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The effects of variability in Antarctic krill (*Euphausia superba*) spawning behavior and sex/maturity stage distribution on Adélie penguin (*Pygoscelis adeliae*) chick growth: A modeling study

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ABSTRACT

Factors that control variability in energy density of Antarctic krill (*Euphausia superba*) populations, and the consequences of this variability for growth and fledging mass of Adélie penguin (*Pygoscelis adeliae*) chicks, were investigated using an individual-based energetics model. Lipid content as a function of sex/maturity stage and season was used to calculate the energy density of krill ingested by chicks. Simulations tested the influence of variability in krill size-class distribution, sex-ratio, length-at-maturity, and the timing of spawning on krill population energy density and penguin chick fledging mass. Of the parameters included in simulations, variability in the timing of krill spawning had the greatest influence on predicted Adélie penguin fledging mass, with fledging mass decreasing from 3.30 to 2.92 kg when peak spawning was shifted from early December to early March. Adélie penguin chicks that fledge from colonies along the western Antarctic Peninsula (wAP) and survive to recruit into the breeding population are 0.117 kg heavier than those that do not survive to breed. Thus, it appears that small differences in fledging mass potentially have significant implications for Adélie penguin chick survivorship. Therefore, the timing of krill spawning may have important consequences for Adélie penguins, and other top-predator species, that may time critical activities to coincide with a period of dependable prey availability with maximum energy density.

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1. Introduction

Among seabirds, chick survival and recruitment is often positively correlated with their mass as they leave the nest site (Perrins et al., 1973; Jarvis, 1974; Hunt et al., 1986; Golet et al., 2000; Litzow et al., 2002). Thus, understanding factors that influence chick growth is integral to assessing the effects of environmental variability on seabird population dynamics. These factors include prey quality (Golet et al., 2000; Osterblom et al., 2001; Litzow et al., 2002; Davoren and Montevecchi, 2003; Martins et al., 2004), prey abundance and distribution (availability) (Croxall et al., 1999), and metabolic costs (energetic loss to non-growth processes) experienced by chicks in the colony (Taylor, 1985). While each of these factors influences growth, changes in prey quality can contribute to a reduction in fledging mass and the probability of recruitment among seabirds as shifts in the timing of processes or species abundance and distribution within a marine ecosystem occur in response to climate or fisheries mediated alteration (Golet et al., 2000; Osterblom et al., 2001; Litzow et al., 2002; Davoren and Montevecchi, 2003; Martins et al., 2004).

Antarctic krill (*Euphausia superba*) is the dominant prey-species for Adélie penguins (*Pygoscelis adeliae*) off the western Antarctic Peninsula (Volkman et al., 1980; Lishman, 1985; Trivelpiece et al., 1990) (wAP, Fig. 1). Therefore, factors that influence the quality of Antarctic krill (due to changes in demography or the timing of krill population processes) may have important implications for fledging mass (and consequently, recruitment) of Adélie penguins in this region. While variability in prey type, prey availability, and metabolic costs experienced at the nest clearly affect fledging mass, variability among factors influencing the quality of Antarctic krill and the consequences of this variability on chick growth and recruitment is the focus of this study.

The quality of Antarctic krill as prey is determined by its energy density, which correlates directly with lipid content (Clark, 1980). Variability in lipid content among Antarctic krill is determined by how different sex/maturity stages balance the physiological requirements of spawning with the need to accumulate lipid prior to the onset of winter (Clark, 1980; Quetin and Ross, 1991; Nicol et al., 1995; Virtue et al., 1996; Hagen et al., 1996, 2001). This balance is critical to Antarctic krill populations,

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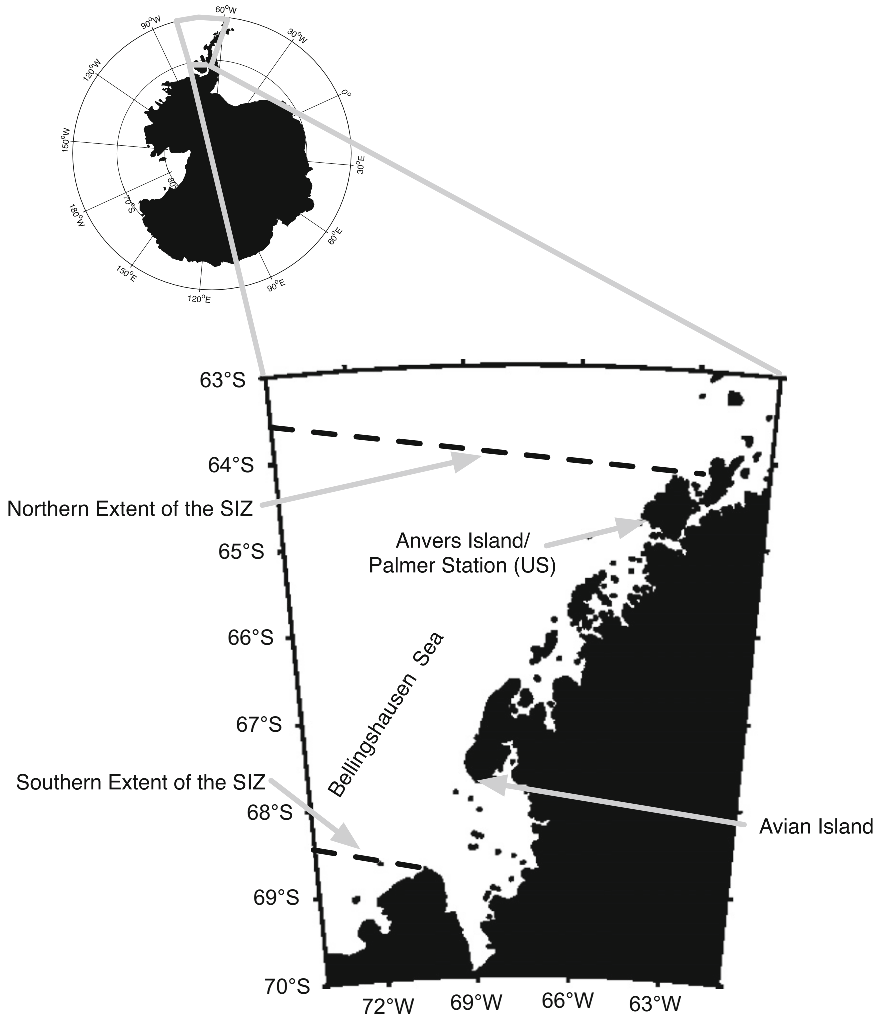

Fig. 1. Map of the western Antarctic Peninsula showing locations of Adélie penguin breeding colonies at Anvers Island (ANV) and the location of Palmer Station (US). Also shown are the northern and southern extent of the seasonal ice zone, adapted from Jacobs and Comiso (1997).

given the brief period during austral summer when food is abundantly available.

Moreover, phytoplankton blooms in Antarctic waters have considerable variability (Garibotti et al., 2005) and are influenced by sea ice (Spiridonov, 1995; Kawaguchi et al., 2006) and hydrographic conditions (Prézelin et al., 2000, 2004). The timing and intensity of Antarctic krill spawning and, presumably, the rate and amount of lipid accumulated by Antarctic krill depend on the timing of the spring bloom and the type of phytoplankton available as food (Quetin and Ross, 2001; Kawaguchi et al., 2006). Specifically, time-varying phytoplankton cell density and type control the ability of krill to ingest and direct energy toward development of lipid stores, growth, or reproduction. The extent to which the Antarctic krill spawning schedule is determined by endogenous reproductive rhythm is unknown. However, significant interannual variability in krill spawning timing, intensity, and duration has been observed (Spiridonov, 1995; Quetin and Ross, 2001), which presumably reflects variability in the timing of physical—biological processes that control phytoplankton blooms (Makarov, 1975; Ross and Quetin, 1983; Siegel et al., 2002; Kawaguchi et al., 2006). Climate change affects the extent of the seasonal pack ice and the timing of ice retreat, which are likely to alter characteristics of spring phytoplankton blooms off the wAP and consequently the accumulation of lipid in krill. These processes could affect chick growth in this region if Adélie penguins do not alter their breeding schedule in response to interannual variability in the availability of high-energy krill.

Antarctic krill size-class distribution also varies interannually and is linked with environmental conditions that govern krill recruitment and mortality (e.g., seasonal-ice characteristics and presumably spring bloom timing, type and magnitude) (Quetin and Ross, 2001, 2003; Fraser and Hofmann, 2003). As a result, the maturity stage distribution among Antarctic krill also varies from year to year. The variability in sex/maturity stage influences lipid accumulation patterns, which is likely to result in inter-annual variability in Antarctic krill lipid content.

In this study, an individual-based energetics model that simulates the growth of Adélie penguin chicks breeding off the wAP was used to investigate the effects of variability in the timing, intensity and duration of Antarctic krill spawning as well as variability in krill size-class distribution and sex-ratio on Adélie penguin prey energy density, chick growth and fledging mass. The wAP Adélie penguin population is the focus of this study because climate variability has been linked with changes in biological production that affect top-predator species in this region (Fraser and Hofmann, 2003; Ducklow et al., 2007). Thus, results from this study provide guidance on possible future scenarios that may result in this region as the marine ecosystem responds to climate variability.

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