

## Cascading Trophic Impacts of Reduced Biomass in the Ross Sea, Antarctica: Just the Tip of the Iceberg?

BRAD A. SEIBEL\* AND HEIDI M. DIERSSEN†

Monterey Bay Aquarium Research Institute, Moss Landing, California 95039

*A significant reduction in phytoplankton biomass in the Ross Sea was reported in the austral summer of 2000–2001, a possible consequence of a disruption in sea-ice retreat due to the presence of an immense iceberg, B15 (1) (Fig. 1). Our observations in McMurdo Sound suggest temporally and trophically cascading impacts of that depression in productivity. Reduced phytoplankton stocks clearly affected the pteropod *Limacina helicina* (Phipps, 1774) (Gastropoda: Mollusca), an abundant primary consumer in the region (2, 3), as indicated by depressed metabolic rates in 2000–2001. The following season, for the first time on record, *L. helicina* was absent from McMurdo Sound. Many important predators, including whales and fishes, rely heavily on *L. helicina* for food (3, 4). However, most obviously impacted by its absence was *Clione antarctica* (Smith, 1902), an abundant pteropod mollusc (Gastropoda) that feeds exclusively on *L. helicina* (5). Metabolic rates of *C. antarctica* were depressed by 50% in 2001–2002. Both *L. helicina* and *C. antarctica* are important components of polar ecosystems and may be good indicators of overall ecosystem “health” in McMurdo Sound and perhaps in the Ross Sea. In this last austral summer, 2002–2003, sea-ice extent was much higher and phytoplankton stocks were dramatically lower than any reported previously, effects possibly associated with El Niño conditions, and we hypothesize that pteropods and their consumers may be further impacted.*

In the Southern Ocean, phytoplankton production is linked strongly to the seasonal oscillations in the extent of the sea ice (6, 7) and survival of higher trophic levels is

dependent on reproductive cycles that are synchronous with phytoplankton blooms. This is especially true of the direct food link between *L. helicina* and *C. antarctica*. *L. helicina* lives and feeds in the water column by extending a web of mucus that traps phytoplankton and, to a lesser extent, small zooplankton (3). *L. helicina* is the exclusive food source of *C. antarctica* throughout the life cycle, and the two species have parallel life histories. They grow in concert, with the preferred prey size increasing with predator size (3). Such specificity within the context of a highly seasonal environment requires precise timing to ensure that predator and prey coexist. The coevolved predator-prey relationship between *L. helicina* and *C. antarctica* provides a unique opportunity to study the ecological and trophic consequences of a depression in primary productivity in the Ross Sea.

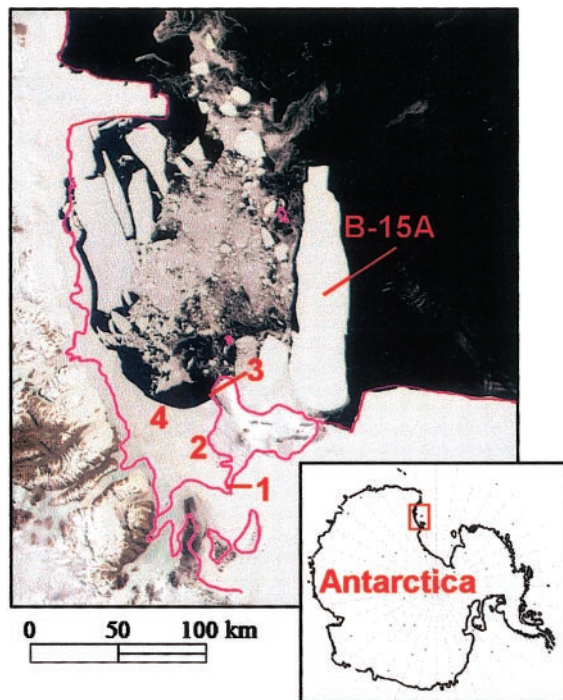
A 50% to 75% reduction in phytoplankton biomass, estimated as chlorophyll *a* (Chl) concentrations, and high sea-ice cover was observed in December 2000–2001 relative to previous years (Table 1; Fig. 2; 8). A limited bloom did form by February, but annual primary production was still only 60% of the previous year (1). We believe that the reduced phytoplankton stocks in 2000–2001 had pronounced impacts on the condition of primary consumers in the region, causing cascading effects through higher trophic levels in the following year. This assertion is supported here by a series of metabolic measurements made on *L. helicina* and *C. antarctica* between 1999 and 2002.

Nutritional state is known to be among the primary determinants of metabolism in all organisms, including pteropods (3), and is especially important in the highly seasonal Antarctic environment (9, 10). Food availability will influence, among other things, the rates of protein synthesis, oxygen consumption, growth, and reproduction (9–11). We collected *L. helicina* and *C. antarctica* at four sampling stations along Ross Island (Fig. 1) and measured the oxygen

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\* To whom correspondence should be addressed. Current address: 100 Flagg Road, Biological Sciences Center, Biological Sciences Department, University of Rhode Island, Kingston, RI 02881. E-mail: seibel@uri.edu

† Current address: Department of Marine Sciences, University of Connecticut at Avery Point, 1080 Shennecosset Road, Groton, CT 06340.



**Figure 1.** True-color imagery of McMurdo Sound and the iceberg B15A in the Ross Sea, Antarctica, on 26 December 2001. Imagery is from the Moderate Resolution Imaging Spectroradiometer (MODIS) (33) at 250-m resolution. Sites on Ross Island where pteropod specimens were collected are marked 1, McMurdo Station; 2, Cape Royds; 3, Cape Bird; and 4, ice edge.

consumption rates of both species in January of 1999, 2001, and 2002, using end-point analysis as described previously (12, 13). The measurement temperature in all analyses was

–1.86 °C, which is the year-round ambient temperature in McMurdo Sound. The oxygen consumption rates of *L. helicina* in 2001 were reduced by more than 30% relative to those measured in 1999 (Table 1). This reduction was presumably a result of food deprivation due to reduced phytoplankton stocks, although we cannot rule out a possible additional influence of changes in food quality (*i.e.*, species composition may also have changed from 1999 to 2001). The following season, phytoplankton stocks were elevated; but for the first time on record (see below), *L. helicina* was not found at any station sampled.

As a monophagous predator, *C. antarctica* was heavily impacted by the absence of its prey in McMurdo Sound. The oxygen consumption rates measured for this species in 2002 are only 50% of those measured in previous years (Table 1; Fig. 3). We also conducted laboratory experiments in 2001 in which specimens of *C. antarctica* were deprived of food for 3 weeks. Over the first 14 days, metabolic rates declined gradually to about 50% of control (wild-caught and laboratory-fed animals) levels. The 2002 rates correspond closely to those of individuals deprived of food in 2001, strongly supporting the suggestion that the depressed rates resulted from the extended absence of *L. helicina* in the region.

*C. antarctica*, like many polar zooplankton (14, 15), accumulates large lipid stores (5% wet mass) during the productive spring and summer months, presumably for survival through the winter and production of eggs that are released the following spring (16). With a depressed metabolic rate of 0.99  $\mu\text{mol}$  (0.022 ml)  $\text{O}_2 \text{g}^{-1} \text{h}^{-1}$  (Table 1), an oxy-calorific conversion of 4.7 kcal  $\text{l}^{-1} \text{O}_2$ , and an energy content of 9.4 kcal  $\text{g}^{-1}$  lipid, a 100-mg animal could survive nearly 6 months on lipid alone, but at the expense of

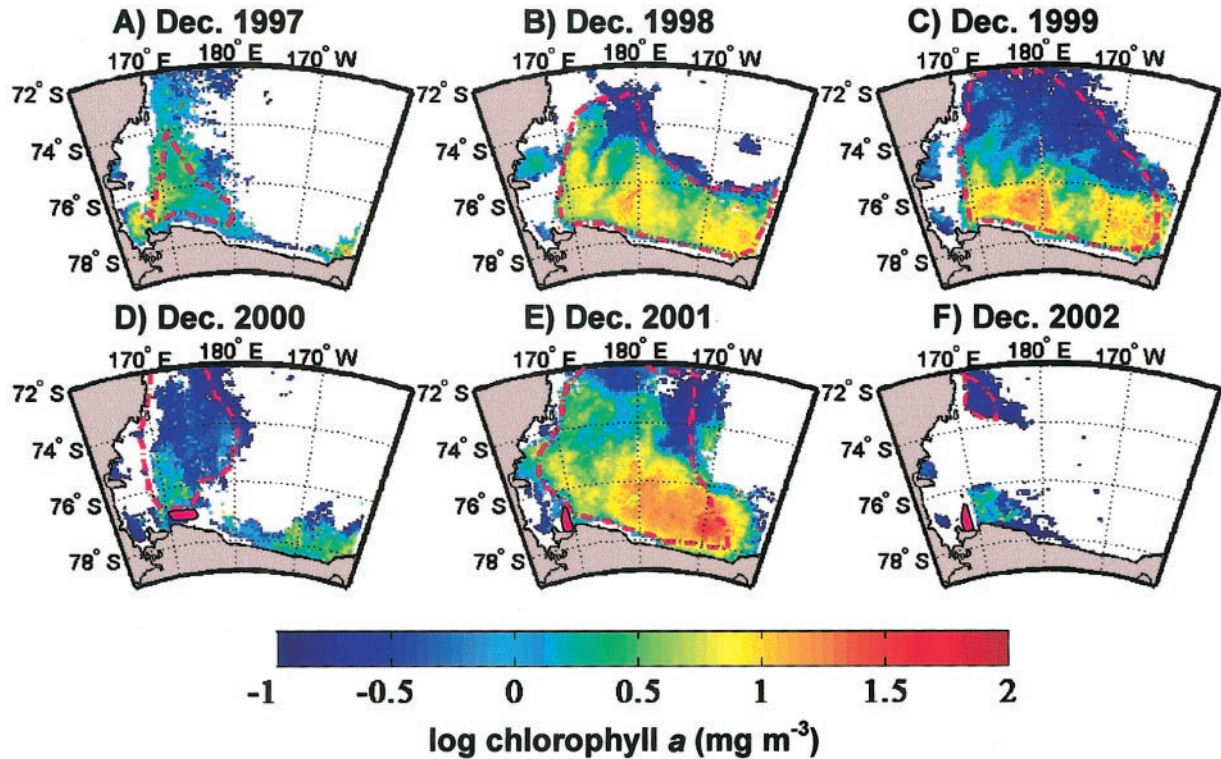
**Table 1**

*Impacts of reduced biomass on trophic dynamics*

	1997–1998	1998–1999	1999–2000	2000–2001	2001–2002	2002–2003
Mean chlorophyll <i>a</i> ( $\text{mg m}^{-3}$ ) in the Western Ross Sea (See Fig. 2 for details)						
December	2.1	3.9	3.4	1.0	5.4	0.56
January	1.6	1.5	3.1	2.2	3.4	0.56
Fraction of the Western Ross Sea covered with sea ice (See Fig. 2 for details) <sup>1</sup>						
December	0.72	0.50	0.31	0.66	0.30	0.88
January	0.52	0.29	0.16	0.57	0.20	0.78
Oxygen consumption rate ( $\mu\text{mol O}_2 \text{g}^{-1} \text{h}^{-1}$ ), mean $\pm$ SE( <i>n</i> ); data pooled from all collection sites (Fig. 1) <sup>2</sup>						
<i>Limacina</i>	n.d.	5.51 $\pm$ 0.4 (12)	n.d.	3.78 $\pm$ 0.20 (22)*	absent	present
<i>Clione</i>	n.d.	1.93 $\pm$ 0.21 (10)	n.d.	2.04 $\pm$ 0.12 (31)	0.99 $\pm$ 0.05 (30)*	present
<i>Clione</i> starved				0.96 $\pm$ 0.10 (7)*		

<sup>1</sup> Sea ice cover determined as the fraction of Western Ross Sea not covered by open water, as shown in Fig. 2.

<sup>2</sup> n.d., no data; \*indicates that oxygen consumption rates were significantly different from those in 1998–1999 ( $P < 0.01$ ).



**Figure 2.** Ross Sea chlorophyll *a* (Chl) concentrations, representing the monthly mean of sea-ice-free pixels at 9-km resolution, derived from satellite ocean color imagery obtained from Sea-viewing Wide Field-of-view Sensor (SeaWiFS; Level 3 Standard Mapped Image, Reprocessing #4) (33) for December 1997 (A)–2002 (F). Gray areas designate land and white areas indicate the presence of sea ice. The dashed magenta line represents the average extent of sea ice determined from passive microwave satellite data (SSM/I NASA Team Algorithm). The sea ice extent and Chl data reported in Table 1 were determined from the area within this line. The location of the B15A iceberg is shown as a solid magenta shape.

reproduction. A positive correlation between egg production and availability of food (*i.e.*, *Limacina*) has been demonstrated in the laboratory for *C. limacina* (3).

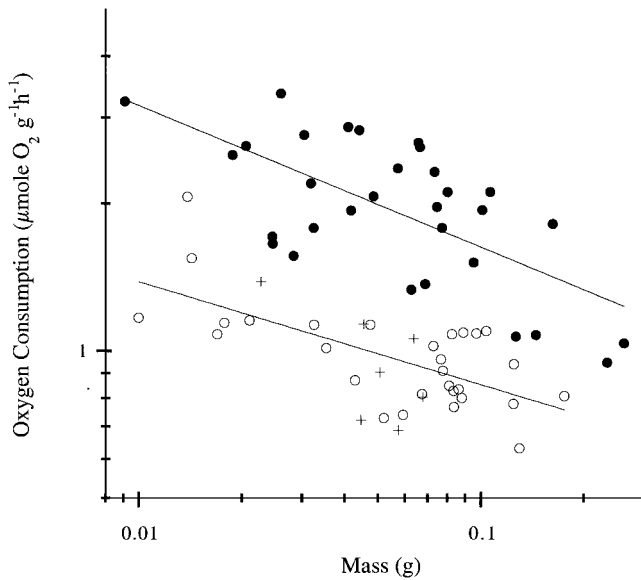
*L. helicina* is typically abundant throughout the Southern Ocean, sometimes displacing krill as the dominant zooplankton (17). In McMurdo Sound, *L. helicina* may constitute more than 20% of the zooplankton biomass and reach concentrations exceeding 300 individuals per cubic meter along the ice edge (18, 19). *L. helicina* is also an important prey item for a number of other species in the Antarctic, including whales and myctophid and notothenioid fishes (4, 20), themselves important components in the diet of penguins and mammals (21, 22). Although *Clione limacina*, the northern hemisphere congener of *C. antarctica*, has also been reported in the diet of fishes and whales (3), *C. antarctica* may have limited importance for higher trophic levels in McMurdo Sound because it produces a novel “anti-feedant” compound (19). However, both *L. helicina* and *C. antarctica* are functionally important components of the ecosystem with the potential to influence phytoplankton stocks (18), carbon flux (23), and dimethyl sulfide (DMS) levels (24) that, in turn, influence global climate through

ocean-atmosphere feedback loops. The state of pteropod populations is almost certainly indicative of overall ecosystem “health” in McMurdo Sound, and perhaps throughout the Ross Sea.

Large aggregations of both pteropod species were found at all four sampling stations (Fig. 1) in January of 1999 and 2001. Equally large aggregations of both species have been reported in McMurdo Sound in every systematic zooplankton sampling study to date (2, 5, 18, 19, 25, 26). The Antarctic Biology Training Course sponsored by the U.S. National Science Foundation also confirmed an abundance of *L. helicina* in McMurdo Sound every year of its operation (1994–1996, 1999–2001; D. Karentz, University of San Francisco, California, pers. comm.). Thus, the absence of *L. helicina* in 2001–2002 appears to be unprecedented in McMurdo Sound, although we cannot rule out the possibility that *L. helicina* was recruited from other parts of the Ross Sea later in the year.

The absence of *L. helicina* in 2001–2002 may have resulted from food limitation. In the Arctic, *L. helicina* has a life cycle of 1.5 to 2 years, and veliger larvae are most abundant in late summer to early fall (27). Assuming a





**Figure 3.** Oxygen consumption rates of *Clione antarctica* plotted as a function of wet body mass. All rates were measured at  $-1.86^{\circ}\text{C}$ , the year-round ambient temperature in McMurdo Sound. The rates from animals captured in 2002 (open circles,  $y = 0.43x^{-0.28}$ ) were significantly lower than those measured in 2001 (black circles,  $y = 0.93x^{-0.25}$ ) or 1999 (grey circles) (ANCOVA;  $P < 0.01$ ). Consumption rates of animals deprived of food in the laboratory in 2001 (+) are similar to those measured in 2002, supporting the suggestion that animals captured in 2002 were suffering food deprivation due to the apparent absence of *Limacina helicina* in the region.

similar life history for *L. helicina* in the Ross Sea, veligers there may not have metamorphosed and grown to adult sizes by summer 2001–2002. Relatively short delays in food availability are known to lead to failed metamorphosis of larval zooplankton (28). Unfortunately, we have no data outside of McMurdo Sound in 2002. An alternative hypothesis is that *L. helicina* was simply excluded from McMurdo Sound by changes in the local currents due to an immense iceberg, B15, a large fragment of which ran aground along the eastern edge of Ross Island in austral spring 2000–2001 (Fig. 1). The iceberg and associated ice cover in 2001–2002 may have prevented the typical flow of water from the Ross Sea gyre around Cape Bird and southward into McMurdo Sound (29), and this may have caused a more localized absence of *L. helicina*. This current typically carries the phytoplankton bloom, and presumably, pteropod populations into McMurdo Sound. This explanation is consistent with the change in the position of the iceberg between 2000–2001 and 2001–2002, but it is not supported by more recent observations. Substantial populations of both *C. antarctica* and *L. helicina* were found in McMurdo Sound in 2002–2003 (Luke Hunt, Hopkins Marine Station, pers. comm.) even though the iceberg continues to block the mouth of McMurdo Sound.

A number of factors may have influenced the sea-ice

conditions and thus contributed to the low biomass observed in 2000–2001. Among the most compelling is that the immense iceberg B15 prevented the retreat of pack ice out of the Ross Sea, causing a reduction in open water and a shortened growing season that delayed and stunted the phytoplankton bloom (1). However, substantial interannual variability exists in both sea-ice extent and phytoplankton production. For example, both 1997 and 2002 had high ice cover (Fig. 2; Table 1) even though the iceberg was no longer preventing the retreat of pack ice in those years. Phytoplankton biomass was reduced somewhat in 1997, but was dramatically reduced in 2002 (mean chlorophyll concentration of  $0.56\text{ mg m}^{-3}$ ). Interestingly, both 1997 and 2002 experienced El Niño events that are known to influence Antarctic waters (30).

Continued monitoring is required to assess the causes of variability in Ross Sea phytoplankton stocks, the role of sea ice in the Southern Ocean ecosystem, and the resulting impacts on trophic interactions. Climate variations may further disrupt the timing of sea-ice formation and retreat (31, 32), and thus primary productivity, with consequences for entire food webs, as observed here.

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### Literature Cited

1. Arrigo, K. R., G. L. van Dijken, D. G. Ainley, M. A. Fahnestock, and R. Markus. 2002. Ecological impact of a large Antarctic iceberg. *Geophys. Res. Lett.* **29**: 1–4.
2. Foster, B. A. 1989. Time and depth comparisons of sub-ice zooplankton in McMurdo Sound, Antarctica. *Polar Biol.* **9**: 431–435.
3. Lalli, C. M., and R. W. Gilmer. 1989. *Pelagic Snails: The Biology of Holoplanktonic Gastropod Mollusks*, Stanford University Press, Stanford, CA.
4. Foster, B. A., and J. C. Montgomery. 1993. Planktivory in benthic nototheniid fish in McMurdo Sound, Antarctica. *Environ. Biol. Fishes* **36**: 313–318.
5. Gilmer, R. W., and C. M. Lalli. 1990. Bipolar variation in *Clione*, a gymnosomatous pteropod. *Am. Malacol. Bull.* **81**: 67–75.
6. Brierley, A. S., and D. N. Thomas. 2002. Ecology of southern ocean pack ice. *Adv. Mar. Biol.* **43**: 171–277.
7. Smith, R. C., K. S. Baker, H. M. Dierssen, S. E. Stammerjohn, and

- M. Vernet. 2001.** Variability of primary production in an Antarctic marine ecosystem as estimated using a multi-scale sampling strategy. *Am. Zool.* **41**: 40–56.
8. **Gow, A. J., S. F. Ackley, J. W. Govoni, and W. F. Weeks. 1998.** Physical and structural properties of land-fast sea ice in McMurdo Sound, Antarctica. Pp. 355–374 in *Antarctic Sea Ice: Physical Processes, Interactions and Variability*, Vol. 74, M.O. Jeffries, ed. American Geophysical Union, Washington D.C.
9. **Brockington, S., and A. Clarke. 2001.** The relative influence of temperature and food on the metabolism of a marine invertebrate. *J. Exp. Mar. Biol. Ecol.* **258**: 87–99.
10. **Peck, L. S. 1998.** Feeding, metabolism and metabolic scope in Antarctic marine ectotherms. Pp. 365–390 in *Cold Ocean Physiology*, H. O. Pörtner, and R. C. Playle, eds. Cambridge University Press, Cambridge.
11. **Ross, R. M., L. B. Quetin, K. S. Baker, M. Vernet, and R. C. Smith. 2000.** Growth limitation in young *Euphausia superba* under field conditions. *Limnol. Oceanogr.* **45**: 31–43.
12. **Marsh, A. G., and D. T. Manahan. 1999.** A method for accurate measurements of the respiration rates of marine invertebrate embryos and larvae. *Mar. Ecol. Prog. Ser.* **184**: 1–10.
13. **Seibel, B. A., E. V. Thuesen, J. J. Childress, and L. A. Gorodezky. 1997.** Decline in pelagic cephalopod metabolism with habitat depth reflects differences in locomotory efficiency. *Biol. Bull.* **192**: 262–278.
14. **Geiger, S. P., H. G. Kawall, and J. J. Torres. 2001.** The effect of the receding ice edge on the condition of copepods in the northwestern Weddell Sea: results from biochemical assays. *Hydrobiologia* **453–454**: 79–90.
15. **Hagen, W., E. S. Van Vleet, and G. Kattner. 1996.** Seasonal lipid storage as overwintering strategy of Antarctic krill. *Mar. Ecol. Prog. Ser.* **134**: 85–89.
16. **Phleger, C. F., P. D. Nichols, and P. Virtue. 1997.** Lipids and buoyancy in Southern Ocean pteropods. *Lipids* **32**: 1093–1100.
17. **Cabal, J. A., F. Alvarez-Marqués, J. L. Acuña, M. Quevedo, R. Gonzalez-Quirós, I. Huskin, D. Fernández, C. R. Del Valle, and R. Anadón. 2002.** Mesozooplankton distribution and grazing during the productive season in the Northwest Antarctic Peninsula (FRUELA cruises). *Deep-sea Res. II* **49**: 869–882.
18. **Hopkins, T. L. 1987.** Midwater food web in McMurdo Sound, Ross Sea, Antarctica. *Mar. Biol.* **96**: 93–106.
19. **Bryan, P. J., W. Y. Yoshida, J. B. McClintock, and B. J. Baker. 1995.** Ecological role for pteroenone, a novel antifeedant from the conspicuous antarctic pteropod *Clione antarctica* (Gymnosomata: Gastropoda). *Mar. Biol.* **122**: 271–277.
20. **Pakhomov, E. A., R. Perissinotto, and C. D. McQuaid. 1996.** Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Mar. Ecol. Prog. Ser.* **134**: 1–14.
21. **Davis, R. W., L. A. Fuiman, T. M. Williams, S. O. Collier, W. P. Hagey, S. B. Kanatous, S. Kohin, and M. Horning. 1999.** Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* **283**: 993–996.
22. **Eastman, J. T. 1993.** *Antarctic Fish Biology: Evolution in a Unique Environment*. Academic Press, San Diego, CA.
23. **Noji, T. T., U. V. Bathmann, B. von Bodungen, M. Voss, A. Antia, M. Krumholz, B. Klein, I. Peeken, C. I.-M. Noji, and F. Rey. 1997.** Clearance of picoplankton-sized particles and formation of rapidly sinking aggregates by the pteropod, *Limacina retroversa*. *J. Plankton Res.* **19**: 863–875.
24. **Levasseur, M., M. D. Keller, E. Bonneau, D. D'Amours, and W. K. Bellows. 1994.** Oceanographic basis of a DMS-related Atlantic cod (*Gadus morhua*) fishery problem: blackberry feed. *Can. J. Fish. Aquat. Sci.* **51**: 881–889.
25. **Whitehead, K., D. Karentz, and J. I. Hedges. 2001.** Mycosporine-like amino acids (MAAs) in phytoplankton, a herbivorous pteropod (*Limacina helicina*) and its pteropod predator (*Clione antarctica*) in McMurdo Bay, Antarctica. *Mar. Biol.* **139**: 1013–1019.
26. **Knox, G. A., E. J. Waghorn, and P. H. Ensor. 1996.** Summer plankton beneath the McMurdo ice shelf at White Island, McMurdo Sound, Antarctica. *Polar Biol.* **16**: 87–94.
27. **Kobayashi, H. A. 1974.** Growth cycle and related vertical distribution of the thecosomatous pteropod *Spiratella* (“*Limacina*”) *helicina* in the central Arctic Ocean. *Mar. Biol.* **26**: 295–301.
28. **Ross, R. M., and L. B. Quetin. 1989.** Energetic cost to develop to the first feeding stage of *Euphausia superba* Dana and the effect of delays in food availability. *J. Exp. Mar. Biol. Ecol.* **133**: 103–127.
29. **Barry, J. P., and P. K. Dayton. 1988.** Current patterns in McMurdo Sound, Antarctica and their relationship to local biotic communities. *Polar Biol.* **8**: 367–376.
30. **Comiso, J. C., C. R. McClain, C. W. Sullivan, J. P. Ryan, and C. L. Leonard. 1993.** Coastal Zone Color Scanner pigment concentrations in the Southern Ocean and relationships to geophysical surface features. *J. Geophys. Res.* **98**(C2):2419–2451.
31. **Scambos, T. A., C. Hulbe, M. Fahnestock, and J. Bohlander. 2000.** The link between climate warming and break-up of ice shelves in the Antarctic Peninsula. *J. Glaciol.* **46**: 516–530.
32. **Dierssen, H. M., R. C. Smith, and M. Vernet. 2002.** Glacial meltwater dynamics in coastal waters west of the Antarctic Peninsula. *Proc. Natl. Acad. Sci. USA* **99**: 1790–1795.
33. **Yoder, J. A. 2000.** Terra's view of the sea. *Science* **288**: 1978–1980.