

Palmer LTER: Relationships between variability in sea-ice coverage, krill recruitment, and the foraging ecology of Adélie penguins

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Seabird research has been an integral part of the science effort at Palmer Station since the early 1970s (Parmelee, Fraser, and Neilson 1977). Originally restricted to studies on the basic biology, ecology, and behavior of seabirds, the program now focuses on environmental variability and its relationship to short- and long-term change in seabird populations. Since 1987, the program has received interagency support from the National Science Foundation and the National Marine Fisheries Service, which together facilitate a coupled terrestrial-marine sampling program with a broad ecosystem perspective (Fraser et al. 1992b). In this article, we summarize the results of a recent analysis with direct relevance to ongoing investigations addressing the broader focus of this program.

Changes in the populations of many southern ocean upper-trophic-level predators, such as penguins and whales, are thought to be ultimately linked to changes in the abundance of their primary prey, the antarctic krill *Euphausia superba*. Increases in penguin populations on the Antarctic Peninsula that have occurred since the 1950s were, therefore, thought to have been due to an increase in krill availability that resulted from the exploitation and depletion of baleen whale stocks (Laws 1985). Fraser et al. (1992a), however, challenged this tenet and instead proposed that the trends evident in these populations (Trivelpiece et al. 1990, pp. 191–202) were caused by a decrease in the frequency of cold years with extensive winter ice resulting from environmental warming. This new hypothesis more logically resolved a number of seemingly anomalous features related to the ecology of the three *Pygoscelid* penguins found on the Antarctic Peninsula (Fraser et al. 1992a), and many of its inherent implications currently guide the analysis and interpretation of long-term data related to these species.

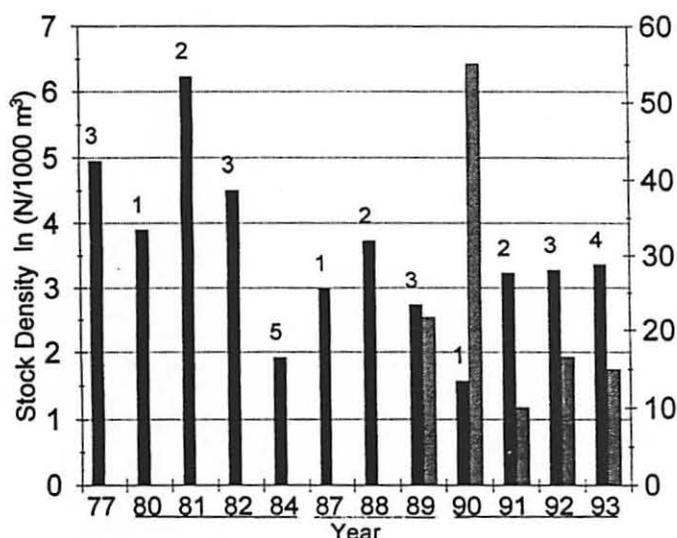
One of these implications is that sea ice may ultimately mediate the outcome of many southern ocean trophic interactions, including, but not limited to, the availability of krill. Krill larvae are obligate inhabitants of the winter pack ice, suggest-

ing that cohort strength may vary annually in response to an increase or decrease in sea-ice coverage (Daly 1990). A recent model (Priddle et al. 1988, pp. 169–182) suggests that failed recruitment years skew krill size-frequency distributions toward the larger size classes, whereas years of good recruitment have the opposite effect. Following years of poor recruitment, moreover, krill abundance decreases because some age classes are no longer represented in the population. These predictions were examined in a log-linear model framework with residual analysis to look for patterns by using 20 years' worth of Adélie penguin (*Pygoscelis adeliae*) diet-sample data from two western Antarctic Peninsula study sites. The implications of this analysis were then compared to a 17-year record of krill stock estimates and a 5-year record of Adélie penguin foraging-trip durations, an indirect measure of krill abundance (CCAMLR 1992).

On the western Antarctic Peninsula, maxima in sea-ice coverage occur every 5–7 years (Fraser et al. 1992a; Stammerjohn 1993). In the analysis, these maxima were categorized as "ice event 1," and the years that followed until another maximum as "ice event 1+n." As suggested by the table, ice cycles start and end with populations of large krill, the spawning stock (ice events 1 and 5); recruitment follows winters of ice maxima, creating a super cohort (ice event 2); this cohort maintains its identity because of missing age classes during subsequent years of failed or poor recruitment (ice events 3, 4, and 5). The pattern evident in the table also implies that within an ice cycle, the krill abundance minimum and maximum should occur during ice events 1 and 2, respectively (i.e., minimum and maximum representation of age classes). The 17-year record of krill stock estimates agrees with this prediction, showing that abundance extremes within an ice cycle are specifically linked to ice events 1 and 2 (figure). As shown by the 1989–1993 series of ice events (figure), Adélie penguin foraging-trip durations exhibit an inverse relationship with krill abundance, suggesting that this variable is a sensitive indicator of prey abundance.

Relationship between ice events and the size-frequency distribution of krill. Blocks indicate the cells had more krill than expected compared to the null hypothesis. Size classes 16–20 and 21–25 as well as 56–60 and 61–65 are combined for analysis because of low frequencies. Ice events type 1 indicate an ice maxima, regarded as the beginning of an ice cycle based on data adapted and updated from Fraser et al. (1992a) and Stammerjohn (1993).

Ice event	Krill size class							
	16–25 mm	26–30 mm	31–35 mm	36–40 mm	41–45 mm	46–50 mm	51–55 mm	56–65 mm
1					■	■		
2	■	■				■	■	■
3		■	■	■				
4			■	■	■			
5				■	■	■		



Relationship between krill stock density (solid bars) and foraging-trip duration (shaded bars). Numbers above each bar represent the ice event category. Underlined years identify each of the three ice cycles that occurred between 1977 and 1993 based on data adapted and updated from Fraser et al. (1992a) and Stammerjohn (1993). Krill stock data are adapted from Siegel and Loeb (in press). (N/1000 m³ denotes number per cubic meter.)

Interactions between the physical and biological components of the marine environment are poorly known at all spatial scales in the southern oceans (Murphy et al. 1988, pp. 120–130). A crucial gap is understanding how the physical environment influences the abundance and distribution of prey on which predators depend (Croxall 1992). This analysis links variability in sea-ice coverage with corresponding variability in krill recruitment and abundance and the effects of these on foraging-trip durations of Adélie penguins. Although some linearity in these relationships is implied and quite likely exists given the potential scale of the recruitment signal, interpretation of population-level changes in Adélie penguins must also consider the effects of more localized factors such as fishing, human disturbance, or variability in the terrestrial breeding habitat (Fraser and Patterson in press). This synthesis has

nevertheless provided a conceptual framework for interpreting short- and long-term change in Adélie penguin populations and other measured parameters.

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