990). Phytoplankton community compositions in the western equatorial Pacific determined from chlorophyll and carotenoid pigment distribution. *Deep-Sea Res.* **37**, 975-997.
- Farman C.B., Gardiner B.G. and Shanklin J.D. (1985). Large losses of total ozone in Antarctica reveal seasonal ClO_x/NO_x interaction. *Nature* **315**, 207.
- Ferreira G.A. and Tomo A.P. (1979). Variacion estacional de las diatomeas planctonicas en Puerto Paraiso-I. *Contribucion del Instituto Antartico Argentio* **264**, 149-184.
- Foxton P. (1966). The distribution and life history of *Salpa thompsoni* Foxton with observations on a related species, *Salpa gerlachei* Foxton. *Discovery Report* **34**, 1-116.
- Fraser W.R. and Trivelpiece W.Z. (1996). Factors controlling the distribution of seabirds: Winter-summer heterogeneity in the distribution of Adélie penguin populations. In: *Foundations for Ecosystem Research in the Western Antarctic Peninsula Region* (eds. Ross R., Hofmann E. and Quetin L.) Antarctic Research Series, Washington D.C., American Geophysical Union, pp 257-272.
- Fraser W.R., Trivelpiece W.Z., Ainley D.G. and Trivelpiece S.G. (1992). Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? *Polar Biol.* **11**, 525-531.
- Gieskes W.W.C., Kraay G.W., Nontji A., Setiapermana D. and Sutomo (1988). Monsoonal alteration of a mixed and a layered structure in the phytoplankton of the euphotic zone of the Banda Sea (Indonesia): A mathematical analysis of algal pigment fingerprints. *Neth. J. Sea Res.* **22**, 123-137.
- Goeyens L., Sorensson F., Tréguer P., Morvan J., Panouse M. and Dehairs F. (1991). Spatiotemporal variability of inorganic nitrogen stocks and uptake fluxes in the Scotia-Weddell Confluence area during November and December 1988. *Mar. Ecol. Prog. Ser.* **77**, 7-19.
- Gon O. and Heemstra C. (1990). *Fishes of the Southern Ocean*. Grahamstown, JLB Smith Institute of Ichthyology, pp 462.
- Granéli E., Granéli W., Rabbani M.M., Daugbjerg N., Fransz G., Cuzin-Roudy J. and Alder V.A. (1993). The influence of copepod and krill grazing on the species composition of phytoplankton communities from the Scotia-Weddell sea: an experimental approach. *Polar Biol.* **13**, 201-213.
- Huntley M.E., Lopez M.D.G. and Karl D.M. (1991). Top predators in the Southern Ocean: A major leak in the biological carbon pump. *Science* **253**, 64-66.
- Huntley M.E., Sykes P.F. and Marin V. (1989). Biometry and trophodynamics of *Salpa thompsoni* Foxton (Tunicata: Thaliacea) near the Antarctic Peninsula in austral summer. *Polar Biol.* **10**, 59-70.
- Kanda K., Takaginy K., Seki Y. (1982). Movement of the larger swarms of Antarctic krill *Euphausia superba* populations of Enderby Land during the 1976-77 season. *J. Tokyo U. Fisheries* **68**, 35-42.

- Kang S-H., Kang J-J., Chung K-H., Lee M-Y., Lee B-Y., Chung H., Kim Y. and Kim D-Y. (1997). Seasonal variation of nearshore Antarctic microalgae and environmental factors in Marian Cove, King George Island, 1996. *Kor. J. of Polar Res.* **8**, 9-27.
- Kang S-H. and Lee S. (1995). Antarctic phytoplankton assemblage in the western Bransfield Strait region, February 1993: composition, biomass, and mesoscale distributions. *Mar. Ecol. Prog. Ser.* **129**, 253-267.
- King J.C. (1994). Recent climate variability in the vicinity of the Antarctic Peninsula. *Int. J. Climatology* **14**, 357-369.
- Kopczynska E.E. (1992). Dominance of microflagellates over diatoms in the Antarctic areas of deep vertical mixing and krill concentrations. *J. Plank. Res.* **14**, 1031-1054.
- Krebs W.N. (1983). Ecology of neritic marine diatoms, Arthur Harbor, Antarctica. *Micropaleontology* **29**, 267-297.
- Lancelot C., Billen G., Vet C., Becquevort S. and Mathot S. (1991). Modeling carbon cycling through phytoplankton and microbes in the Scotia-Weddell Sea area during sea ice retreat. *Mar. Chem.* **35**, 305-324.
- Laws R.M. (1985). The ecology of the Southern Ocean. *Am. Sci.* **73**, 26-40.
- Leynaert A., Tréguer P., Quéguiner B. and Morvan J. (1991). The distribution of biogenic silica and the composition of particulate organic matter in the Weddell-Scotia Sea during spring 1988. *Mar. Chem.* **35**, 435-447.
- Loeb V., Siegel V., Holm-Hansen O., Hewitt R., Fraser W., Trivelpiece W., Trivelpiece S. (1997). Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* **387**, 897-900.
- MacClatchie S. and Boyd C.M. (1983). Morphological study of sieve efficiencies and mandibular surfaces in the Antarctic krill, *Euphausia superba*. *Can. J. Fish. Aquat. Sci.* **40**, 955-967.
- Madin L.P. and Kremer P. (1995). Determination of the filter-feeding rates of salps (Tunicata, Thaliacea) ICES. *J. Mar. Sci.* **52**, 583
- Manly BFJ (1991) Randomization and Monte Carlo Methods in Biology. London, Chapman and Hall, pp 282.
- McMinn A. and Hodgson D. (1993). Summer phytoplankton succession in Ellis Fjord, eastern Antarctica. *J. Plank. Res.* **15**, 925-938
- Meyer M.A. and El-Sayed S.Z. (1983). Grazing of *Euphausia superba* Dana on natural phytoplankton populations. *Polar Biology* **1**, 193-197.
- Moline M.A. (1996). Temporal dynamics and regulation of coastal Antarctic phytoplankton communities: Spring/Summer 1991-1994. Ph.D. Thesis, University of California, Santa Barbara. pp. 356.
- Moline M.A. and Prézélin B.B. (1996). Palmer LTER 1991-1994: Long-term monitoring and analyses of physical factors regulating variability in coastal Antarctic phytoplankton biomass, *in situ* productivity and taxonomic composition over subseasonal, seasonal and interannual time scales. *Mar. Ecol. Prog. Ser.* **145**, 143-160.
- Moline M.A. and Prézélin B.B. (1997). High-resolution time-series data for primary production and related parameters at a Palmer LTER coastal site: Implications for modeling carbon fixation in the Southern Ocean. *Polar Biol.* **17**, 39-53.
- Moline M.A., Prézélin B.B., Schofield O. and Smith R.C. (1997). Temporal dynamics of coastal Antarctic phytoplankton: Environmental driving forces and impact of a 1991-1992 summer diatom bloom on the nutrient regimes. In: *Antarctic Communities* (eds. Battaglia B., Valencia J., Walton D.W.H.) Cambridge, Cambridge University Press, pp 67-72.
- Moline M.A. (1998). Photoadaptive response during the development of a coastal diatom bloom and relationship to water column stability. *Limnol. Oceanogr.* **43**, 146-153.
- Mura M.P., Satta M.P. and Agusti S. (1995). Water-mass influences on summer Antarctic phytoplankton biomass and community structure. *Polar Biology* **15**, 15-20.
- Nelson D.M., Ahern J.A. and Herlihy L.J. (1991). Cycling of biogenic silica within the upper water column of the Ross Sea. *Mar. Chem.* **35**, 461-476.
- Nishikawa J., Naganobu M., Ichii T., Ishii H., Terazaki M. and Kawaguchi K. (1995). Distribution of salps near the South Shetland Islands during austral summer, 1990-1991 with special reference to krill distribution. *Polar Biol.* **15**, 31-39.
- Owens N.J.P., Priddle J. and Whitehouse M.J. (1991). Variations in phytoplanktonic nitrogen assimilation around South Georgia and in the Bransfield Strait (Southern Ocean). *Mar. Chem.* **35**, 287-304.
- Pakhomov E.A., Perissinoto R. and McQuaid C.D. (1994). Comparative structure of the macro-zooplankton/micronekton communities of the Subtropical and Antarctic Polar Fronts. *Mar. Ecol. Prog. Ser.* **111**, 155-169.
- Prézélin B.B. and Bozcar B. (1986) Molecular bases of cell absorption and fluorescence in phytoplankton: potential applications to studies in optical oceanography. In: *Progress in Phycological Research* (eds. Round F. and Chapman D.) Bristol, Biopress Ltd., pp 349-465.
- Quéguiner B., Tréguer P. and Nelson D.M. (1991). The production of biogenic silica in the Weddell and Scotia Seas. *Mar. Chem.* **35**, 449-459.
- Quetin L.B. and Ross R.M. (1985). Feeding by antarctic krill, *Euphausia superba*: Does size matter? In: *Antarctic Nutrient Cycles and Food Webs* (eds. Siegfried W.R., Condy P.R. and Laws R.M.) Berlin, Springer-Verlag, pp 372-377.
- Quetin L.B., Ross R.M., Frazer T.K. and Haberman K.L. (1996). Factors affecting distribution and abundance of zooplankton, with an emphasis on Antarctic krill, *Euphausia superba*. In: *Foundations for Ecosystem Research in the Western Antarctic Peninsula Region* (eds. Ross R., Hofmann E. and Quetin L.) Antarctic Research Series, Washington D.C., American Geophysical Union, pp 357-371.
- Ross R.M., Quetin L.B. and Lascara C.M. (1996). Distribution of Antarctic krill and dominant zooplankton west of the Antarctic Peninsula. In: *Foundations for Ecosystem Research in the Western Antarctic Peninsula Region* (eds. Ross R., Hofmann E. and Quetin L.) Antarctic Research Series, Washington D.C., American Geophysical Union, pp 199-217.
- Smith R.C., Baker K.S., Fraser W.R., Hofmann E.E., Karl D.M., Klink J.M., Quetin L.B., Prézélin B.B., Rorr R.M., Trivelpiece W.Z. and Vernet M. (1995). The Palmer LTER: A long-term ecological research program at Palmer Station, Antarctica. *Oceanography* **8**, 77-86.
- Smith R.C., Baker K.S., Handley P. and Newberger T. (1992). Palmer LTER program: Hydrography and optics within the peninsula grid, zodiac sampling grid during the 1991-1992 field season. *Ant. J. U. S.* **27**, 253-255.

- Smith R.C., Stammerjohn S.E. and Baker K.S. (1996). Surface air temperature variations in the western Antarctic Peninsula region. In: *Foundations for Ecosystem Research in the Western Antarctic Peninsula Region* (eds. Ross R., Hofmann E. and Quetin L.) Antarctic Research Series, Washington D.C., American Geophysical Union, pp 105-121.
- Sommer U. (1986). Nitrate- and silicate-competition among antarctic phytoplankton. *Mar. Biol.* **91**, 345-351.
- Sommer U. (1988). The species composition of Antarctic phytoplankton interpreted in terms of Tilman's competition theory. *Oecologia* **77**, 464-467.
- Sommer U. (1991). Comparative nutrient status and competitive interactions of two Antarctic diatoms (*Corethron criophilum* and *Thalassiosira antarctica*). *J. Plank. Res.* **13**, 61-75.
- Sommer U. and Stabel H-H. (1986). Near surface nutrient and phytoplankton distribution in the Drake Passage during early December. *Polar Biol.* **6**, 107-110.
- Stark P. (1994). Climate warming in the central Antarctic Peninsula area. *Weather* **49**, 215-220.
- Tréguer P., Lindner L., Bennekom A.J., van Panouse M., Leynaert A. and Jacques G. (1991). The production of biogenic silica in the Weddell-Scotia Seas measured by using radiotracer ³²Si. *Limnol. Oceanogr.* **36**, 1217-1227.
- Trivelpiece W.Z., Trivelpiece S.G., Geupel G.R., Kjelson J. and Volkman N.J. (1990). Adélie and Chinstrap penguins: Their potential as monitors of the southern ocean marine ecosystem. In: *Antarctic Ecosystems: Ecological Change and Conservation* (eds. Kerry K. and Hempel G.) Berlin, Springer-Verlag, pp 191-202.
- Vaughan D.G. and Doake C.S.M. (1996). Recent atmospheric warming and retreat of ice shelves on the Antarctic Peninsula. *Nature* **379**, 328-331.
- Villafañe V.E., Helbling E.W. and Holm-Hansen O. (1995). Spatial and temporal variability of phytoplankton biomass and taxonomic composition around Elephant Island, Antarctica, during the summers of 1990-1993. *Mar. Biol.* **123**, 677-686.