

Spring 2009

## Factors Affecting Adult Foraging and Chick Growth of Adélie Penguins (*Pygoscelis adeliae*) off the Western Antarctic Peninsula: A Modeling Study

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**FACTORS AFFECTING ADULT FORAGING AND  
CHICK GROWTH OF ADÉLIE PENGUINS  
(*PYGOSCELIS ADELIAE*) OFF THE WESTERN  
ANTARCTIC PENINSULA: A MODELING STUDY**

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A Dissertation Submitted to the Faculty of  
Old Dominion University in Partial Fulfillment of the  
Requirement for the Degree of

DOCTOR OF PHILOSOPHY

OCEANOGRAPHY

OLD DOMINION UNIVERSITY

May 2009

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## ABSTRACT

# FACTORS AFFECTING ADULT FORAGING AND CHICK GROWTH OF ADÉLIE PENGUINS (*PYGOSCELIS ADELIAE*) OFF THE WESTERN ANTARCTIC PENINSULA: A MODELING STUDY

Erik W. Chapman  
Old Dominion University, 2009  
Director: Dr. Eileen E. Hofmann

Coupled individual-based models that simulate Adélie penguin (*Pygoscelis adeliae*) chick growth and adult foraging behavior during the chick growth period were developed and used to explore factors that influence chick fledging mass and adult foraging energetics off the western Antarctic Peninsula (WAP). Adélie penguin colonies in this region are undergoing changes in population size that have been correlated with climate-driven alteration of the marine and terrestrial environment. Simulations were selected to highlight possible mechanistic linkages between climate variability and chick growth and adult foraging processes. These processes were the focus of this study because chicks that fledge at a greater mass are more likely to recruit to the breeding population and Adélie penguin population dynamics can link directly with recruitment and fledging mass.

Simulations using the chick-growth model tested the influence on penguin chick fledging mass of variability in 1) timing of Antarctic krill (*Euphausia superba*) spawning, 2) chick diet composition [Antarctic silverfish (*Pleuragramma antarcticum*) combined with Antarctic krill compared to an all-Antarctic krill diet], 3) provisioning rate; and 4) the extent to which chicks become wet (from rain or melting snow). Simulations coupling the adult-foraging and chick-growth models investigated the influence on adult mass, foraging energetics, and chick growth of variability in 1) prey-availability characteristics (prey ingestion rate and distance between colony and prey), 2) the extent to which adults prioritize self-maintenance over chick provisioning, 3) adult digestion rate while foraging (a poorly studied physiological rate), and 4) adult diet composition [Antarctic krill combined with Antarctic silverfish (50% female) compared to all-Antarctic krill (50% and 100% female)].

In the chick-growth model simulations, shifting peak Antarctic krill spawning from

early December to early March reduced fledging mass by 12%, enough to reduce a chick's probability of recruitment. Introducing a minimal amount of third-year age class (AC3) Antarctic silverfish to an Antarctic krill diet increased Adélie penguin fledging mass by 5%. Environmental stress that results in more than a 4% reduction in provisioning rate or wetting of just 10% of the chick's surface area decreased fledging mass enough to reduce the chick's probability of recruitment. The negative effects of reduced provisioning and wetting on chick growth can be compensated by an increase in AC3 Antarctic silverfish in the chick diet. Results from the coupled models showed that increasing adult ingestion rate, decreasing distance to prey, increasing adult digestion rate, feeding only on female Antarctic krill, and including Antarctic silverfish in the diet increased the range in prey-availability characteristics over which adults can raise full-sized chicks.

Overall, results suggest future observational and modeling studies that focus on factors that influence the ability of foraging adult Adélie penguins to provide high-quality prey to their young. Furthermore, results indicate that future studies should be directed at improving our knowledge of the energetic and physiological constraints on adult Adélie penguin foraging and chick growth. Results suggest that factors that influence the timing and extent of lipid acquisition and spawning among Antarctic krill may have important consequences for Adélie penguin chick growth. Additionally, climate-driven alteration of processes that determine the availability of phytoplankton biomass may have important consequences for Adélie penguins and other top-predator species that time critical activities to coincide with dependable availability of prey with maximum energy density. Also, results suggest that the loss of Antarctic silverfish from the diets of Adélie penguins in some parts of the WAP may have limited the ability of adults to compensate for the negative effects of climate-related changes in the marine (reduced Antarctic krill abundance) and terrestrial (increased wetting of chicks) environment.

This work is dedicated to my sunshine, Michèle, and my beautiful children Reece and Kira, whose love and support have sustained me through this process.

## ACKNOWLEDGMENTS

I first would like to thank my principal advisor, Eileen E. Hofmann, for providing me with the opportunity and the guidance necessary to begin work in the field of marine ecosystem modeling. I am grateful to William R. Fraser for always being willing to spend time discussing the ecology of the western Antarctic Peninsula and for giving me my first opportunity to work in the Antarctic. I could not have completed this work without the guidance, support, and constructive criticism from Christine A. Ribic. I would also like to thank John M. Klinck for always welcoming me into his office and taking the time to answer my questions. His teaching was invaluable to my introduction to the basics of programming and ocean modeling. Combined, these four researchers represent a top-level understanding of the methods, techniques, and the ecological system that formed the basis of this work. I am deeply indebted to them and their collective interest in this work and my professional development.

I would also like to thank each of my committee members who have provided the constructive criticism necessary to make this work the best that it can be. I am thankful for the assistance of Baris Salihoglu who provided the original framework for the chick-growth model. William R. Karasov provided critical suggestions and insights into the complex physiological transition that occurs as chicks develop from hatchling to fledgling, which was helpful in developing the parameterizations used in the chick-growth model. I would also like to thank the Palmer Station support staff for facilitating the long-term data collection efforts. Furthermore, I am grateful for the assistance provided by many field team members who have helped with the data collection over the years. The collection and analysis of the Adélie penguin data used in this study was funded through the National Science Foundation Grants ANT-0323254, OPP-9011927, OPP-9605596, OPP-0130525, OPP-0217282, OPP-0224727 and OPP-052361. The development of the penguin chick model was supported by the National Science Foundation Grant ANT-0523254 and is part of the U.S. Southern Ocean Global Ecosystem Dynamics (GLOBEC) synthesis and integration program.

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## CHAPTER I

### INTRODUCTION AND RESEARCH QUESTIONS

The Adélie penguin (*Pygoscelis adeliae*) is a top predator in the Antarctic marine food web. Therefore, observed changes in reproductive success, population trajectory, and distribution of this species provide insight into the marine environment and its adjustment to variability, such as that resulting from climate change. As a result, concurrent studies of environmental conditions and Adélie penguin and other top predator populations are now integral components of multidisciplinary Antarctic ecosystem research programs, such as the Palmer Long Term Ecological Research (PAL-LTER) program (Smith et al., 1995) and the Southern Ocean Global Ocean Ecosystems Dynamics (SO GLOBEC) program (Hofmann et al., 2006, 2008).

This research project uses modeling studies to explore the influence on Adélie penguin chick growth and foraging behavior of variability among physical and biological environmental factors. Chick growth and adult foraging were selected for study because these processes are critical to recruitment and thus to the population trajectory for this species. The project focuses on conditions affecting approximately 200,000 pairs /citepwoe93 of Adélie penguins that breed in a cluster of heterogeneously distributed colonies located on the west Antarctic Peninsula (WAP) between Anvers Island (ANV, 64° 46' S; 64° 04' W; Fig. 1) and Avian Island (AVI, 67° 46' S; 68° 54' W; Fig. 1).

Since the late 1970s, the number of breeding penguins off the WAP has increased in some colonies while decreasing in others. For example, over this time period a breeding population of about 15,000 Adélie penguins at ANV (Fig. 1) declined by 40% (Fraser and Patterson, 1997) while the populations of two penguin species with a more sub-Antarctic distribution, gentoo (*Pygoscelis papua*) and chinstrap (*Pygoscelis*

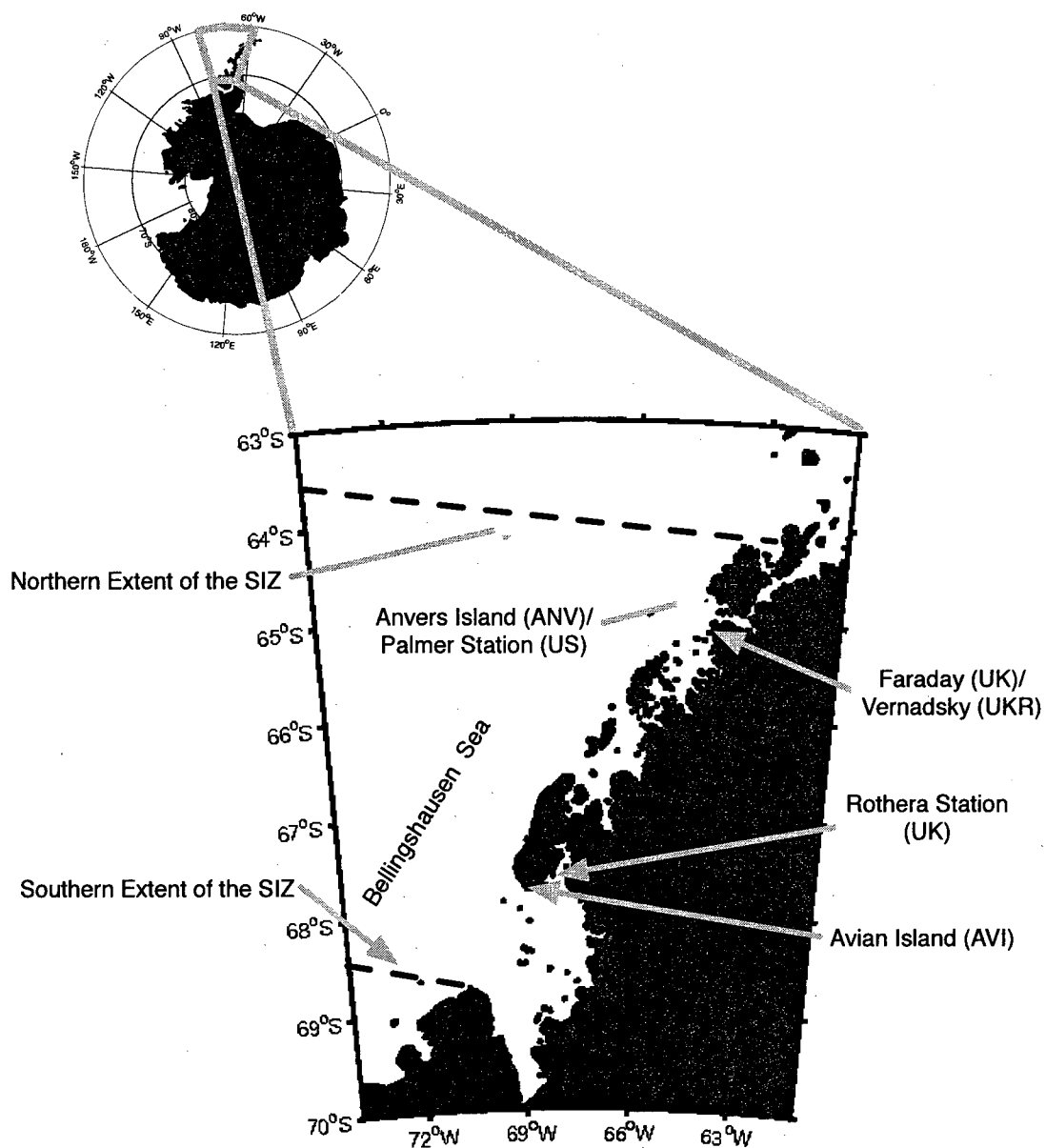


Fig. 1. Map of the western Antarctic Peninsula (WAP) including Avian Island (AVI) and Palmer Station (US) on Anvers Island (ANV). Research stations that were the source of environmental data are indicated [Faraday (UK)/Vernadsky (UKR) and Rothera (UK)]. Also shown are the northern and southern extent of the seasonal ice zone (SIZ) which was based on Jacobs and Comiso (1997).

*antarctica*) penguins, increased (Fraser et al., 1992; Ducklow et al., 2007). At AVI (Fig. 1), Adélie penguin populations have increased over the same period (Fraser, unpublished data).

These population changes occurred during a period of regional warming on the WAP that is characterized by an atmospheric warming rate of  $0.56^{\circ}\text{C decade}^{-1}$  during the last 50 years (Turner et al., 2005a), a trend significant to the 5% level. This warming trend is especially pronounced ( $+ 1.08^{\circ}\text{C decade}^{-1}$ , significant at 5% level) during the winter months (Turner et al., 2005a) (Fig. 2), which has a direct affect on winter sea ice extent (Turner et al., 2005a). As a result, winter sea ice coverage in the Bellingshausen Sea west of the WAP (Fig. 1 and Fig. 3) has been reduced at a rate of approximately  $15,000 \text{ km}^2 \text{ year}^{-1}$  (Kwok and Comiso, 2002). Sea ice is a preferred foraging habitat for Adélie penguins (Ribic and Ainley, 1988/1989; Ainley et al., 1994; Ainley, 2002), and changes in its distribution affect Adélie penguin populations by influencing their foraging behavior as well as the distribution and abundance of their primary prey items, Antarctic krill (*Euphausia superba*) and Antarctic silverfish (*Pleuragramma antarcticum*).

While alteration of the prey field and sea ice conditions surely has important consequences for Adélie penguin populations on the WAP, other changes in the physical-biological environment have been observed at ANV that may also impact the breeding ecology of this species. For example, due to increased atmospheric temperatures, precipitation has increased on the WAP (Turner et al., 2005b). This has resulted in increased snowfall on and snow-melt water in colonies during the early part of the breeding season (Patterson et al., 2003).

These environmental changes affect many processes that influence Adélie penguin population dynamics, including recruitment of offspring into the breeding population. Adélie penguins are a long-lived species typically having high, stable adult survivorship and variable recruitment. Therefore, recruitment is a process that is directly

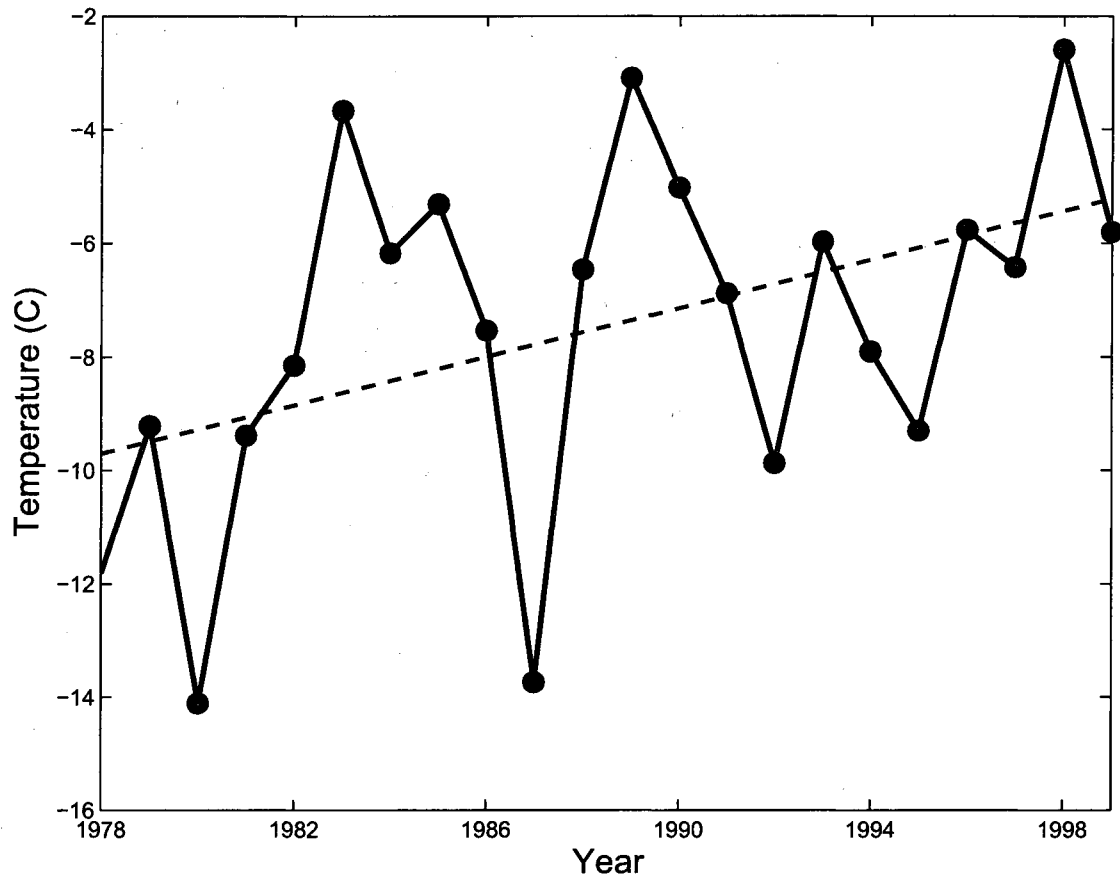


Fig. 2. Trend in mean winter near surface temperature at Vernadsky/Faraday (Fig. 1) (Turner et al., 2005a). A linear regression fitted in Turner et al. (2005a) is shown (---).

linked with Adélie penguin population trajectories.

For many seabirds, survival and recruitment of chicks is positively correlated with fledging mass, the mass chicks attain before permanently leaving the nest site (Perrins et al., 1973; Jarvis, 1974; Hunt et al., 1986; Golet et al., 2000; Litzow et al., 2002). This holds for Adélie penguins off the WAP, where larger chicks are more likely to survive to recruit into the breeding population (see Chapter III) and mean fledging mass is positively correlated with population trajectory (Hinke et al., 2007). Heavier chicks are more likely to survive because they have larger energy reserves with which to endure the energetic stresses of the post-fledging period. These include learning

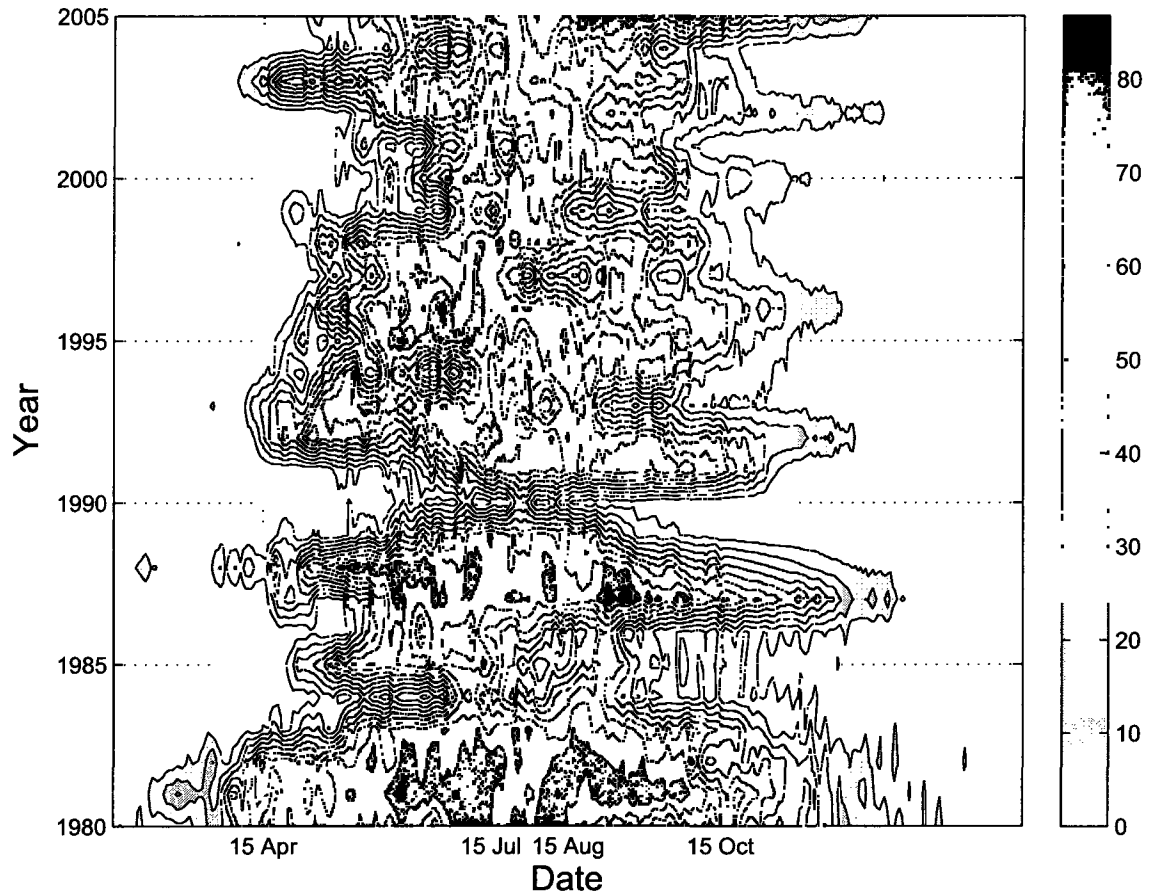


Fig. 3. Contour of mean daily sea ice concentration within 200 km of Anvers Island between 1980 and 2005. Data obtained from the National Snow and Ice Center and were derived from analysis of satellite passive microwave data (Cavalieri et al., 2005).

to find and capture prey, migrating long distances, and adding weight and strength in preparation for the non-breeding season, a period of potentially low/patchy prey availability.

Thus, understanding factors that influence chick growth and fledging mass is integral to assessing the effects of environmental variability on penguin population dynamics. The most important factors that affect penguin chick growth and fledging mass are 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 losses experienced at the nest

(Taylor, 1985). Climate variability can alter the physical-biological connections in the ecosystem that determine the species, age-class, quality, and availability of prey. It also influences weather conditions that affect the thermoregulatory costs experienced by chicks in the colony. Specifically, increased snowfall increases exposure of chicks to water in colonies. Contact with water can disrupt the insulating properties of chick down and therefore introduce an increased thermoregulatory cost that competes with growth and can reduce chick fledging mass.

While diet and metabolic rate at the nest influence chick growth, adult foraging behavior mediates feeding rates and is critical to chick growth and breeding success. The energetic investment in breeding by adult birds in a particular year can reduce survivorship and/or future breeding success, and is referred to as the cost of breeding (Williams, 1966). In order to maximize life-long fecundity, foraging penguins should balance investment in current breeding effort against chances for survival and breeding in subsequent years. Members of long-lived, low reproductive rate seabird species such as the Adélie penguin typically follow strategies that favor their own survival at the expense of a single year's breeding effort (Mauck and Grugg, 1995; Watanuki et al., 2002). Therefore, under moderate environmental stress, Adélie penguins alter their behavior (e.g., do not breed, reduce provisioning of chicks) to maintain their own fitness at the expense of energetic investment in their offspring (Clarke, 2001; Watanuki et al., 2002; Takahashi et al., 2003). Under favorable environmental conditions, adults are able to capture enough prey to meet their own metabolic requirements while provisioning young at rates that will grow large chicks. Therefore, foraging behavior translates environmental conditions into chick production and individual fitness which in turn help determine population dynamics of Adélie penguins.

This discussion provides a basis for developing a conceptual framework (Fig. 4) that links the physical and biological processes by which climate change may affect Adélie penguin population dynamics at ANV. Processes controlling chick growth and

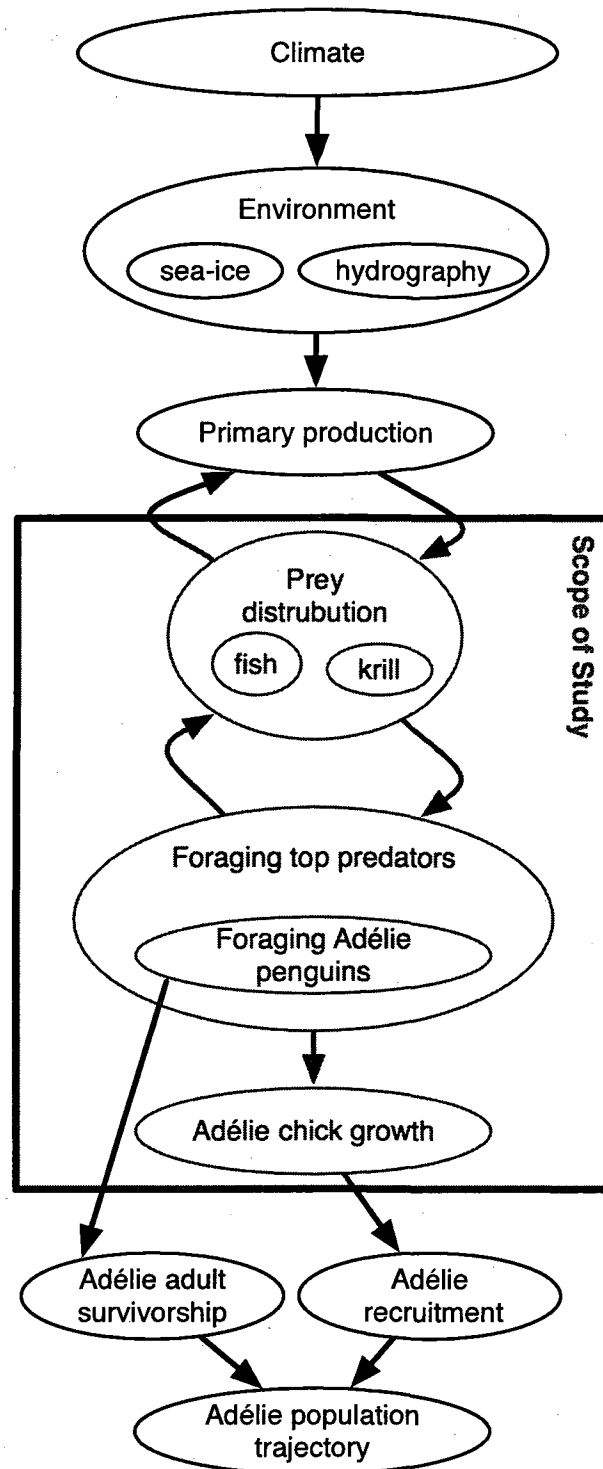


Fig. 4. Conceptual diagram of linkages between climate, the physical-biological environment and the population trajectory of Adélie penguins that was used in this study. The part of this conceptual model considered in this research is outlined by the box.

fledging mass and adult foraging energetics and environmental factors affecting both were investigated in this study through development and implementation of coupled chick-growth and adult-foraging models.

These models were used to address two primary research questions. The first provides insights into controls on chick growth which ultimately affects recruitment: *How does variability in physical and biological variables associated with the marine and terrestrial environments influence Adélie penguin chick growth at colonies off the WAP?* The second research question focuses on the link between the environment and adult foraging ecology: *How does variability in environmental and physiological factors influence adult Adélie penguin foraging energetics and chick growth during breeding at colonies off the WAP?*

Adélie penguin chick-growth and adult-foraging individual based models (IBM) were developed and parameterized to reflect conditions within the study region. The models were used to simulate the flow of energy from prey to predator, enabling exploration of the effect of environmental variability on chick growth and adult self-maintenance (Fig. 5).

Parameterization and development of the models relied on previously collected data sets from ANV. Therefore, simulations were designed primarily to assess the influence of environmental variability at ANV, though implications for Adélie penguins breeding at other locations were considered.

Chapter II provides general background information relevant to this study. Chapters III and IV provide descriptions of the chick-growth model and simulations done with the model. Specifically, the quality of the Antarctic krill prey that results from variability in Antarctic krill sex/maturity stage and timing of krill spawning and lipid accumulation on Adélie penguin chick growth is considered in Chapter III. The influence of prey type, wetting of chicks in the nest, and variability in provisioning rate on chick growth is the focus of Chapter IV. The coupled adult-foraging and chick-growth

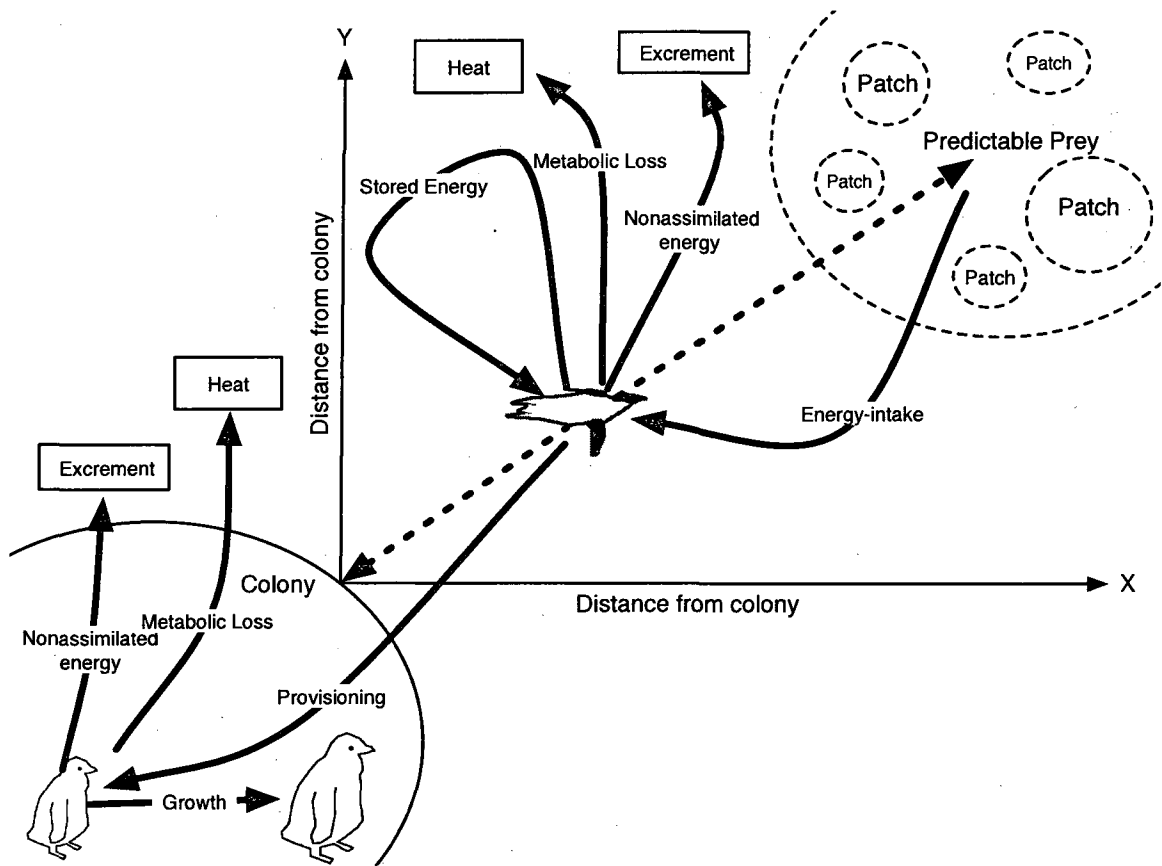


Fig. 5. A schematic of the processes included in the Adélie penguin chick-growth and adult-foraging models. The solid arrows indicate the energy transfers. Dashed arrows indicate movement of the foraging adult. The adult forager moves between the colony, where chick provisioning occurs, and the area of prey.

models are described in Chapter V and used to assess environmental and physiological constraints on the ability of foraging adult Adélie penguins to produce viable chicks. Within each chapter, implications of the effects of climate change on the breeding energetics of Adélie penguins off the WAP are considered. The final chapter summarizes the results with respect to the research questions and reviews the contribution of this study to the understanding of climate-driven variability in physical-biological linkages within the marine ecosystem off the WAP.

## CHAPTER II

### BACKGROUND

This chapter reviews the current understanding of basic components of the physical-biological system off the WAP, much of which has been generated by multidisciplinary research efforts including the PAL-LTER and SO GLOBEC programs.

#### II.1 SEA ICE

Sea ice is a prominent and variable feature that influences physical and biological processes throughout many regions of the Southern Ocean (Ainley et al., 2005; Emslie and Woehler, 2005; Ducklow et al., 2007). Each year sea ice grows from about  $4 \times 10^6$  km<sup>2</sup> in the summer to a peak coverage of  $20 \times 10^6$  km<sup>2</sup> in the winter (Zwally et al., 1983). Growth of the seasonal ice coverage in the Southern Ocean occurs slowly (over 8 months, between February to September) while melting of the sea ice in spring happens relatively quickly (over 3 months, October to December) (Gordon, 1981; Zwally et al., 1983; Jacobs and Comiso, 1997). Off the WAP, the northern edge of the sea ice proceeds from a minimum near 70°S in February to a maximum between 66° and 65°S in September (Jacobs and Comiso, 1997) (Fig. 1). However, seasonal ice development is characterized by inter-annual variability in the timing of sea-ice growth and retreat and the amplitude of annual fluctuation. For example, between 1973 and 1996, the maximum sea ice extent varied about 600 km (Fraser and Hofmann, 2003).

Variability in maximum sea-ice extent is associated with atmospheric pressure features that affect wind and temperature and propagate around the Antarctic continent in an eastward direction with variable frequency that may be linked to the occurrence of El Niño events (Murphy et al., 1995; Peterson and White, 1998; Yuan and Martinson, 2000; Kwok and Comiso, 2002; Turner, 2004; Yuan, 2004). In recent decades,

the amount of seasonal ice production and the duration of seasonal ice coverage along the WAP have been significantly decreasing (Jacobs and Comiso, 1997; Smith and Stammerjohn, 2001; Liu et al., 2004; Stammerjohn et al., 2008).

Sea ice has ecological significance because it provides protection from predators for macro-zooplankton and is a substrate for ice algae and micro-zooplankton which is food critical to early life-stages of macro-zooplankton and fish species (Daly, 1990; Fach et al., 2002; Arrigo and Thomas, 2004). Recent decadal changes in seasonal ice-coverage patterns have been correlated with changes in the marine ecosystem species composition and structure (Ducklow et al., 2007).

## II.2 ADÉLIE PENGUIN DIET

Most information about the diet of Adélie penguins comes from studies done during the summer breeding period throughout the Adélie penguin's circum-Antarctic range. These studies show that diet consists primarily of Antarctic krill, Antarctic coastal krill (*Euphausia crystallorophias*), and Antarctic silverfish. The species of krill in Adélie diets varies according to the location of a colony with respect to the slope-break (Ainley, 2002). In general, Antarctic krill is more likely to be present in diets when colonies are located in waters influenced by the open ocean and are close to the slope break (e.g., the WAP). Antarctic coastal krill tends to dominate Adélie diets when a colony is located in the interior of the continental shelf, further away from the slope-break (e.g., the Ross Sea). The presence or absence of Antarctic silverfish seems to depend more on seasonal sea-ice conditions. For example, off the WAP, Antarctic silverfish are absent from Adélie penguin diets at, and north of, AVI (Fig. 1) (Volkman et al., 1980; Fraser, unpublished data) where sea ice is present for a short time each year. Sampling of Adélie penguin gut content (diet) at locations where krill and fish are consumed indicates a shift over the course of the breeding season to a diet that includes a higher percentage of fish (Emison, 1968; Puddicome

and Johnstone, 1988; Ainley et al., 1998, 2003). It is not known whether this occurs at locations off the WAP where fish are included in Adélie penguin diets.

### II.3 ADÉLIE PENGUIN FORAGING BEHAVIOR

Adélie foraging behavior shows strong regional variability in the Southern Ocean, presumably in response to differences in the physical affects on biological processes. These difference largely depend on ice conditions around colonies. When fast ice occurs around colonies, as is the case in the Ross Sea and Eastern Antarctica, Adélie penguins forage in tidal cracks and through open water adjacent to ice bergs set in the ice (Watanuki et al., 2003). When fast ice conditions persist during the chick provisioning period, foraging trip duration is reduced, meal sizes are smaller, and feeding frequency is increased (Watanuki et al., 1997). When fast-ice is not present around colonies, as is typical off the WAP, Adélie penguins typically forage within generally predictable locations (Ainley et al., 2003) usually within 40 km of the colony (Trivelpiece et al., 1987b; Watanuki et al., 2002; Ainley et al., 2003) and in close association with a combination of open water and sea ice (Ribic and Ainley, 1988/1989; Ainley et al., 1994; Ainley, 2002). Because Adélie penguins generally forage in association with sea ice, this species is considered an ice-obligate species (Ainley, 2002).

As discussed above, Adélie penguins can shift their diet from krill to fish later in the breeding season. However, this shift does not appear to cause any change in diving pattern (Ropert-Coudert et al., 2002). Furthermore, the percentage of time spent hunting and feeding during foraging trips does not appear to change significantly over the breeding season (Chappell et al., 1993c). However, studies do indicate that in some cases foraging-trip duration and distance covered increase significantly over the breeding season (Ainley et al., 2004). This may indicate a breeding response to depletion of prey stocks by predators (Ainley et al., 2004) and increased energetic requirement of the chick(s) (Lishman, 1985; Culik et al., 1990; Salihoglu et al., 2001),

or to the offshore migration of krill (Lascara et al., 1999).

## **II.4 SEA-ICE OPTIMUM CONDITIONS FOR ADÉLIE PENGUIN REPRODUCTION**

Sea ice is considered important to Adélie penguin reproductive success because their principle prey items (krill and Antarctic silverfish) also appear in association with sea ice (Ainley, 2002). In some circumstances, relatively heavy ice years correlate with a higher percentage of breeding Adélie adults (Fraser et al., 1992) within a colony, increasing reproductive effort. However, heavy sea-ice conditions can negatively affect breeding effort by forcing Adélie penguins to walk over sea ice to reach breeding grounds; walking has a high energetic cost (Ainley, 2002). Extensive sea ice can also limit reproductive success by preventing access to productive foraging waters (Wilson et al., 2001). These observations have given rise to the optimum ice condition hypothesis, which states that peak reproductive success for Adélie penguins is achieved under moderate ice conditions (Fraser and Trivelpiece, 1996). However, this relationship is theoretical and no specific criteria have been proposed to characterize moderate ice conditions. Off the WAP, where persistence and concentration of sea ice increase with increasing latitude, optimum ice conditions likely correspond with an optimum latitude for Adélie breeding (Fig. 6). Under climate warming scenarios, this optimum latitude would be expected to shift to a higher latitude (to the south).

## **II.5 ADÉLIE PENGUIN PREY FIELD OFF THE WESTERN ANTARCTIC PENINSULA**

The following sections discuss Antarctic krill and Antarctic silverfish ecology, the two primary components of the Adélie penguin prey field off the WAP. The influence of environmental variability on each species and the importance of each species as Adélie penguin prey are considered.

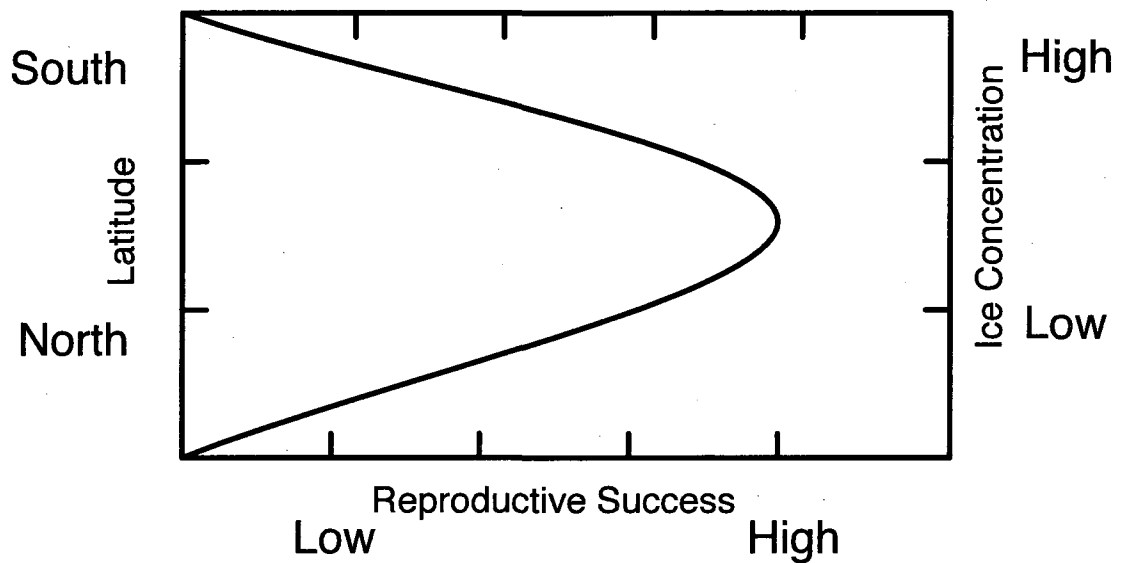


Fig. 6. A schematic of the ice optimum theory that relates latitude and sea-ice concentration to Adélie penguin reproductive success. The relationship between ice concentration and reproductive success is adapted from Fraser and Trivelpiece (1996).

### II.5.1 Antarctic Krill

Antarctic krill is a central component of the Antarctic marine system, a position that likely reflects adaptation to characteristic features and variabilities of its environment (Verity and Smetacek, 1996). In the Southern Ocean, circulation patterns and water mass distributions (Marr, 1962; Fach et al., 2002; Hofmann and Hüsrevoğlu, 2003; Hofmann and Murphy, 2004), bathymetry (Hofmann and Hüsrevoğlu, 2003), and sea ice (Marr, 1962; Mackintosh, 1972; Siegel and Loeb, 1995; Loeb et al., 1997; Atkinson et al., 2004) influence food availability, spawning habitat, and advection of larval and juvenile stages of Antarctic krill. They also influence Antarctic krill abundance and distribution.

Circulation (Hofmann et al., 1992) and bathymetry combine to provide environmental conditions necessary to support the descent-ascent embryo and larval development of krill (Marr, 1962; Hofmann and Hüsrevoğlu, 2003). These conditions, facilitated by bathymetrically controlled transport of heat and nutrients associated with Upper Circumpolar Deep Water (UCDW), are met at the shelf-break off the WAP (Hofmann et al., 1992; Hofmann and Hüsrevoğlu, 2003) and there is evidence that krill move offshore to these locations to spawn in December and January (Siegel, 1988; Spring and Schalk, 1992). However, over the continental shelf, deep-water troughs have also been identified as possible locations for on-shore transport of (UCDW) (Dinniman and Klinck, 2004) where successful spawning could take place (Hofmann and Hüsrevoğlu, 2003). However, the exact nature of krill spawning behavior over the continental shelf and at the shelf-break remains somewhat uncertain (Siegel, 2005).

Following spawning and the descent-ascent developmental stage, advection transports or retains larval krill (Marr, 1962; Mackintosh, 1972; Fach et al., 2002; Reid et al., 2002; Hofmann and Murphy, 2004; Fach et al., 2006; Fach and Klinck, 2006). Larvae spawned off the WAP can either be retained over the shelf or transported north along the continental shelf break by the ACC (Fach et al., 2002, 2006; Fach and Klinck, 2006). Retention over the shelf could be mediated by a possible two-gyre circulation system over the continental shelf on the WAP (Smith et al., 1999a). Therefore, alteration of circulation patterns, such as a change in the location of the ACC with respect to the continental shelf or a change in the intensity or location of the gyre system over the shelf, can have important implications for regional krill populations (Fach et al., 2002, 2006; Fach and Klinck, 2006).

While circulation determines the potential routes of dispersal for Antarctic krill, survival during and after dispersal depends on the presence of habitat that supports development to the adult stage. There is strong evidence that sea ice provides habitat that is critical to this development. For example, there is a positive relationship

between over-winter sea ice extent and summer recruitment of krill, suggesting that sea ice plays a role in providing food and protection from predation and so increases survival of larval stages of krill (Daly, 1990; Siegel and Loeb, 1995; Loeb et al., 1997; Quetin and Ross, 2003; Atkinson et al., 2004). Also, a modeling study found that the availability of sea ice biota as food for larval krill in the Scotia Sea is important for over-winter survival of Antarctic krill spawned off the WAP as they are advected by ocean currents to South Georgia (Fach et al., 2002). Because krill are believed to live between 5 and 7 years (Nicol, 2000; Siegel, 2000), it has been hypothesized that Antarctic krill populations are dependent on recruitment events associated with high ice years every 4 or 5 years in order to maintain their populations (Siegel and Loeb, 1995; Fraser and Hofmann, 2003; Quetin and Ross, 2003).

### *II.5.2 Antarctic Silverfish*

The high rate of endemism (Eastman and McCune, 2000) within the suborder Notothenioidei (88%), a group that dominates the fish community in the Southern Ocean particularly in shelf areas where it comprises 77% of the fish species and 90-95% of fish abundance and biomass (DeWitt, 1970; Eastman and McCune, 2000), indicates a strong linkage between these species and environmental conditions unique to the Southern Ocean. Antarctic silverfish is the most abundant member of the Notothenioidei and has developed neutral buoyancy, ecologically separating itself from this primarily demersal fish group. In this way, Antarctic silverfish has escaped competition with other demersal species and capitalized on an under-exploited pelagic food source (Wöhrmann et al., 1997). Sub-adults and adults avoid feeding overlap with each other by inhabiting different depth ranges and exploiting different prey. For example, juveniles and post-larval stages reside in the top 150 m (Kellermann, 1986) and feed on zooplankton eggs and small copepods (Kellermann, 1987; Hubold and Ekau, 1990), while adults tend to reside below 300 m (Fuiman et al., 2002) and feed

on krill species, amphipods, and copepods (Takahashi and Nemoto, 1984; Hubold, 1985). Based on this information, sub-adults and spawning adults (see below) should be most available to top predators that feed in the top 150 m of the water column.

Antarctic silverfish life history is characterized by slow growth, delayed maturation to reproductive condition, a long life-span (up to 30 years), and high reproductive rate (Radtke et al., 1993). Spawning appears to be linked to the under-surface of permanent ice-shelves at high latitudes (south of 65°S) (Keller, 1983; Hubold, 1984; Fuiman et al., 2002). These shelves act as nursery habitat for very early stages of development (Vacchi et al., 2004). Distribution of post-larva and juveniles is linked to advective transport (Kellermann, 1986, 1996), and it has been suggested that the SIZ plays an important role as an additional nursery for these life stages (Kellermann, 1987).

Antarctic silverfish are particularly abundant in regions of high sea-ice concentration, where circulation patterns promote retention of larval and post-larval stages such as the Weddell and Ross Seas (DeWitt, 1970; Hubold and Ekau, 1987). Off the WAP, it has been suggested that coastal waters in the northeastern Bellingshausen Sea (including the AVI-ANV region) are important spawning areas for the Antarctic silverfish (Kellermann, 1986, 1996). These locations are believed to be the source for recruited post-larval and juvenile Antarctic silverfish that have been spawned to the south and advected to more northern locations near ANV island (Kellermann, 1987).

Antarctic silverfish are second only to Antarctic krill in importance to the marine ecosystem of the Southern Ocean (Barrera-Oro, 2002). Some evidence suggests that Antarctic silverfish were more prominent in Adélie penguin diets in several regions of the Antarctic, including the WAP, prior to the removal of large cetaceans and seals approximately 200 years ago (Emslie and Patterson, 2007). This evidence further suggests that Adélie penguins off the WAP are able to prey upon significant amounts of Antarctic silverfish of at least the 4-year Age Class (AC4) (McDaniel and Emslie,

2002). In general, fish are most important to foraging Adélie penguins during periods when krill are absent or in low abundance within foraging areas (DeWitt, 1970), perhaps when krill move offshore to spawn (Barrera-Oro, 2002) or when krill stocks are depleted due to high predation pressure (Ainley et al., 2003, 2006).

## II.6 CLIMATE VARIABILITY AND ECOSYSTEM IMPLICATIONS

The climate and sea-ice variability observed on the Antarctic Peninsula has been linked to variability in the Southern Oscillation Index (SOI) (Kwok and Comiso, 2002) and the occurrence of El Niño events (Kwok and Comiso, 2002; Turner et al., 2005a). As a result, it has been suggested that the cause of warming on the Antarctic Peninsula may be the result of propagation of climate conditions (such as increased intensity and frequency of El Niño events) from the tropical Pacific Ocean to this region (Murphy et al., 1995; Peterson and White, 1998; Yuan and Martinson, 2000; Kwok and Comiso, 2002; Turner, 2004; Yuan, 2004). It has been further suggested that this telecommunication has resulted in reduction of the annual sea-ice extent (Stammerjohn and Smith, 1997; Jacobs and Comiso, 1997) and the frequency of heavy ice years (Fraser and Hofmann, 2003) over the warming period on the Antarctic Peninsula. This represents a potential causal mechanism for alteration in the sea-ice environment, with important implications for the physical-biological system and Adélie penguin ecology.

The declining frequency of high-ice years on the Antarctic Peninsula may be shifting environmental conditions in this location toward a regime that is not favorable to sustaining krill (Fraser and Hofmann, 2003; Quetin and Ross, 2003) or Antarctic silverfish populations. In fact, SOI and El Niño have also been linked to recruitment events of krill on the Antarctic Peninsula (Quetin and Ross, 2003). Possibly as a consequence of the changing ice-regime, Antarctic krill populations have been found to be decreasing on the Antarctic Peninsula (Loeb et al., 1997; Atkinson et al.,

2004). As discussed above, a decline in Antarctic silverfish near ANV is suggested by the virtual disappearance of this species from Adélie penguin stomach contents near Palmer Station (Fraser, unpublished data). These changes are likely to have important impacts on Adélie penguin population dynamics off the WAP.

# CHAPTER III

## ANTARCTIC KRILL ENERGY DENSITY AND ADÉLIE PENGUIN CHICK GROWTH

### III.1 INTRODUCTION

Chick growth and fledging mass are influenced by 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). Changes in prey quality alone 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 is the dominant prey species for Adélie penguins off the WAP (Volkman et al., 1980; Lishman, 1985; Trivelpiece et al., 1990). 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. Variability of these factors influencing the quality of Antarctic krill and the consequences of this variability on chick growth are assessed here. Other remaining factors that influence chick growth (diet complexity, availability, and metabolic costs experienced at the nest) are considered in Chapter IV.

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 of 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, 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 controls 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 inter-annual 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 inter-annual variability in the availability of high-energy krill.

Antarctic krill size-class distribution also varies inter-annually 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; Fraser and Hofmann, 2003; Quetin and Ross, 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.

An IBM 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 Adélie penguin nesting development period is described in the following section, which sets the framework for the modeling structure, equations, and parameters used in the chick-growth model. Next, the procedure for estimating Antarctic krill energy density is described, as are the approaches and data sets used to specify model processes and parameter values. The results section presents a reference simulation and sensitivity studies based on this simulation. The discussion section considers the implications of the simulation results for breeding Adélie penguins off the WAP.

## III.2 METHODS

### *III.2.1 Adélie Penguin Nestling Development*

Adélie penguin chicks hatch in nests of one or two chicks in late December off the WAP (Chappell et al., 1990; Culik, 1994). For the first 20-25 days after hatching (the guard stage), adults take turns attending the chick(s) at the nest while the other adult forages to meet its own energetic requirements and those of its offspring. During this stage, chicks develop homeostasis as they replace their hatchling feathering with a thick, downy plumage (Bucher et al., 1990; Ainley, 2002). The energetic demands of the growing chick(s) increases dramatically until both adults must forage simultaneously, ending the guard stage. At this time, unattended chicks gather in wandering groups called *crèches*.

About 40 days after hatching, chicks begin a second molt, replacing their downy plumage with water-proof feathering (Ainley, 2002). Finally, about 3 to 7 days prior

to fledging, adults stop feeding their chicks (Trivelpiece et al., 1987a; Ainley, 2002) resulting in a brief starvation period during which the chicks lose about  $50 \text{ g d}^{-1}$ . At this time, chicks begin to gather on beaches from which they fledge approximately 54 days after hatching (Chappell et al., 1990; Culik, 1994). The mass of the chick immediately prior to entering the water is the fledging mass.

Once fledglings enter the water and leave the colonies, they typically do not return until they begin breeding in their third or fourth year (Ainley, 2002). These returning chicks have successfully recruited into the breeding population of Adélie penguins. The physiological changes that coincide with chick development from hatchlings into fledglings, such as a change in biochemical body composition, metabolic rate, and assimilation efficiency, provide the basis for the structure of the chick-growth model.

### *III.2.2 Data Used in Simulations and Analyses*

#### *III.2.2.1 Adélie Penguin Diet Sample Data*

Diet samples were collected from Adélie penguins that were provisioning chicks at colonies near Anvers Island off the WAP (Fig. 1). Gut content samples were collected from 4 to 5 adult Adélie penguins every week of the breeding season between 1987 and 2004 (Fraser and Hofmann, 2003) using the water off-loading technique (Wilson, 1984). Approximately 80 diet samples were collected each year. For reference, the first year during each breeding season is used to refer to particular breeding seasons (e.g. 1987 = 1987/88 breeding season).

Birds were captured and gut contents collected as they returned to colonies after foraging and immediately prior to feeding of chicks. Therefore, the diet samples are representative of the Antarctic krill population that was ingested by chicks. Sub-samples of between 50 and 100 whole Antarctic krill were measured from each diet sample. Individual length was obtained by measuring from the base of the eye to the tip of the telson (Morris et al., 1988) and samples were binned in 8, 5-mm size-classes,

between 16 and 65 mm. Diet samples from each year were pooled and the size-class distribution for all biomass sampled during the breeding period was calculated to create a krill size-class frequency distribution for that year.

The dominant Antarctic krill length changes from year to year as recruited cohorts in the krill population grow and senesce (Fraser and Hofmann, 2003). Cycling of krill greater than 40 mm (2+ year-old krill) in the diet samples over time (Fig. 7) provides evidence for the movement of individual krill cohorts through the population. This pattern of a shifting dominant size-class frequency of Antarctic krill over a 4 to 6 year cycle has been described in several studies (Reid et al., 1999, 2002; Fraser and Hofmann, 2003; Quetin and Ross, 2003).

### *III.2.2.2 Fledging Mass and Resighting Data*

Adélie penguin chicks congregate on fledging beaches immediately prior to entering the water for the first time. A sub-sample of one-third of these chicks on Humble Island off Anvers Island (Fig. 1) was weighed each year between 1987 and 2004. A total of 5,422 fledglings were weighed during this time period ( $285 \pm 95$  per year). Each chick was marked so that chicks were not weighed more than once. Sampling at beaches began when the first group of chicks arrived and ended when the last chick fledged, a period that usually lasts two weeks. Measurements were assumed to represent fledging mass and a mean fledge mass for each year was calculated (Fig. 8).

Between 1988 and 1998, a sub-sample of fledglings were fitted with metal bands with a unique identification number. Each resighting of banded chicks that return to colonies as adult breeders was recorded. These birds were considered to be chicks that had recruited into the breeding population. Banded birds that were resighted ( $n=152$ ) averaged  $3.152 \pm 0.352$  kg at fledging (Resighted Fledge Mass, RFM), while birds that were not resighted ( $n=2030$ ) averaged  $3.035 \pm 0.258$  kg (Not Resighted

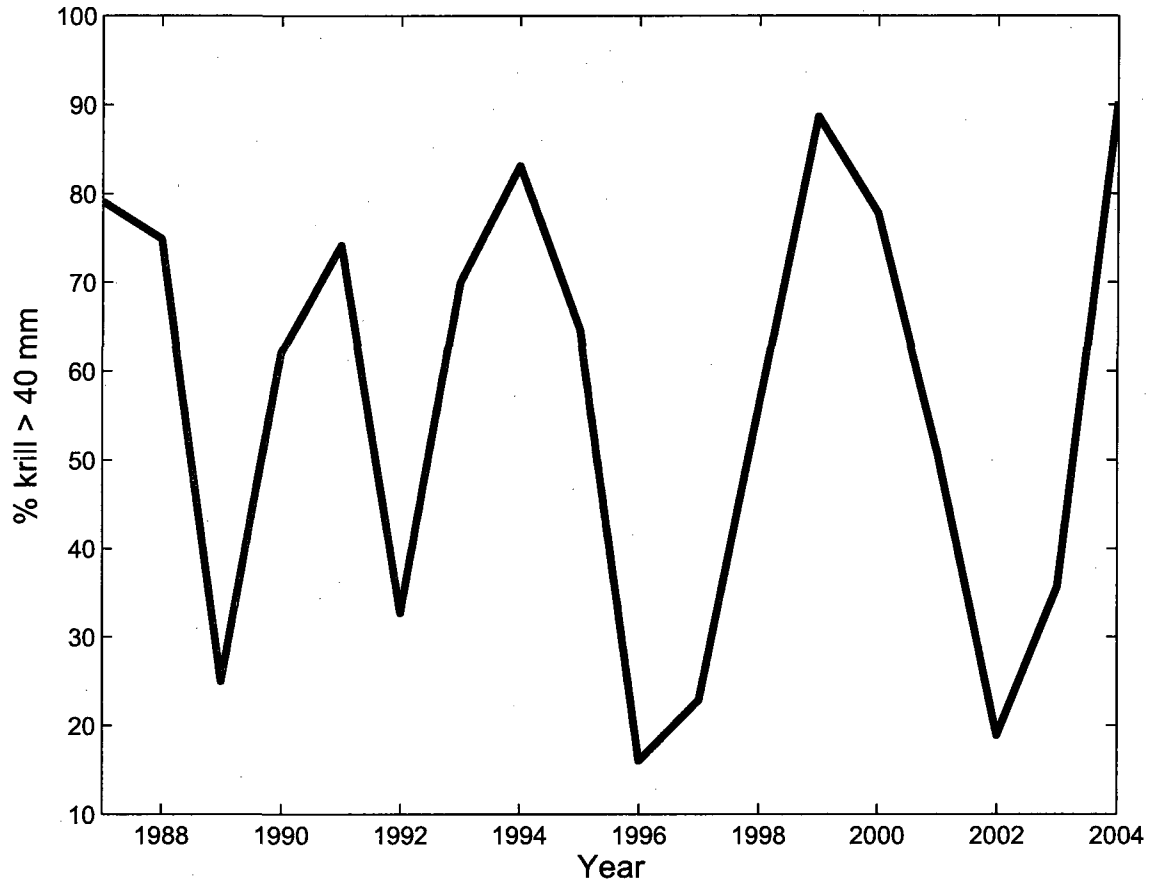


Fig. 7. The variability in the percentage of krill larger than 40 mm (> 2 years old) in diet samples obtained from penguins provisioning chicks in colonies near Palmer Station between 1987 to 2004.

Fledge Mass, NRFM) (Fig. 8). The difference between these two means, 0.117 kg, is statistically significant (t-test, p-value < 0.001).

### III.2.3 Model Structure and Governing Equation

A conceptual diagram of energy pathways included in the chick growth are provided in Fig. 5. Chick growth is expressed as the change over time ( $t$ ) in chick mass ( $M$ , kg) as

$$\frac{dM}{dt} = \frac{1}{ED_{cwm}}(E_p - E_c) \quad (1)$$

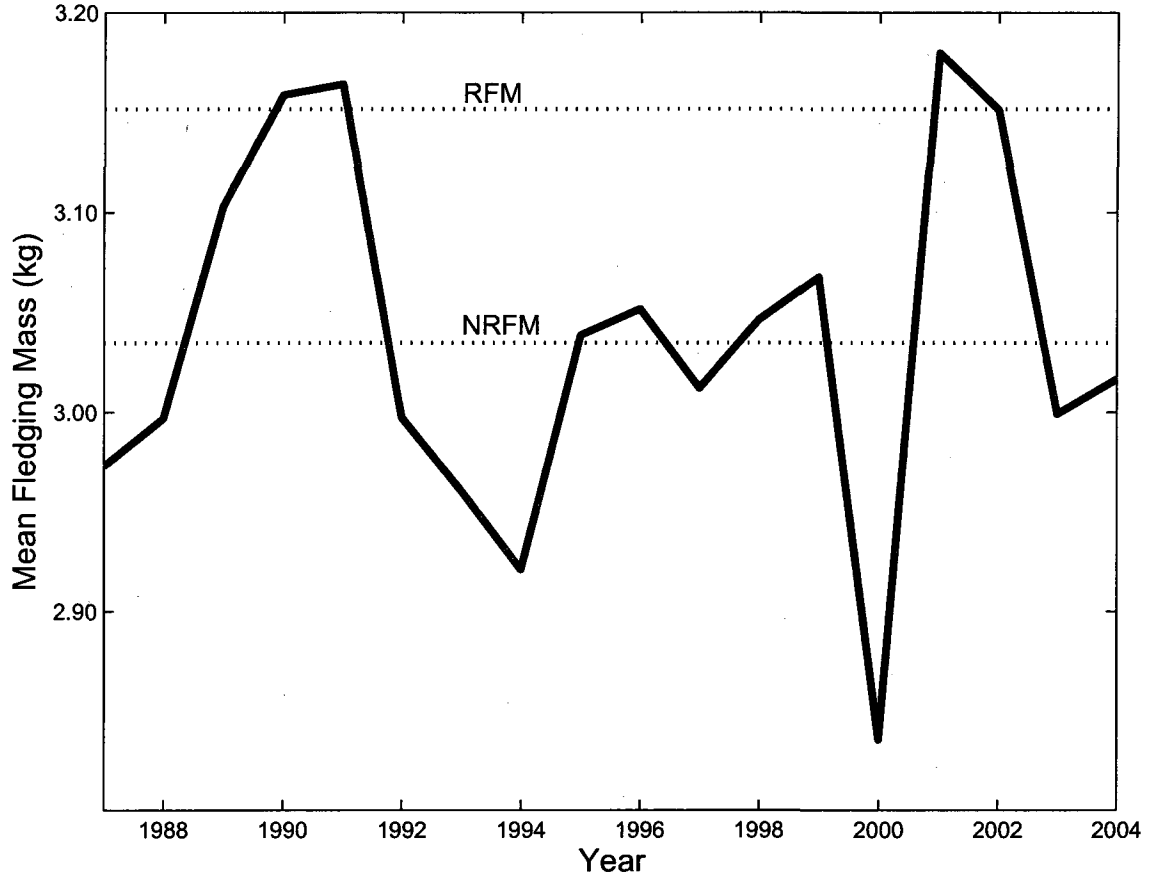


Fig. 8. Mean fledging mass measured for Adélie penguin chicks leaving Humble Island, near Palmer Station for each year between 1987 to 2004 (Section III.2.2.2). The mean fledging mass of banded chicks that were resighted (RFM) and the mean fledging mass of chicks that were not resighted (NRFM) are indicated. See text for details.

where  $E_p$  is the energy available for somatic tissue production (kJ),  $E_c$  is metabolic energy loss (kJ), and  $ED_{cwm}$  is the chick's wet-mass energy density ( $\text{kJ kg}^{-1}$ ). The latter term converts tissue to energy.

The energy production available to the chick is calculated as

$$E_p = ED_{kwm} \cdot P \cdot AE \quad (2)$$

where  $ED_{kwm}$  is the prey wet-mass energy density ( $\text{kJ kg}^{-1}$ ),  $P$  is the amount of prey provisioned to a chick (kg), and  $AE$  is the assimilation efficiency (unitless), or pro-

portion of gross energy intake available to meet metabolic costs (Castro et al., 1989). Energy density of Antarctic krill ( $ED_{kwm}$ ) is dependent on seasonal accumulation of lipid content among sex/maturity stages within the krill population and is described in Section III.2.4.

Energy that is ingested but not used (unassimilated energy,  $E_u$ , kJ) is calculated as

$$E_u = P \cdot ED_{kwm}(1 - AE) \quad (3)$$

and the energy taken in by the chick (energy-intake,  $E_i$ , kJ) is calculated as

$$E_i = P \cdot ED_{kwm}. \quad (4)$$

The daily amount of food provisioned to a chick,  $P$  (kg), was assumed to slowly increase initially then increase rapidly as the chick's energy demands increase, and reach a plateau prior to fledging. This dependency is expressed as

$$P = Prov_{max} - [1 + \frac{Prov_{max} - Prov_0}{Prov_0} e^{-k_{prov}(t-1)}] \quad (5)$$

where  $Prov_{max}$  is the maximum feeding rate ( $\text{kg d}^{-1}$ ),  $Prov_0$  is the feeding rate at time zero ( $\text{kg d}^{-1}$ ), and  $k_{prov}$  is the rate of increase in provisioning rate (unitless). Values for  $Prov_0$ ,  $Prov_{max}$ , and  $k_{prov}$  were calculated empirically by matching simulated chick growth with observed chick growth (see below). No prey was provisioned to the chick after day 50, the beginning of the chick's starvation period. The provisioning schedule was held constant in all simulations.

Among birds,  $AE$  generally increases with chick age as the chick's digestive system becomes functionally mature (Penney and Bailey, 1970; Blem, 1975; Cain, 1976; Cooper, 1977; Heath and Randall, 1985; Karasov, 1990). For penguins,  $AE$  begins to decrease with approximately 20% of the nestling period remaining (Cooper, 1977; Heath and Randall, 1985). Thus, the  $AE$  used in the chick-growth model was 0.69 at

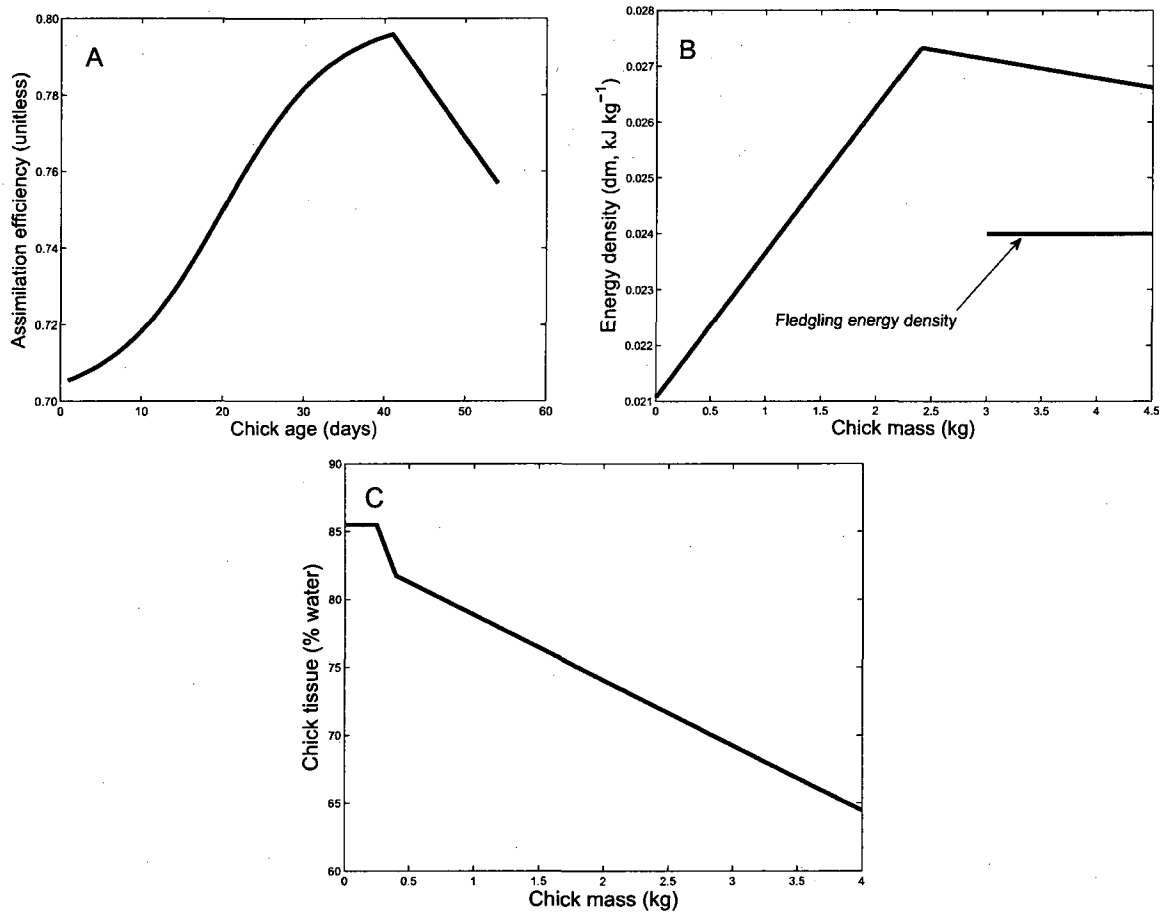


Fig. 9. Dependency on chick mass of relationships used in the chick-growth model to describe A) chick assimilation efficiency as a function of chick age, B) chick dry-mass energy density as a function of chick mass (fledgling energy density also shown), and C) percent of chick somatic tissue that is water. See text for details.

hatching, increased to 0.80 at day 40, and declined to 0.76 at fledging (Cooper, 1977; Heath and Randall, 1985; Janes, 1997) (Fig. 9A). This gives an overall mean value for  $AE$  of 0.75 which agrees with results from previous studies (Cooper, 1977; Heath and Randall, 1985; Jackson, 1986; Janes, 1997).

The total energy cost for an individual chick was calculated as

$$E_c = MMR + TR \quad (6)$$

where  $MMR$  is the mean metabolic rate (kJ d<sup>-1</sup>) and  $TR$  is the energy needed to

convert chick tissue to the new energy density ( $\text{kJ d}^{-1}$ ), which changes over time. Therefore, a growing chick must not only add mass at the current energy density, but convert its existing mass to the new energy density.

The *MMR* was derived from a study using the doubly-labeled water method which integrates all contributions to metabolic rate under actual field conditions experienced by a chick (Janes, 1997). In contrast with adult metabolic rate, which typically scales exponentially with mass, mean metabolic rate for chicks scales linearly with mass (Culik et al., 1990; Janes, 1997) according to

$$MMR = a \cdot M \quad (7)$$

where  $a$  was initially set to  $910 \text{ kJ d}^{-1} \text{ kg}^{-1}$  (Janes, 1997). Fledglings during the starvation period have a slightly lower metabolic rate; therefore, after day 50 the value for  $a$  was reduced to  $800 \text{ kJ d}^{-1} \text{ kg}^{-1}$  (Janes, 1997). The conversion to the new energy density ( $TR$ ) was calculated as

$$TR = \Delta ED_{cwm} \cdot M \quad (8)$$

where  $\Delta ED_{cwm}$  is the change in chick wet-mass energy density during the previous time interval ( $\text{kJ kg}^{-1}$ ).

The wet-mass energy density of chick tissue was calculated as

$$ED_{cwm} = ED_{cdm} \cdot (1 - WC_c) \quad (9)$$

where  $ED_{cdm}$  is the dry mass energy density of the chick ( $\text{kJ kg}^{-1}$ ) and  $WC_c$  is the percentage of chick tissue that is composed of water. Chick dry mass energy density ( $ED_{cdm}$ ) increases from  $0.0213 \text{ kJ kg}^{-1}$  to  $0.0273 \text{ kJ kg}^{-1}$  as the chicks grow from  $0.09 \text{ kg}$  to  $2.40 \text{ kg}$  (Fig. 9B). As chicks continue to grow, chick dry mass energy

density begins to decrease (Myrcha and Kaminski, 1982) (Fig. 9B). As chicks begin their transition to fledgling plumage (day 40), dry mass energy density decreases at a faster rate, reaching the fledgling dry mass energy density ( $0.0240 \text{ kJ kg}^{-1}$ ) on day 54 (Myrcha and Kaminski, 1982) (Fig. 9B). The proportion of water in chick tissue ( $W_c$ ) declines from an initial value of 85% to 67% at fledging (Myrcha and Kaminski, 1982; Konarzewski et al., 1998) (Fig. 9C).

Following day 50, when chicks are no longer receiving food from their parents, they use their lipid stores to cover metabolic needs, which results in a loss of mass. Therefore, during the starvation period, the wet mass energy density of lipid ( $0.0398 \text{ kJ kg}^{-1}$ ) was substituted for the chick's wet mass energy density ( $ED_{cdm}$ ).

#### *III.2.4 Antarctic Krill Energy Density Estimation*

Lipid content is the most variable of all the biochemical components of Antarctic krill (Clark, 1980). In order to minimize the variability of the non-lipid biochemical components in this study, the proportion of these components remain at the same ratio to each other as lipid content varies (Table 1). This allows for the proportion of all biochemical components to be estimated if lipid content is known. Once the biochemical composition of an individual Antarctic krill (or a krill population) is estimated, the energy density of that krill can be estimated based on the energy density of each component (Clark, 1980; Savage and Foulds, 1987) (Table 1).

The size-class distribution of Antarctic krill obtained from gut content samples from adult penguins was used to calculate the biochemical composition, and consequent energy density, of krill ingested by the simulated chicks (Fig. 10). This distribution was apportioned into mature males, gravid and spent females, and males/females that are mature (based on the length-at-maturity function) but are not involved in spawning, and immature krill, to produce a sex/maturity stage distribution (Fig. 10). The proportion of gravid and spent females was allowed to vary relative to spawning.

Table 1. Ratios and energy density of Antarctic krill biochemical components calculated from Clark (1980). The lipid proportion is calculated for the Antarctic krill population as described in Section III.2.4.

Biochemical component	Ratio	Dry mass energy density (kJ kg <sup>-1</sup> )
lipid	Calculated	0.0395
protein	10.0	0.0236
carbohydrate	0.5	0.0172
chitin	2.0	0.0171
ash	3.0	0.0

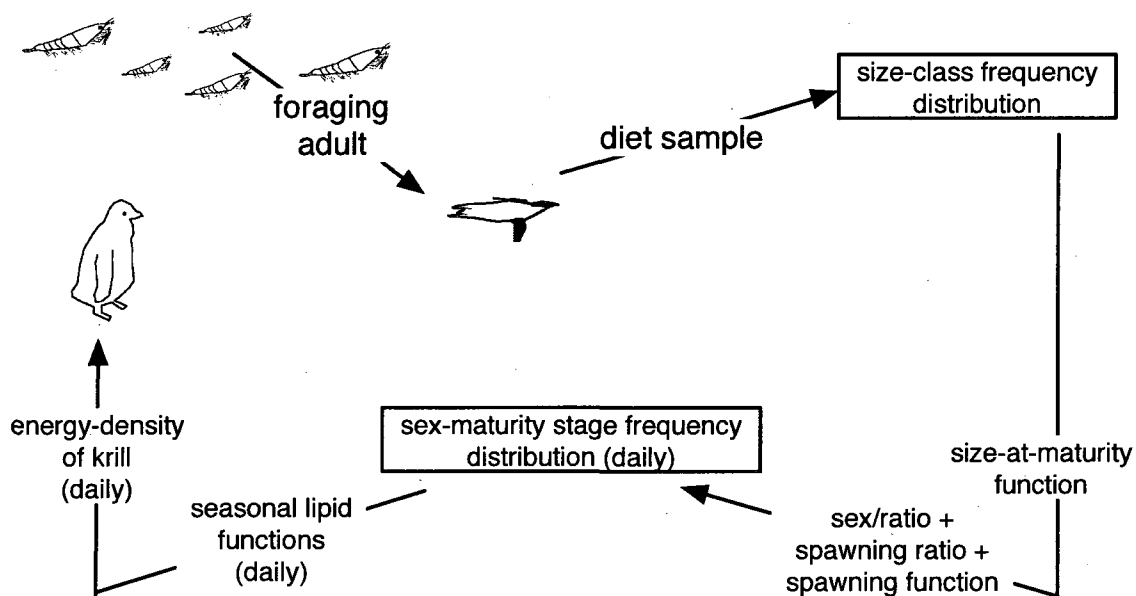


Fig. 10. Schematic representation of the calculation of energy-density of Antarctic krill ingested by Adélie penguin chicks.

The lipid content of the Antarctic krill ingested by chicks was then estimated based on the lipid content of each sex/maturity stage. Finally, the population-wide lipid content was converted to population energy density, which provided energy to the chick (Fig. 10).

Length-at-maturity relationships (Siegel and Loeb, 1994) were used to calculate the proportion of mature male and female individuals ( $p_{m/f,n}$ ) for each size class ( $n$ ) in the Antarctic krill size-class distribution obtained from the adult penguin diet samples. These relationships were based on the length that male or female krill achieve at the first stage of maturity (Makarov and Denys, 1981). The length-at-maturity relationships are of the form

$$p_{m/f,n} = \frac{1}{1 + e^{-k_{m/f}(TL_n - L_{50,m/f})}} \quad (10)$$

where  $k_{m/f}$  is the coefficient that controls the rate of increase in proportion of sexually mature Antarctic krill with increasing krill length for males ( $m$ ) and females ( $f$ ),  $TL_n$  is the mean total length of krill within each size-class ( $n$ , mm), and  $L_{50,m/f}$  is the length at which 50% of the krill stock has attained sexual maturity (Fig. 11A-B).

The total proportion of mature males and females ( $T_{m/f}$ ) in the population is then calculated as

$$T_{m/f} = \sum_{n=1}^N p_{m/f,n} \cdot R_{m/f} \cdot SC_n \quad (11)$$

where  $R_{m/f}$  is the ratio of each sex in the population and  $SC_n$  is the overall proportion of Antarctic krill within each size class. The proportion of immature individuals is then the proportion of the population that are not mature male or female Antarctic krill.

The proportion of mature males and females within the Antarctic krill population that continue through all maturity stages (and participate in spawning) ( $SP_{m/f}$ ) is then given by

$$SP_{m/f} = T_{m/f} \cdot sp_{m/f} \quad (12)$$

where  $sp_{m/f}$  is the proportion of mature males and females that participate in spawning.

With the exception of the mature females, the proportion of each sex/maturity

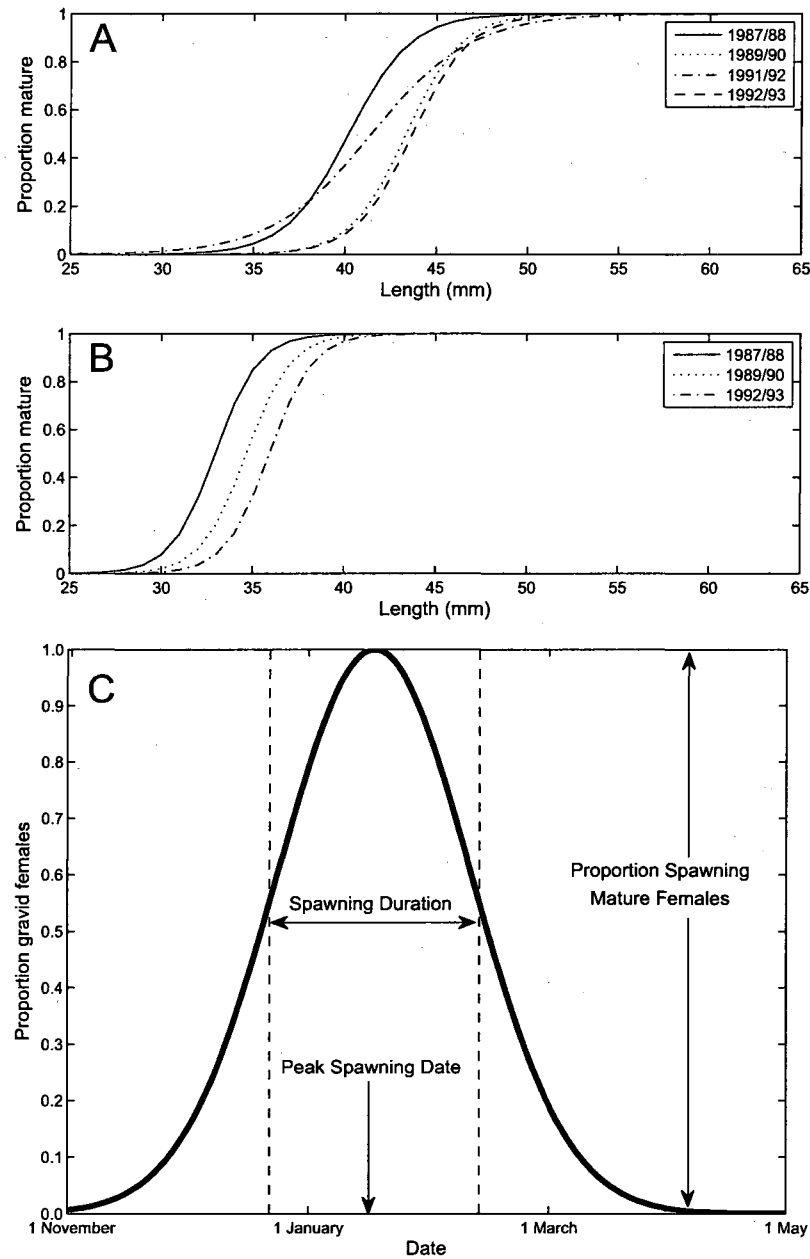


Fig. 11. Length-at-maturity functions from Siegel and Loeb (1995) for A) male and B) female Antarctic krill used to calculate the proportion of mature (potentially spawning) males and females from size-class distributions obtained from Adélie penguin diet samples collected at Palmer Station, and C) the spawning function showing variability in the proportion of gravid females among spawning females over the austral summer. The duration of spawning, proportion of mature females that spawn and the date of peak spawning are characteristics of the spawning function that were varied in simulations.

stage was assumed to remain constant throughout the chick-rearing period. Females, however, lose a significant amount of lipid content at spawning, so spawning females were further separated into a time-varying proportion of gravid and spent (post-spawning) individuals. These proportions vary as Antarctic krill spawning activity peaks and subsides. This seasonal variability in spawning, and the proportion of gravid/spent females in the population for each day during the chick-rearing period is given by

$$P_{gravid}(t) = T_f \cdot e^{\frac{(t-S_{pk})^2}{S_{dur}}} \quad (13)$$

where  $P_{gravid}$  is the proportion of gravid females in the population,  $t$  is time (days),  $S_{pk}$  is the day when the maximum proportion of gravid mature females occurs, and  $S_{dur}$  is the spawning duration (the period during which >50% of the spawning female population is gravid). Values for  $S_{pk}$ ,  $sp_{m/f}$ , and  $S_{dur}$  were varied in the chick growth simulations to assess the influence on chick growth of variability in the timing, intensity (proportion of mature adults that spawn), and duration of the spawning period, respectively (Fig. 11C). Prior to peak spawning, the proportion of gravid females was set at the value for  $T_f$ . After peak spawning, the proportion of spent females was equal to the difference between the proportion of spawning females and the current proportion of gravid females in the population,  $P_{gravid}$ .

The proportion of each sex/maturity stage was then multiplied by the corresponding time varying sex/maturity stage lipid content. The sum of the product from these calculations for each sex/maturity stage was then used as an estimate of the lipid content of the overall Antarctic krill population (Fig. 12A-C). Lipid content of Antarctic krill generally increases over the austral summer (Clark, 1980; Quetin and Ross, 1991; Hagen et al., 1996, 2001) but variation to this pattern occurs between immature and mature krill (Fig. 12A-C)(Clark, 1980; Quetin and Ross, 1991; Nicol et al., 1995; Virtue et al., 1996; Hagen et al., 1996, 2001). In general during the chick rearing period, the lipid content of immature krill (Fig. 12A) is more than mature

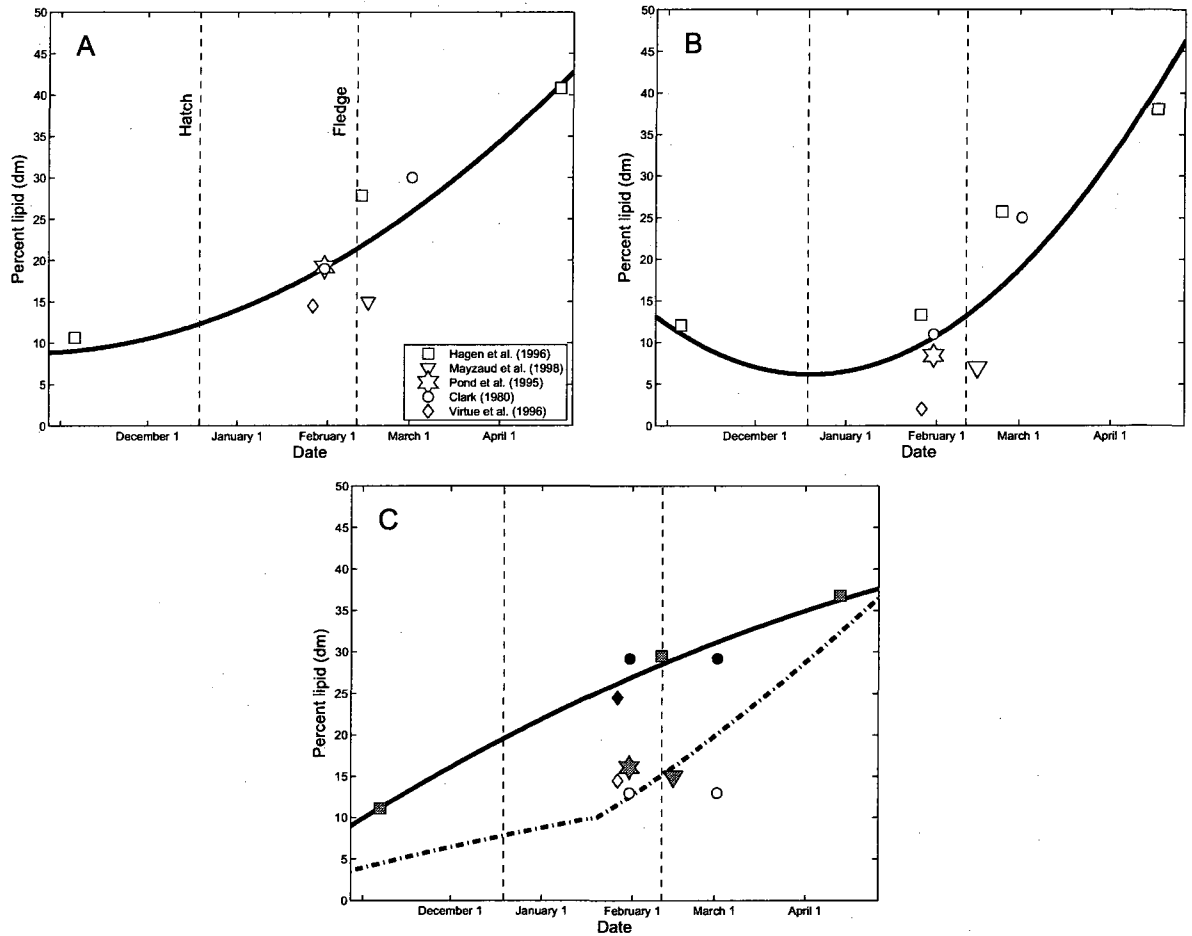


Fig. 12. Relationships used to describe the seasonal change in lipid content for A) immature krill, B) spawning male krill, and C) gravid and spent (— · —) female krill. The data sets used to develop the relationships are indicated. Shading indicates the maturity stage of females in the samples (● = gravid females, ○ = spent females, ○ = mature females of an unspecified maturity stage). Typical hatching and fledging dates for Adélie penguin nestling period at Palmer Station are indicated (— · —).

male krill (Fig. 12B) or spent females (Fig. 12C), but less than gravid females (Fig. 12C).

Gravid females lose approximately 54% of their lipid during spawning (Clark, 1980). Spent female Antarctic krill presumably begin feeding immediately after spawning in order to accumulate lipid in preparation for a subsequent spawning effort or to meet the energetic demands of over-wintering. As a result, the population of spent females at any given time consists of females that have just spawned and those that are in

some stage of lipid re-accumulation. The proportion of Antarctic krill that have re-accumulated lipid, and the extent to which this occurred, was assumed to increase following the date of peak spawning activity. Accordingly, there is a steady decrease in the percent lipid loss assigned to the population of spent females following peak spawning. As a result, spent females have 54% less lipid than gravid females at peak spawning and none less at the end of April when it is assumed that all spent females have recovered to reach lipid levels of other Antarctic krill sex/maturity stages. This assumption is supported by an observational study that shows that by the end of April, lipid content among immature, male, and female krill are approximately 40% dm (Hagen et al., 2001).

The lipid content for non-spawning mature females and males was assumed to follow the same dependency used for immature Antarctic krill. This implies that the lipid content of these krill is similar to that of individuals that are storing lipids solely in preparation for over-wintering, as is the case with immature krill.

The daily energy density of the Antarctic krill population is then calculated as:

$$E_{kdm}(t) = \sum_1^n p_{ms}(t) \cdot L_{ms}(t) \cdot LED \quad (14)$$

where  $E_{kdm}$  is the dry-mass energy density of the krill population ( $\text{kJ kg}^{-1}$ ),  $p_{ms}$  is the proportion of each sex/maturity stage in the population ( $n$ ),  $L_{ms}$  is the dry-mass lipid content (%) for each sex/maturity stage and  $LED$  converts lipid content to energy density based on the ratio and energy density of biochemical components (Table 1). The dry-mass energy density is converted to wet-mass energy density using (Ikeda and Mitchell, 1982)

$$E_{kwm}(t) = E_{kdm}(t)/0.216. \quad (15)$$

### III.2.5 Model Implementation and Simulations

The chick-growth model was integrated for 54 days using a one-day time-step and a fourth-order Runge-Kutta integration algorithm. Chick mass on the 54th day of the simulation is the simulated fledging mass. The model was run using mean conditions (Table 2) measured for Adélie penguin chicks at ANV and this provides a reference simulation for comparison. The total wet mass provisioned, the total energy provided to the chick, and the energy density of krill were calculated from the reference simulation and used as diagnostics for comparison to observed and sensitivity simulations. Subsequent simulations assessed the influence on chick growth and fledging mass of variability in a subset of parameters that were each varied independently while all other parameters were held constant at reference values as described below.

Changes from the mean growth trajectory resulting from variability in the date of peak spawning ( $S_{pk}$ ) (Table 3, A-B) and seasonal lipid accumulation were the first sensitivity simulations done. Next, the influence of variability in spawning duration and the proportion of mature adults that spawn on chick growth were examined (Table 3, C-E). Subsequent simulations investigated the influence of krill population sex-ratio and size-class frequency distribution on chick growth (Table 3, F). Sensitivity of chick growth to variability in krill length-at-maturity was investigated by varying  $L_{50}$  for males and females independently and together (Table 3, G-I). The final set of simulations investigated the effect of variability in population-wide lipid content on penguin chick growth (Table 3, K).

When possible, the difference in fledging mass obtained from different parameter values in a simulation was compared with the difference between the RFM and the NRFM (0.117 kg; Fig. 8). This difference provides an estimate of the change in simulated fledging mass that would reduce a chick's probability of recruitment.

Table 2. Definition of parameters used in the chick-growth model and the value used in the reference simulation. The sources for the parameter values are given and those that were varied in subsequent simulations are underlined.

Parameter	Definition	Reference	Source(s)
-	Chick provisioning period	19 December - 10 February	Field data
$P$	Provisioning Rate	0.030-0.86 kg d <sup>-1</sup>	Calculated
$AE$	Assimilation efficiency	0.69-0.80	Cooper (1977); Heath and Randall (1985); Jackson (1986); Janes (1997)
$Prov_{max}$	Peak provisioning rate	0.86 kg d <sup>-1</sup>	Calculated
$Prov_0$	Provisioning at time zero	0.03 kg d <sup>-1</sup>	Calculated
$k_{prov}$	Rate of increase in provisioning rate	0.185	Calculated
$MMR$	Mean metabolic rate	86-2952 kJ d <sup>-1</sup>	Janes (1997); Culik et al. (1990)
$ED_{cdm}$	Chick dry mass energy density	18.8-29.3 kJ kg <sup>-1</sup>	Myrcha and Kaminski (1982)
$WC_c$	Fraction water content in chick tissue	0.67-0.85	Myrcha and Kaminski (1982)
$k_{m/f}$	Rate of increase in proportion of sexually mature male and female krill with increasing krill size	Males=0.60, females=0.83	Siegel and Loeb (1994)
<u><math>sp_{m/f}</math></u>	Proportion of mature males and females that spawn	1.0	Siegel and Loeb (1994); Quetin and Ross (2001)
<u><math>L_{50,m/f}</math></u>	Length at which 50% of male or female krill has attained sexual maturity	Males=42mm, females=34mm	Siegel and Loeb (1994)
<u><math>S_{pk}</math></u>	The date of peak krill spawning	20 January	Quetin and Ross (2001)
<u><math>S_d</math></u>	Duration of spawning (>50% spawning females are gravid)	60 days	Quetin and Ross (2001)
<u><math>R_{m/f}</math></u>	Proportion of males and females in krill population	0.5	—
<u><math>SC_n</math></u>	Proportion of krill in each size-class (n)	0.00-0.46	Derived from 1996 field data

### III.3 RESULTS

#### III.3.1 Reference Simulation and Model Validation

The reference simulation was established using parameter values that represent mean conditions for breeding Adélie penguins near Anvers Island off the WAP (Table 2). Antarctic krill size-class frequency distribution from the 1995 breeding season was used because mean fledge mass during this year (3.030 kg) was closest to the

Table 3. Summary of chick growth and Antarctic krill energy density simulations. For each the range of krill wet mass energy density is given as is the range of the simulated chick fledging mass. See text for descriptions of each simulation set.

Parameter(s) varied [experimental variability]	Mean krill wet-mass energy density (kJ g <sup>-1</sup> )	Fledging mass (kg)
(A) Date of peak spawning ( $S_p$ ) [6 December - 6 March]	4.51-4.69	2.96-3.11
(B) Date of peak spawning ( $S_p$ ) [6 December - 6 March] and timing of seasonal lipid function [centered on 6 December - 6 March]	4.97-4.45	3.30-2.93.
(C) Spawning duration ( $S_d$ ) [17d-99d]	4.62-4.68	3.01-3.10
(D) Proportion of both male and female adults that spawn ( $P_{spm/f}$ ) [0.0-1.0]	4.65-4.67	3.09-3.09
(E) Proportion of females that spawn ( $P_{spf}$ ) [0.0-1.0]	4.54-4.68	3.02-3.09
(F) Proportion of large (> 40 mm) krill in diets [0.16-0.90] and male proportion in krill population ( $R_m$ ) [0.1 - 0.9]	4.81-4.92	3.18-3.24
(G) Male length-at-maturity function ( $L_{50m}$ ) [40-44 mm]	4.67-4.69	3.09-3.10
(H) Female length-at-maturity function ( $L_{50f}$ ) [32 - 36mm]	4.68-4.67	3.10-3.90.
(I) Male and female length-at-maturity functions ( $L_{50m}$ and $L_{50f}$ ), [40/32 - 44/36mm (m/f)]	4.67-4.68	3.09-3.09
(J) Population-wide lipid adjustment [-5 - +5 %lipid (dry mass)]	4.44-4.91	2.95-3.24

mean value over the time-series between 1987 to 2005 (3.036 kg, Fig. 8) and the krill population ingested by chicks was not dominated by either large or small krill (Fig. 7). Applying the length-at-maturity relationship (Eq. 12) to the distribution measured in 1995 resulted in an Antarctic krill population consisting of 0.40 mature females, 0.30 mature males and 0.30 immature individuals. Target fledge mass for the growth curve was set at 3.094 kg, the mean of the RFM and the NRFM (Fig. 8). This value was selected so that the potential impact of simulated fledging mass on recruitment could be assessed. Setting the provisioning rate function to fit the target growth curve required multiplying the assigned provisioning rate function (Eq. 5 with parameter values in Table 2) by 0.965 following day 41.

Simulated growth matched the target growth curve (Fig. 13;  $r^2$  of 0.99 prior to the starvation period). During the starvation period, an average of 54 g d<sup>-1</sup> was lost by

Table 4. Comparison of model diagnostics calculated from the reference simulation (underlined text) with equivalent values obtained from field and other modeling studies.

Model Diagnostic Variable	Value	Source	Comments
Total wet mass	33.6	Janes (1997)	Estimated based on observed growth and other physiological data
provisioned to chick (kg)	29.8	Culik (1994)	Estimated from observed growth
	<u>27.8</u>	This study	Estimated based on chick-growth model assumptions
	24.1	Salihoglu et al. (2001)	Estimated based on chick-growth model assumptions
	24.0	Chappell et al. (1993a)	Measured from change in adult mass before and after feeding
	23.0	Trivelpiece et al. (1987a)	Measured from mass of adult stomach contents
Krill wet-mass	4.99	Nagy and Obst (1992)	Measured: Bomb calorimetry
energy density (kJ g <sup>-1</sup> )	<u>4.51 - 4.82</u>	This study	Calculated based on estimated lipid content
	4.08	Janes and Chappell (1995)	Measured using bomb calorimetry
	3.70	Davis et al. (1989)	Measured using bomb calorimetry
Total energy provided to chick (MJ)	162	Janes (1997)	Estimated
	<u>131</u>	This study	Estimated
	98	Salihoglu et al. (2001)	Estimated

the chick (Fig. 13). The simulated chick wet mass energy density increased from 3.1 kJ g<sup>-1</sup> to 8.6 kJ g<sup>-1</sup>, with the fastest rate of increase between day 8 and 30 (Fig. 14A). Daily energy production increased immediately after hatching to day 40 from 112 kJ to 3255 kJ (Fig. 14B). Following day 50, the daily energy production dropped to zero during the starvation period. Daily energy costs increased from 87 kJ just after hatching to a maximum of 2952 kJ at the onset of the starvation period (Fig. 14B). The greatest difference between energy production and cost was the period of fastest chick growth which occurred between days 12 and 25 of the simulation. The amount of krill provisioned to the chick ranged between 0.03 kg d<sup>-1</sup> and 0.85 kg d<sup>-1</sup> (Fig. 14C). The total amount of krill provisioned to the chick (27.8 kg), the energy density of krill (Fig. 14D, 4.51 - 4.82 kJ g<sup>-1</sup>), and the total energy provisioned to the chick (131 MJ) are all within the range of available estimations and measurements (Table 4).

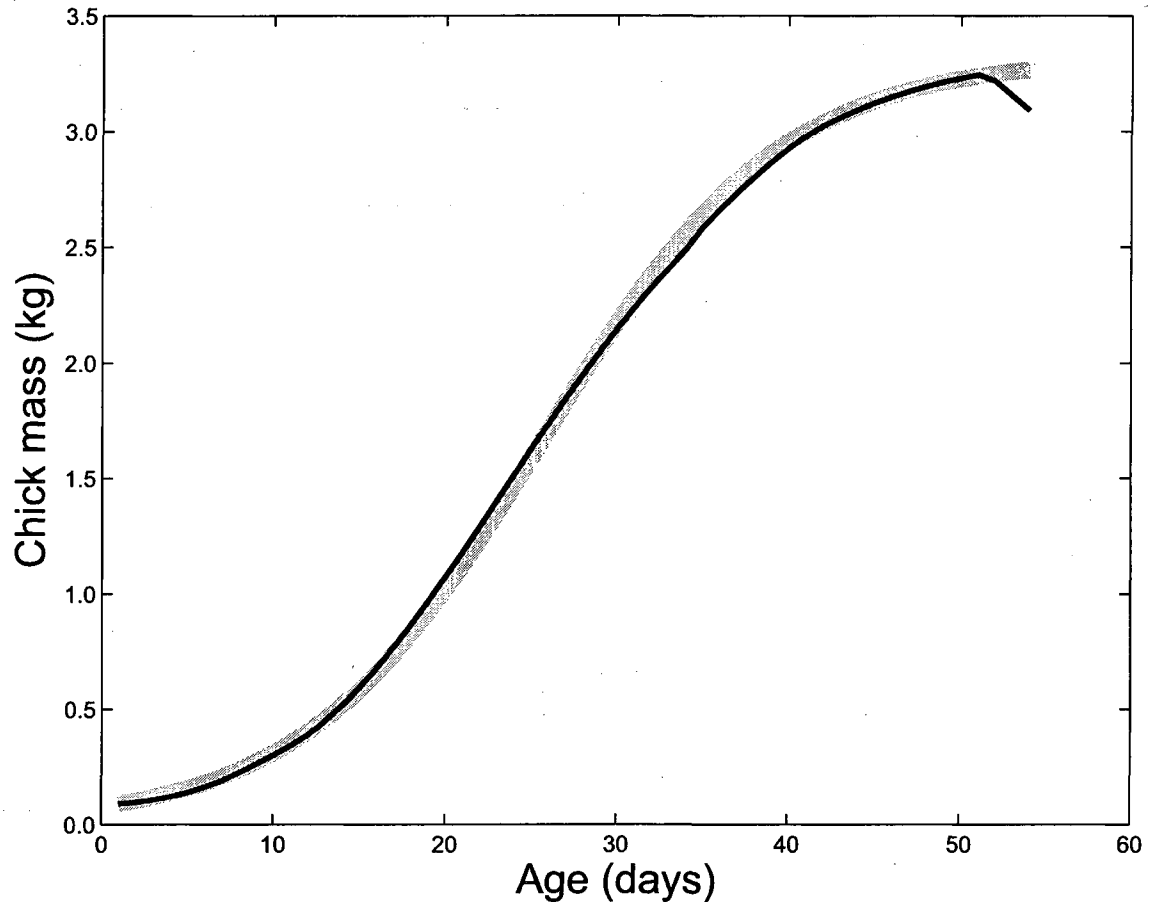


Fig. 13. Simulated time evolution of Adélie penguin chick growth (—) obtained from the reference simulation. The target growth curve used to set the provisioning rate in the reference simulation is shown (■).

### III.3.2 Variability in the Timing of Antarctic Krill Spawning

Chick fledging mass increased as the date of peak Antarctic krill spawning progressed further into the austral summer, reaching an asymptote below the RFM as the spawning peak approached the Adélie penguin hatching date (10 February) (Fig. 15A). Peak spawning between 6 December and 1 January resulted in a fledging mass below the NRFM and the difference between the maximum and minimum simulated fledging mass (0.11 kg) was approximately the same as the difference between the RFM and NRFM. Here, chick growth was influenced solely by variability in the proportion of gravid and spent females in the chick diet. A decrease in the average pro-

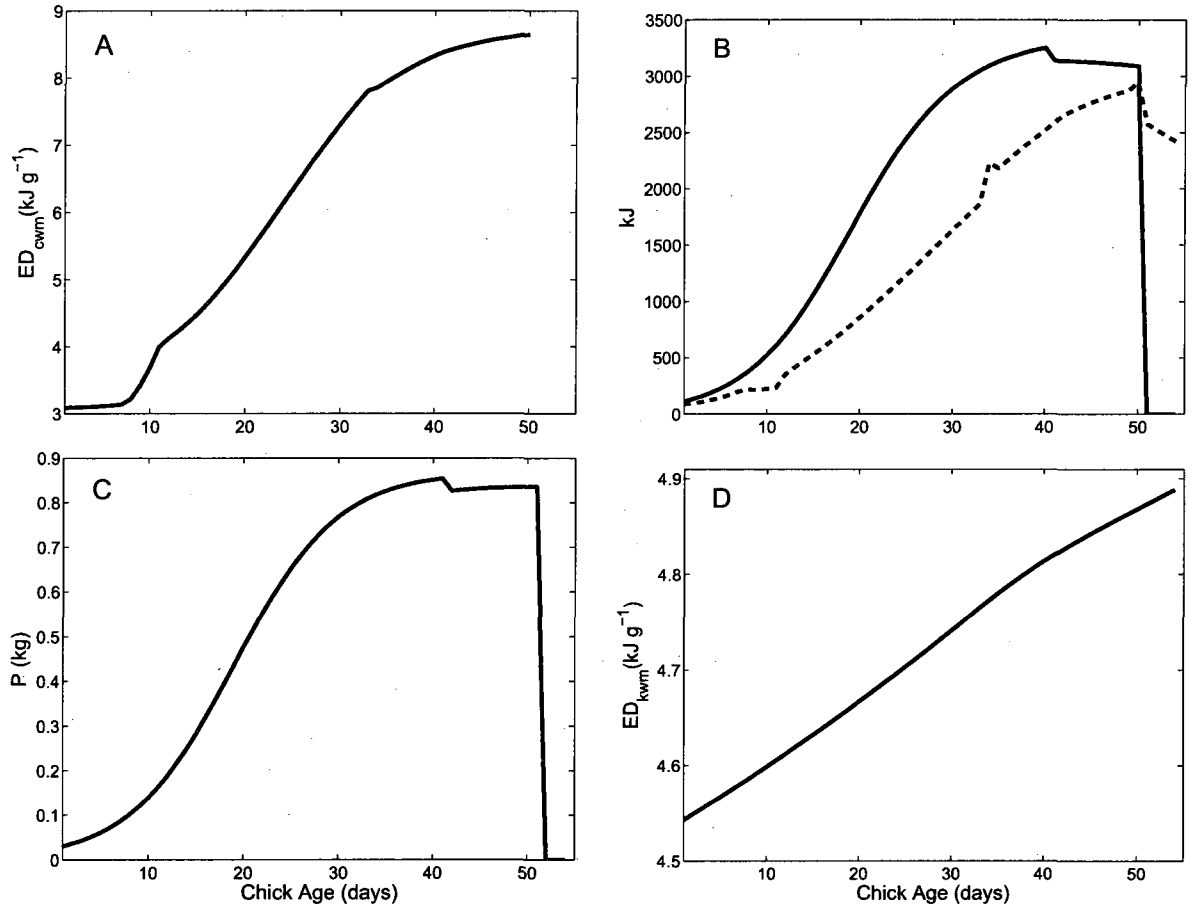


Fig. 14. Simulated evolution of A) wet mass energy density of the chick ( $ED_{cwm}$ ), B) energy available for production ( $E_p$ , —) and energetic costs ( $E_c$ , ---), C) provisioning rate ( $P$ ) and D) wet mass energy density of Antarctic krill ( $ED_{kwm}$ ) as a function of chick age.

portion of spent females in the chick diet from 0.66 to zero as peak spawning moved from early December to late January produced the increase in simulated fledging mass. When peak spawning occurred after 10 February (chick hatching), only gravid or pre-spawning females were consumed by the chick and no spent females occurred in the chick diet.

Variability in peak spawning date, coupled with variability in the timing of seasonal lipid accumulation, produced decreased simulated fledging mass as spawning moved to later in the summer (Fig. 15A). Simulated fledging mass varied by 0.37 kg, well above the difference between RFM and NRFM. Simulated fledging mass reached the

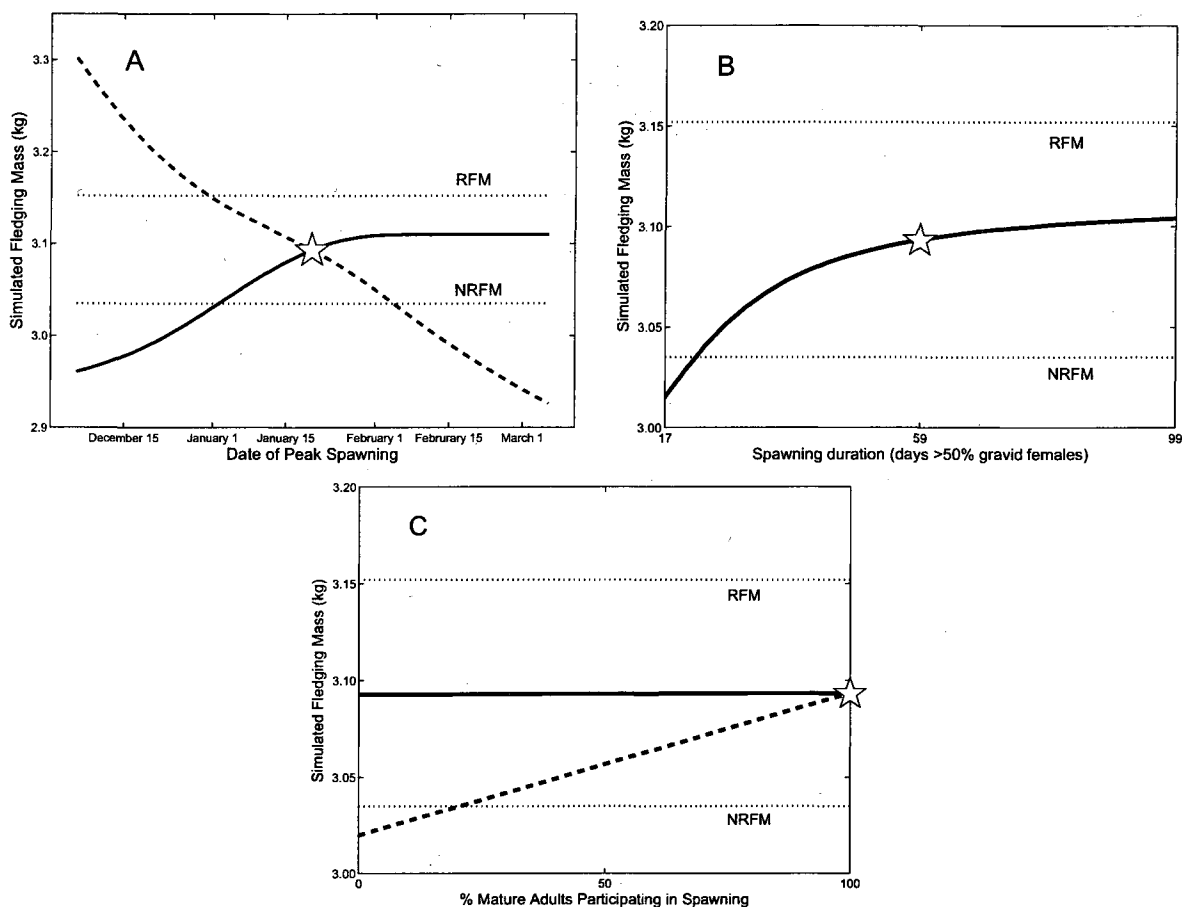


Fig. 15. Simulated chick fledging mass produced by variability in A) peak spawning date (—) and peak spawning date coupled with lipid accumulation (---), B) spawning duration, and C) the percentage of mature adults (both male and female, —) and mature females that participate in spawning (with 100% mature males spawning participation, ---). The mean fledging mass of banded chicks that were re-sighted (RFM) and the mean fledging mass of chicks that were not re-sighted (NRFM) are indicated ( $\cdots$ ), as is the fledging mass obtained from the reference simulation ( $\star$ ).

RFM as peak spawning shifted from 20 January (reference condition) to the beginning of January and the NRFM was reached as peak spawning was delayed to the first week in February. This trend is opposite to that found when the spawning timing alone was varied, and demonstrates the importance of the timing of Antarctic krill lipid accumulation on Adélie penguin chick growth.

### *III.3.3 Variability in the Intensity and Duration of Antarctic Krill Spawning*

Variability in the percentage of male and female spawners had no effect on simulated fledging mass (Fig. 15B). However, decreasing the percentage of females that spawn from 100 to 0% decreased simulated chick fledging mass by 0.07 kg (Fig. 15B). Increasing the duration of spawning from 59 to 99 days increased the simulated fledging mass by 0.01 kg, while decreasing the duration of spawning to 17 days decreased fledging mass by 0.08 kg (Fig. 15C). This change reflected the greater proportion of gravid females in the chick's diet with a lengthened spawning period.

### *III.3.4 Variability in Antarctic Krill Demography*

A krill population composed of 90% males resulted in a decline in simulated fledging mass of 0.12 kg as the proportion of large Antarctic krill increased from 14% to 90% (Fig. 16A). A population of 50% males resulted in a small increase in simulated fledging mass as the proportion of large krill increased (Fig. 16A). When the percentage of males in the krill population was decreased to 10%, fledging mass increased with increasing proportion of large Antarctic krill by 0.06 kg resulting from a greater proportion of high-lipid gravid females in the chick diet (Fig. 16A).

When 90% of the Antarctic krill were large, simulated fledging mass increased by 0.29 kg as the proportion of males in the population decreased from 90% to 10% (Fig. 16A). However, when 14% of the krill were large, simulated fledging mass increased by just 0.06 kg when the proportion of males fed to chick decreased.

### *III.3.5 Variability in Length-at-maturity and Total Antarctic Krill Lipid Content*

Increasing the male krill length-at-maturity ( $L_{50m}$ ) from 40 to 44 mm increased the simulated fledging mass by 0.02 kg while increasing female length-at-maturity ( $L_{50f}$ ) from 32 to 36 mm decreased fledging mass by 0.01 kg (Fig. 16B). Increasing both male and female length-at-maturity at the same time ( $L_{50m}$  and  $L_{50f}$ ) resulted in an

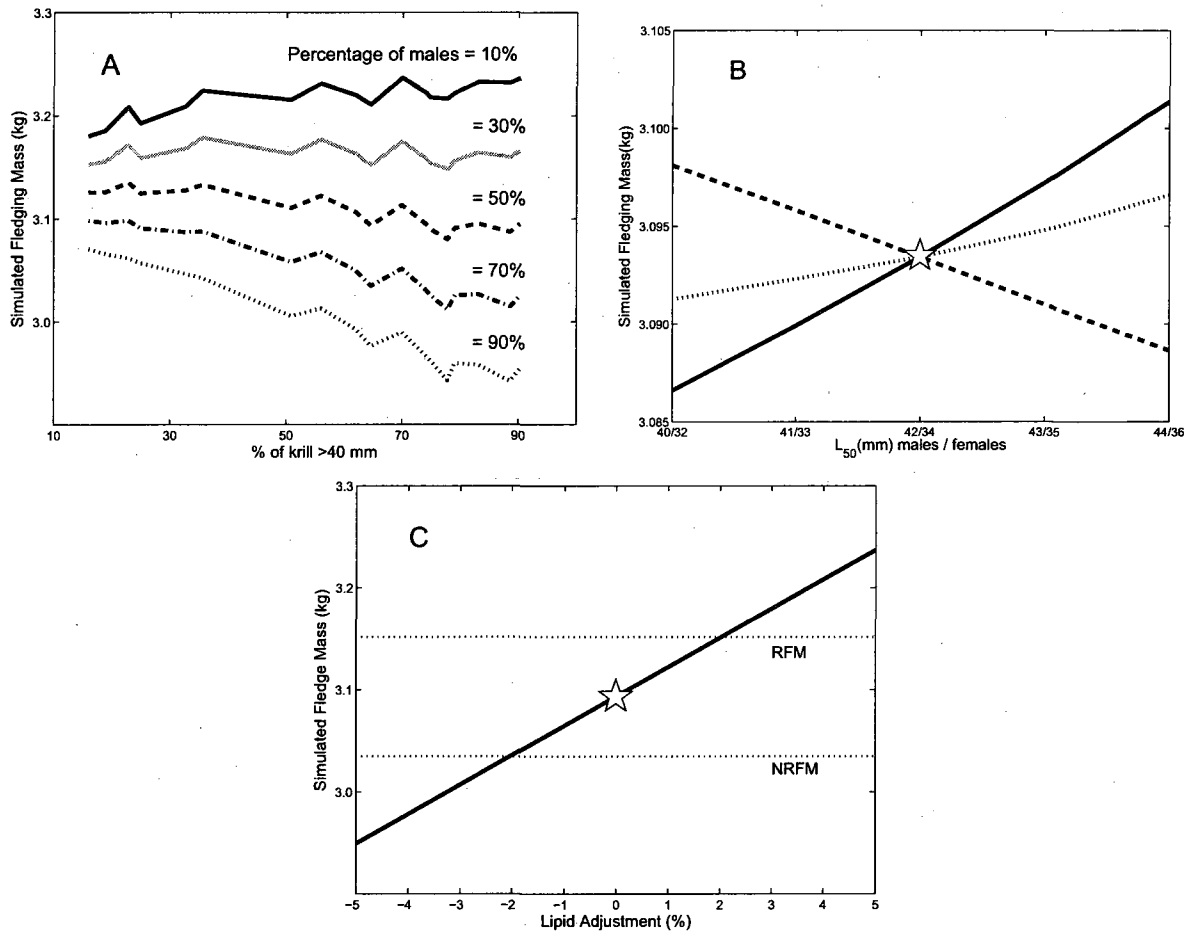


Fig. 16. Simulated chick fledging mass obtained for A) changing percentage of krill larger than 40 mm and varying percentage of male krill in the population, B) variability in the length-at-maturity for male (—), female (---), and male and female (···) krill, and C) variability in the population lipid content. The mean fledging mass of banded chicks that were re-sighted (RFM) and the mean fledging mass of chicks that were not re-sighted (NRFM) are indicated (···), as is the fledging mass obtained from the reference simulation (☆).

0.01 kg increase in simulated fledging mass. These results reflect the cost/benefit of consuming lipid-poor mature males versus lipid-rich gravid females.

Varying the dry mass lipid content of the entire Antarctic krill population from -5% to +5% increased simulated fledging mass by 0.29 kg (Fig. 16C). A 2% increase and decrease in the Antarctic krill dry mass lipid content was sufficient to simulated fledging mass to the RFM and the NRFM, respectively.

### III.4 DISCUSSION

#### *III.4.1 The Timing of Antarctic Krill Spawning*

Simulations suggest that the timing of Antarctic krill spawning can influence the availability of high-energy prey to foraging Adélie penguin adults, decreasing the fledging mass of their chicks sufficiently to reduce chick recruitment. The timing of krill spawning appears to be more important to chick fledging mass than the duration of spawning. The initiation of krill spawning is mediated by the timing and type of food available to Antarctic krill (Nicol et al., 1995; Spiridonov, 1995; Quetin and Ross, 2001; Siegel, 2005; Kawaguchi et al., 2006), which influences the timing of krill lipid accumulation. Therefore, regional and inter-annual differences in physical-biological processes that control spring phytoplankton blooms and consequently krill spawning behavior potentially have important implications for ecosystem linkages that affect Adélie penguin chick growth.

An analysis of larval krill stages obtained from net tows that provided circum-Antarctic coverage suggested regionally varying patterns in Antarctic krill spawning behavior (Spiridonov, 1995). These patterns include virtually all combinations of spawning timing (early, late November to early December; late, late December to January; variable) and duration (short, 1-1.5 months; long, 3-3.5 months; variable). The patterns may result from regional differences in physical processes (e.g. seasonal ice coverage, ice-melt patterns) that determine the availability of primary production to krill in the austral spring (Spiridonov, 1995). An implication is that regional differences in the phenology of lipid-accumulation and energy density among Antarctic krill available to breeding Adélie penguins may also exist. However, the extent to which regional patterns in primary production and krill spawning behavior influence the transfer of energy to Adélie penguins (and other top predators) population remains to be determined.

The WAP region between Anvers and Avian Island experiences high variability in the timing and duration of Antarctic krill spawning (Spiridonov, 1995). Simulations suggest that if breeding Adélie penguins do not shift initiation and duration of the breeding period in order to capitalize on the availability of high energy-density krill, inter-annual variability in krill spawning off the WAP could result in similar variability in prey quality and chick growth for their chicks.

#### *III.4.2 The Contrasting Energy Density of Spawning Female and Male Antarctic Krill*

Observations show that between 10-100% of mature adult Antarctic krill off the WAP participate in spawning (Siegel and Loeb, 1995; Quetin and Ross, 2001). Simulations suggest that when females and males participate in spawning in the same proportion, this variability has a small effect on Adélie penguin chick growth. However, when a higher proportion of females participate in spawning with no change in male spawning rate, simulations found that Antarctic krill energy density increases and Adélie penguin chick growth is enhanced. Conversely, reduced chick growth occurs with increased spawning participation by mature males and no change in female spawning rate.

Results also indicate that chick growth is influenced by an interaction between the effect of the length (maturity) and sex-ratio of Antarctic krill ingested by the chicks. When large, mature krill dominate, there is a greater proportion of adults that spawn in the population. Because mature males tend to have a low lipid content and mature (gravid) females have a high lipid content, the sex-ratio of a large size-class krill population that is provided to the chicks influences their growth. When large krill dominate and the population is dominated by females, the simulated chick fledging mass is optimal. However, if the population is dominated by males, simulated chick fledging mass is low due to lower krill-population lipid content.

Observations have found that the availability of large, presumably mature, Antarctic krill along the WAP varies with a 3 to 5 year periodicity. Survivorship rates of different krill age-classes underlie this periodicity. Antarctic krill survivorship is linked to sea-ice, stratification, and circulation patterns that determine phytoplankton availability as well as predation pressure. For Antarctic krill recruitment (over-winter survival of larval stages), extensive winter sea-ice cover is thought to provide food and protection from predators for larval krill. As a result, heavy sea-ice conditions have been positively correlated with episodic recruitment of Antarctic krill (Daly, 1990; Siegel and Loeb, 1995; Fraser and Hofmann, 2003; Quetin and Ross, 2003; Atkinson et al., 2004). Conditions that promote early spawning are also believed to be positively associated with recruitment as larval krill are allowed a longer period of growth prior to the onset of the seasonal ice-pack increasing their survivorship (Siegel and Loeb, 1995); a belief that is supported by krill energetics modeling (Fach et al., 2002). Factors that affect adult survivorship however, are not as well understood, but are likely to also be important for determining the 3 to 5 year periodicity in Antarctic krill size-classes. These factors include intra- and inter-specific competition, predation, and environmental conditions that facilitate lipid-accumulation prior to the onset of winter. Simulations suggest that environmental conditions that promote persistent abundance and availability of larger, mature size-classes could be important to Adélie penguin chick growth energetics. In particular, when the large size-classes are dominated by gravid females, the result is heavier fledging mass for Adélie penguin chicks.

Observations have found that large mature female Antarctic krill tend to dominate penguin diets during the austral summer (Hill et al., 1996; Reid et al., 1996), a pattern that appears to hold for Adélie penguins (Endo et al., 2002). Furthermore, analysis of net tows that were coincident with Adélie penguin diet samples showed the presence of significantly smaller krill with a higher proportion of males in net tows than in

the diet samples (Hill et al., 1996; Endo et al., 2002). These observations may reflect active selection by penguins of larger krill which, in some cases, have been shown to be dominated by females (Virtue et al., 1996). They may also suggest that Adélie penguins actively select mature female krill within swarms *or* forage in areas where this sex/maturity stage dominates. Regardless of the mechanism that underlies these patterns, simulations suggest that, search time being equal, over-representation of large, female Antarctic krill in adult Adélie penguin diets is beneficial for chick growth energetics.

#### *III.4.3 Antarctic Krill Population Lipid Content*

Many of the factors that were varied independently in this portion of the study likely co-vary in nature. For example, conditions that promote high spawning participation by mature Antarctic krill females probably also promote early spawning and enhanced lipid accumulation. In addition, large female krill are able to spawn earlier in the spring (Cuzin-Roudy and Labat, 1992; Spiridonov, 1995), so the timing of the initiation of spawning and its effects on prey quality and Adélie penguin chick growth should also be linked with krill size class distribution. Overall, a complex set of interactions between krill demography and environmental conditions combine to determine the seasonal variability of the energy density of Antarctic krill. While much has been learned about variability in lipid-content among sex/maturity stages, little is known about factors that control inter-annual variability in phytoplankton patterns that control lipid accumulation among Antarctic krill. Results from this portion of the study suggest that variability in the population-wide lipid-content of just  $\pm 2\%$  could influence Adélie penguin chick growth sufficiently to have a possible impact on recruitment.

#### *III.4.4 Climate Warming and Adélie Penguin Chick Growth*

The amount of seasonal ice production and the duration of seasonal ice coverage along the WAP is significantly decreasing (Jacobs and Comiso, 1997; Smith and Stammerjohn, 2001; Liu et al., 2004; Stammerjohn et al., 2008). Along the WAP, early krill spawning is associated with extensive and late retreating sea-ice coverage during the previous winter (Quetin and Ross, 2001). Conversely, early retreat is associated with late spawning. Presumably this relationship is tied to the influence of the timing of sea ice retreat on the spring phytoplankton bloom. Mechanisms that control the spring phytoplankton bloom off the WAP are not well understood. However, in the southeastern Bering Sea, another sea-ice-driven marine ecosystem, early sea-ice retreat is associated with a late spring phytoplankton bloom (Hunt et al., 2002). In this region, with an early ice retreat, surface stratification associated with the ice meltwater is eroded by winds prior to the availability of sufficient sunlight to drive an early-spring phytoplankton bloom (Hunt et al., 2002). As a result, the spring phytoplankton bloom is delayed until summer sunlight is sufficient to stratify the water column. This alteration in the phenology of biophysical processes that determine the type and timing of the phytoplankton bloom causes ecosystem effects in the southeastern Bering Sea that are observed through the system up to top predators (Hunt et al., 2002).

Similarly, earlier retreat of the seasonal pack-ice may change the phenology of biophysical processes off the WAP that may delay Antarctic krill spawning and lipid accumulation in some areas compared to previous times. Assuming that krill spawning and lipid accumulation patterns are coupled, the simulations project that this would have negative implications for the quality of Antarctic krill available to breeding Adélie penguins and chick growth in those areas (Fig. 17). However, while a shift in the availability of high-energy krill later in the summer may negatively influence chick growth, the same change may increase the energy available to fledglings im-

mediately after they enter the water. This may enhance their ability to meet their energetic requirements and to survive during the critical period immediately following fledging when chicks are learning to feed themselves.

Changes in the physical environment resulting from warming off the WAP may also influence the distribution of high-energy gravid female Antarctic krill that are available to breeding Adélie penguins. The spatial distribution of larger, spawning krill is known to differ from other sex/maturity stages (Lascara et al., 1999) and this distribution is thought to be determined by productivity patterns that facilitate the physiological demands of spawning (Cuzin-Roudy and Labat, 1992; Ichii et al., 1998; Siegel, 2000). Changes in the physical environment that alter the distribution of Antarctic krill spawning may have important implications for Adélie penguin chick growth energetics. For example, loss or reduced quality of spawning habitat within the foraging range of breeding Adélie penguins may reduce the energy density of prey ingested by chicks reducing their growth. The influence of climate warming on the distribution of Antarctic krill spawning regions off the WAP is not well understood but deserves attention in future field studies.

#### *III.4.5 Further Considerations*

Adult foraging Adélie penguins can counteract the energetic shortfall than comes from low quality prey in various ways. For example, adults could increase the feeding rate of their chicks in response to poor chick growth conditions. However, long-lived seabird species, such as the Adélie penguin, typically follow strategies that favor their own survival at the expense of single year's breeding effort (Mauck and Grugg, 1995; Watanuki et al., 2002). As a result, while Adélie penguins demonstrate some ability to adjust their foraging behavior during years when prey are less available (Lynnes et al., 2002), adults are not likely to significantly increase their energetic investment in chick provisioning under conditions of environmental stress. In fact, it has been

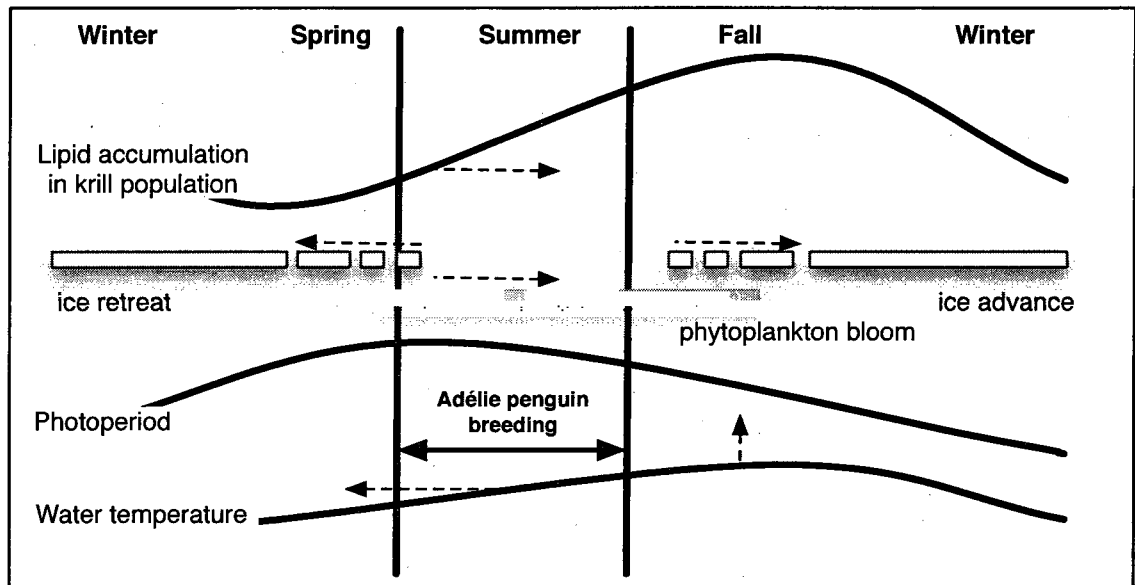


Fig. 17. The phenology of physical biological processes that link the physical environment (sea ice, water column environment) with primary production, Antarctic krill lipid accumulation and the quality of prey ingested by breeding adult penguins and their chicks. Dashed arrows indicate the shift in phenology of processes off the WAP under climate warming based on observational studies. The figure was adapted from current theory linking physical processes with krill spawning behavior (Kawaguchi et al., 2006).

shown that chinstrap penguins do not alter their foraging effort with reduced prey availability (Croll et al., 2006), suggesting that in some cases penguin adults invest a consistent amount of energy in their breeding-period foraging effort regardless of inter-annual variability in prey.

Adult Adélie penguins could also adjust their breeding schedule in order to match the availability of high quality prey. This kind of plasticity in breeding behavior has been shown among common murre (*Uria aalge*) in the North Atlantic that have delayed their breeding by a month to adjust to the shifting availability of high-quality gravid female capelin (*Mallotus villosus*) (Davoren and Montevecchi, 2003). However, Adélie penguins along the WAP do not demonstrate significant variability in their breeding schedule, with peak fledging occurring within 5 days of the average date

between 1987 to 2004. This lack of variability may accrue from the following, 1) the short period of high prey availability/quality necessary for breeding does not allow for flexibility in the Adélie penguin breeding schedule, 2) Adélie penguins must complete breeding at a certain time in order to meet the energetic requirements of a post-breeding molt and prepare for the over-winter period of low prey-availability, 3) Adélie penguins cannot shift their breeding later in the austral summer because this brings them into greater competition with the peak energetic requirements of chinstrap and gentoo penguins (*Pygoscelis papua*) that breed later in the austral summer, or 4) there is limited variability in timing of prey availability/quality patterns off the WAP, so it is not necessary for Adélie penguins to adjust their breeding schedule. All but the last imply that Adélie penguins have limited flexibility in the timing of breeding. If so, this leaves the WAP Adélie penguins particularly vulnerable to the energetic effects of a change in the phenology of prey availability/quality during the austral summer.

#### *III.4.6 Implications and Summary*

The chick-growth model simulations highlight the importance of processes that determine the timing of spawning and lipid accumulation to chick growth, fledging mass and recruitment of Adélie penguin chicks. Climate warming off the WAP has led to earlier retreat of the annual sea ice pack, which may be shifting Antarctic krill spawning and lipid accumulation in response to later availability of phytoplankton blooms in some regions. As a result, in those regions, the quality of prey available to foraging adults and provisioned to chicks may be reduced, which may be limiting the ability of breeding adults to raise chicks of sufficient size to recruit to the breeding population. Furthermore, results suggest that the availability of high-lipid, gravid female Antarctic krill as prey for foraging adult penguins is a critical determinant for penguin chick growth and fledging mass.

As has been found in other regions where sea ice characteristics determine ecosystem

structure and function (Hunt et al., 2002), climate related alteration of physical-biological linkages that determine availability of primary production to higher trophic levels may have important implications for the transfer of energy to top predators. In some regions off the WAP, this may be influencing the ability of breeding Adélie penguins to provision prey of sufficient quality to raise chicks that are able to recruit. However, factors that influence the energy density of Antarctic krill represents only a portion of the complete set of variables that influence Adélie penguin chick growth processes. The remaining factors will be considered in Chapter IV.

## CHAPTER IV

# DIET COMPLEXITY, VARIABLE PROVISIONING RATE, THERMOREGULATORY PROCESSES AND ADÉLIE PENGUIN CHICK GROWTH

### IV.1 INTRODUCTION

The growth of Adélie penguin chicks and fledging mass result from a combination of marine (prey) and terrestrial (thermoregulation) environmental effects. This chapter will consider the influence of variability among marine and terrestrial factors that were not considered in Chapter III that also influence Adélie penguin chick growth and fledging mass.

Warming of the WAP region over the past 50 years has been associated with significant alteration of the region's physical environment (Murphy et al., 1995; Jacobs and Comiso, 1997; Stammerjohn and Smith, 1997; Kwok and Comiso, 2002; King et al., 2003; Turner et al., 2005b; Stammerjohn et al., 2008), which has changed the WAP marine ecosystem within which breeding Adélie penguin populations exist. One result of these environmental changes is a shift in abundance, and most likely the distribution, of mid-trophic level prey species that mediate the transfer of energy from primary production to Adélie penguins (Smith et al., 1999b; Clarke et al., 2007; Ducklow et al., 2007). For example, Antarctic krill, the primary prey item for WAP Adélie penguins off the mid- to northern WAP (Volkman et al., 1980; Lishman, 1985; Trivelpiece et al., 1990; Fraser and Trivelpiece, 1996; Hinke et al., 2007), has experienced a reduction in population size while populations of salps (dominated by *Salpa thompsoni*), a group of species that is not an important prey item for Adélie penguins, has increased (Atkinson et al., 2004). In addition, Antarctic silverfish, a species that was present historically in WAP Adélie penguin diets (Emslie and Patterson, 2007), is not currently a diet component off Anvers Island during breeding (Fraser, unpub-

lished data). This suggests a change in Antarctic silverfish distribution and therefore their availability to foraging Adélie penguins and hence to their chicks in this region (Emslie and Patterson, 2007). Moreover, other diet items may become increasingly available at high latitudes as the climate warms. For example, *Electrona antarctica* (Family: *Myctophidae*, no common name), which is consumed by chinstrap (Jansen et al., 1998; Rombola et al., 2006) and gentoo penguins (Croxall et al., 1999) but not Adélie penguins (Volkman et al., 1980; Lishman, 1985; Trivelpiece et al., 1990) may become increasingly available to penguins at higher latitude locations. These observed and potential changes in mid-trophic level species distribution and abundance provide a basis for the first objective of this portion of the study which is to assess the effect of increasing dietary complexity through the addition of fish to an Antarctic krill diet on Adélie penguin chick growth and fledging mass.

The provisioning rate of the food encountered by foraging adults is also an important factor determining chick growth and fledging mass (Croxall et al., 1999; Salihoglu et al., 2001; Clarke et al., 2002). Provisioning rate of chicks is determined by the complex interaction between environmental conditions (e.g., sea ice characteristics, water temperature, nutrient distribution, circulation and water mass distributions) that affect prey availability and hence the behavior of a foraging adult penguin as it attempts to meet its own energetic requirements and the energetic requirements of its chick(s). When prey is less available, adults provision smaller meals and less energy to growing chicks (Croxall et al., 1999). Thus, the second objective of this study is to assess the influence of variation in provisioning rate of chicks at the nest on Adélie penguin chick growth.

The WAP has experienced increased precipitation as a result of climate warming (Turner et al., 2005b), which potentially enhances the role of terrestrial effects on Adélie penguin chick growth through increased exposure to water from rainfall or snow-melt (Patterson et al., 2003). While snow-pack could provide some insula-

tion from thermoregulatory costs, snowfall has typically melted by the time chicks are hatched near Palmer Station. Increased water in the colonies causes wetting of chicks thereby amplifying thermoregulatory costs (i.e. the wetting effect) and reducing growth (Lustick and Adams, 1977; Stalmaster and Gessaman, 1984; Wilson et al., 2004). This forms the basis for the third objective, which is to assess the influence of the wetting effect and associated metabolic costs on Adélie penguin chick growth.

The three research objectives were addressed using an individual-based energetics model (see Chapter III) to simulate the effects of variations in diet complexity (prey type and quality; research objective 1), availability (research objective 2), and increased wetting (research objective 3) on Adélie penguin chick growth and fledging mass. The common diagnostic used to analyze simulation results was chick fledging mass, which affects the probability that a chick will survive to recruit into the breeding population.

The model structure, simulations, parameters and approach for quantifying the implications of the simulations are described in the next section. Results of the simulations are then presented and implications of the model results for Adélie penguin populations in the context of changing environmental conditions off the WAP are discussed.

## IV.2 METHODS

The chick-growth model outlined in Chapter III was modified by substituting prey wet-mass energy density ( $ED_{pwm}$ ) for krill wet-mass energy density ( $ED_{kwm}$ ) (allowing for the diet complexity) and adding a wetting effect term ( $MMR_{wet}$ ) to the calculation of metabolic costs. Details of these modifications and the simulations used to investigate the research objectives are given below.

#### IV.2.1 Chick Diet Complexity

Adélie penguin foraging behavior does not appear to differ significantly when capturing fish or krill during the breeding season (Ropert-Coudert et al., 2002). Thus, for this study, it was assumed that the addition of fish to the diet does not affect the chick-provisioning rate schedule that was established for the chick-growth simulations. When fish are an important component of the Adélie penguin diet, the proportion of fish in the diet increases over the chick growth period (Ainley et al., 2003). Therefore, in this study, the proportion of fish in the chick diet was increased as the chick aged during the chick growth period (Fig. 18). The proportions of fish in the chick diet used in this study (mean of 0.17) were within the lower range of observations (Ainley et al., 2003) and, thus, provide a test of the effect on Adélie penguin chick growth of a small, but realistic increase of fish in the chick diet.

Alternative diets were provisioned at the same rate as that which, when being fed an all-Antarctic krill diet, produced a chick with a simulated fledging mass equal to the mean of the RFM and the NRFM. Simulated fledging masses when alternative diets were provisioned to chicks were then compared to that produced by the all-krill diet (3.09 kg), the RFM, and the NRFM. The parameterizations used to determine the energy density provided by the addition of Antarctic silverfish and *E. antarctica* to the chick's diet are given in the following sections.

##### IV.2.1.1 Antarctic Silverfish

The energy density for Antarctic silverfish was obtained from an empirical relationship developed from measurements (Hubold and Hagen, 1997; Wöhrmann et al., 1997; Hagen et al., 2000) that relate lipid content and fish total length ( $TL$ ) as

$$Lip(TL) = (Lip_{max} - Lip_{min}) \left( \frac{1}{1 + e^{-k(TL - k_{50})}} \right) + Lip_{min} \quad (16)$$

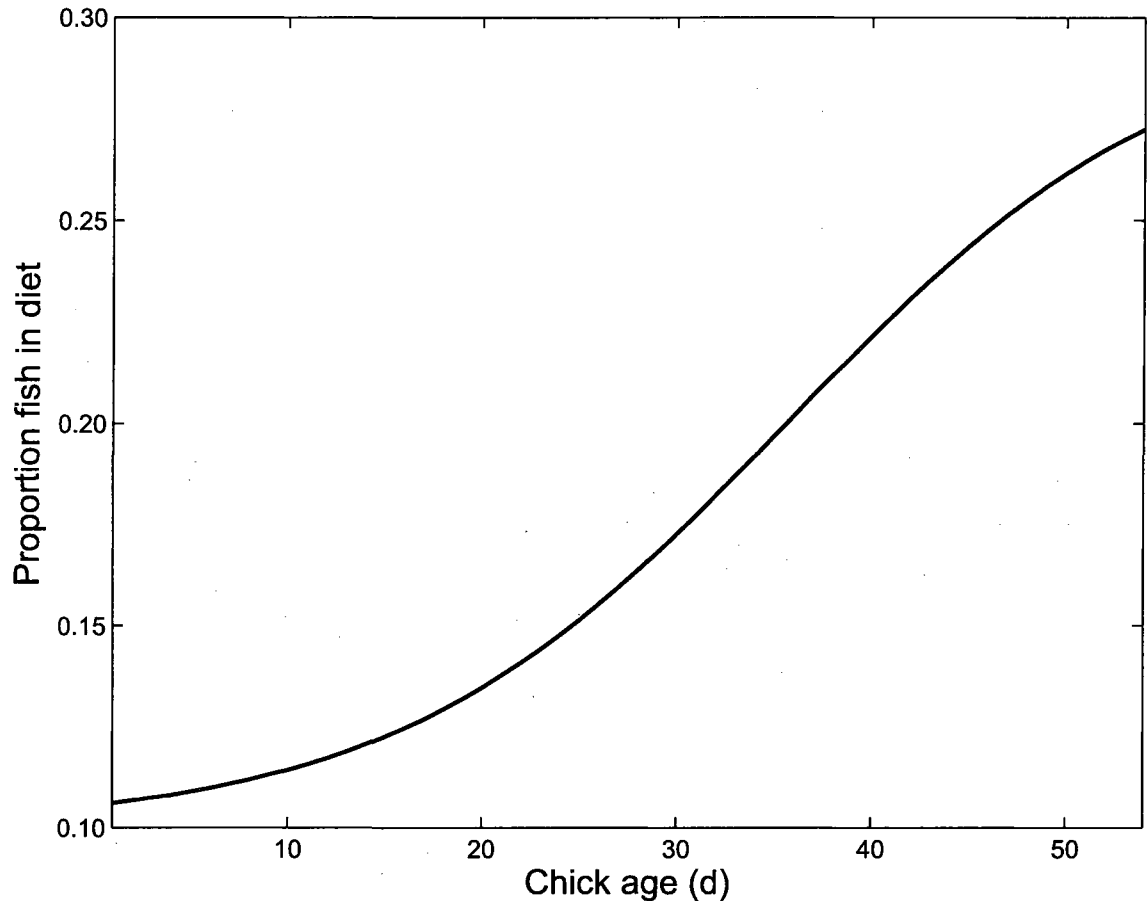


Fig. 18. Change in the proportion of fish in the Adélie penguin chick diet as the chick ages during the nestling period.

where  $Lip_{max}$  is the maximum lipid content (proportion dry mass, 0.43, Fig. 19),  $Lip_{min}$  is the minimum lipid content (proportion dry-mass, 0.12, Fig. 19),  $k$  ( $0.1 \text{ mm}^{-1}$ ) controls the rate of increase in lipid content with increasing  $TL$  (mm), and  $k_{50}$  (50 mm) is the  $TL$  (mm) at which the lipid content is 50% of its maximum value. Equation (16) gives a lipid content for Antarctic silverfish that increases slowly until 30 mm, after which it increases rapidly until reaching an asymptote at 80 mm (Fig. 19).

The dry mass proportion of protein, carbohydrate, and skeletal ash in the non-lipid portion of Antarctic silverfish was assumed to be similar to that of *Electrona antarctica* (Table 5). The percent-water composition of Antarctic silverfish decreases

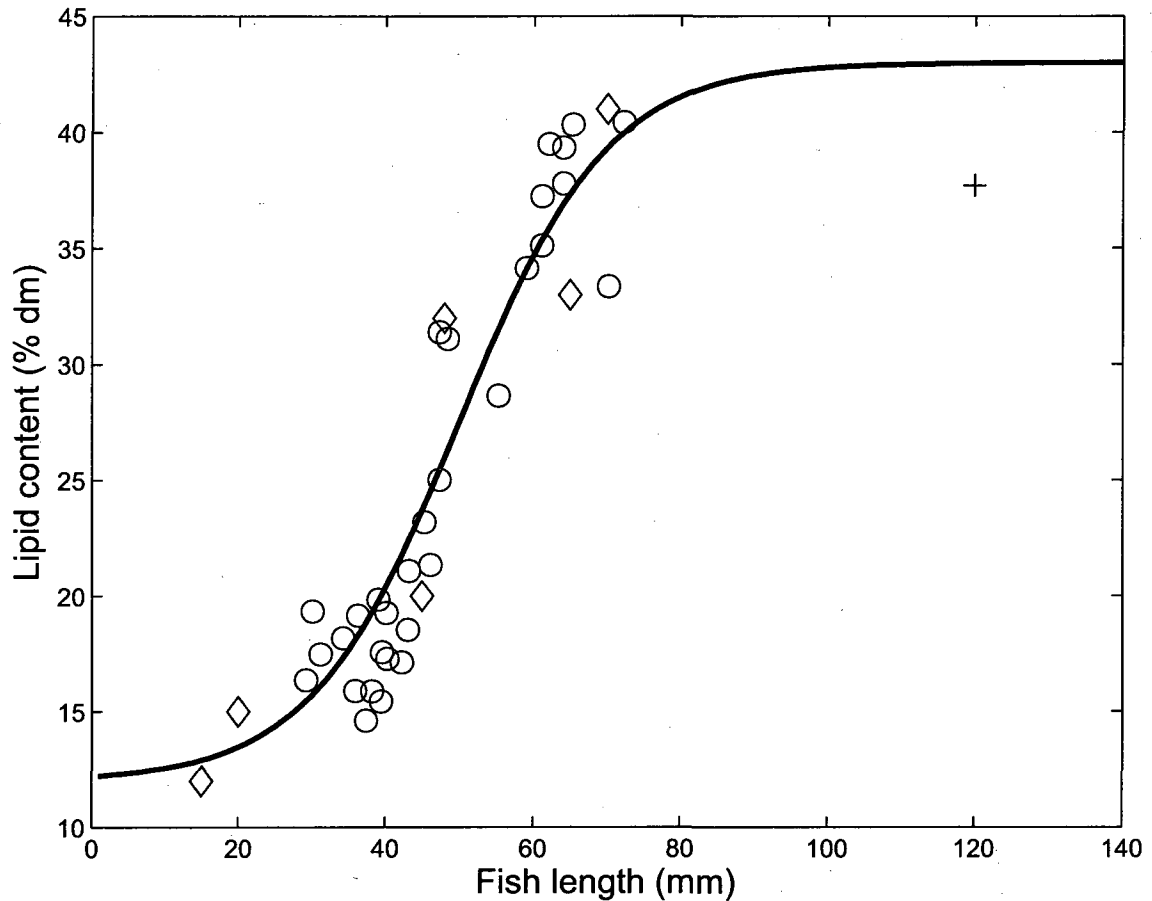


Fig. 19. Lipid content (% dry-mass) measured for Antarctic silverfish (*Pleuragramma antarcticum*) by (○) Hubold and Hagen (1997), (+) Wöhrmann et al. (1997), and (◇) Hagen et al. (2000). The relationship used to estimate the energy density for each age class of Antarctic silverfish using equation (16) is shown (—).

from 90% to 78% as  $TL$  increases (Torres, unpublished data). The lipid content, the non-lipid biochemical composition, and the percent-water composition were then used to calculate wet-mass biochemical composition as a function of Antarctic silverfish length. Finally, the energy density of each biochemical component (Table 5) was used to translate this function to one relating the Antarctic silverfish length to wet mass energy density (Fig. 20).

Antarctic silverfish  $TL$  was then related to specific age classes (AC) using von Bertalanffy growth parameters (eq. 17) determined from studies done in the Wed-

Table 5. The ratio and dry mass energy density of lipid, protein, carbohydrate and ash components used for Antarctic silverfish in this study. Ratios were calculated from Donnelly et al. (1990) based on a study of *E. antarcticum* and dry-mass energy density measurements are from Ricklefs et al. (1998). The lipid ratio is calculated from the relationship between age class and lipid content for Antarctic silverfish (equation 16).

Biochemical component	Ratio	Energy density (kJ kg <sup>-1</sup> )
lipid	calculated	0.0395
protein	0.85	0.0236
carbohydrate	0.01	0.0172
ash	0.14	0.0

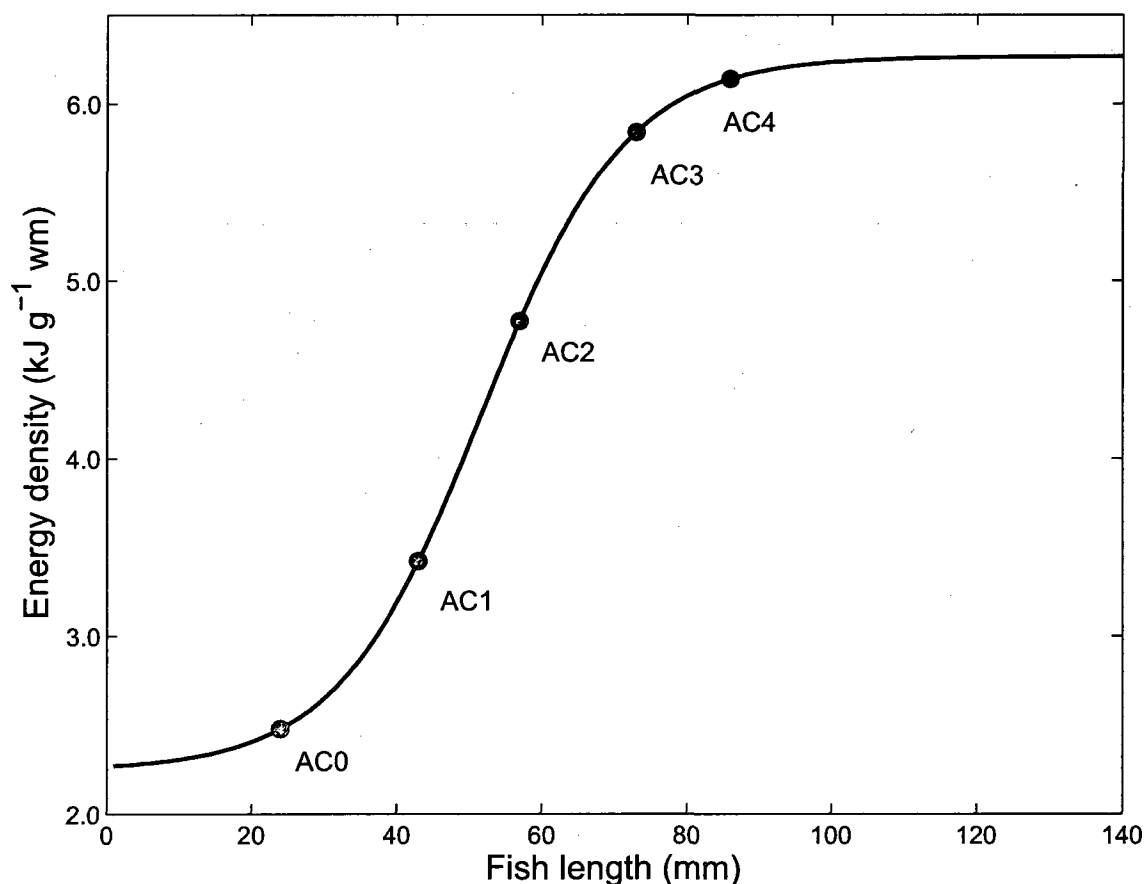


Fig. 20. The relationship between length and energy density for Antarctic silverfish (*Pleuragramma antarcticum*) used to obtain energy density for age classes (AC) 0 to 4 years. The energy density for the mean length of AC0 through AC4 fish is indicated by filled circles.

Table 6. Parameter values used in eq. (17) to estimate the length for each age class of Antarctic silverfish (*Pleuragramma antarcticum*). See text for parameter definitions.

$t_0$ (years)	$L_{max}$ (mm)	$k$ (mm <sup>-1</sup> )	Source
-1.49	210.8	0.07	Radtke et al. (1993)
-1.50	303.0	0.06	Hubold and Tomo (1989)
-1.495	256.9	0.065	This study

dell Sea (Hubold and Tomo, 1989) and the WAP (Radtke et al., 1993). The von Bertalanffy growth equation is

$$TL(t) = TL_{\infty}[1 - e^{-K(t-t_0)}] \quad (17)$$

where  $TL_{\infty}$  is the maximum length of the fish (mm),  $t$  is in years,  $t_0$  (years) moves the growth curve along the age axis and allows for non-zero length at hatching ( $TL$  at time = 0 years), and  $K$  (years<sup>-1</sup>) controls the rate of length increase.

The mean values of von Bertalanffy growth parameters from previous studies (Table 6) were used to obtain an estimate of  $TL$  for Antarctic silverfish AC0 through AC4. Lipid content is unknown for older Antarctic silverfish (Fig. 19), so only age classes up to AC4 were included as part of the chick diet. These lengths were then used to obtain an estimate of energy density for each Antarctic silverfish age class (Fig. 20, Table 7).

#### IV.2.1.2 *Electrona Antarctica*

*Electrona antarctica* represents a second potentially available prey species for penguin chick diets. van de Putte et al. (2006) provide a relationship between wet-mass energy density ( $E_{density}$ , kJ g<sup>-1</sup>) and  $TL$  (mm) for *E. antarctica* of the form

Table 7. Mean length (mm) and wet-mass energy density for each age class (AC0 - AC4) of Antarctic silverfish used in simulations. See text for a description of the methods and data used in generating these values.

Fish	Age Class	Mean length (mm)	Energy density (kJ kg <sup>-1</sup> )
<i>Pleuragramma antarcticum</i>	AC0	24	2.48
	AC1	43	3.42
	AC2	57	4.77
	AC3	73	5.84
	AC4	86	6.14
<i>Electrona antarctica</i>	AC0	20	6.79
	AC1	43	9.05
	AC2	66	10.62
	AC3	89	11.88

$$E_{density} = a \cdot \left(\frac{TL}{TL_0}\right)^{0.3745} \quad (18)$$

where  $TL_0$  is the base length (1 mm) used to calculate energy density and  $a$  (2.12 kJ g<sup>-1</sup> wet mass) is the energy density at this base length (van de Putte et al., 2006). This relationship gives an energy density that increases with increasing fish  $TL$  (Fig. 21). The  $TL$  values for *E. antarctica* between AC0 and AC3 were obtained from a relationship provided in Greely et al. (1999) of the form

$$TL = (0.063)A_d + 8.869 \quad (19)$$

where  $A_d$  is the fish age (days). Equations (18) and (19) allow length and energy density for *E. antarctica* AC0 to AC3 to be estimated (Fig. 21, Table 7).

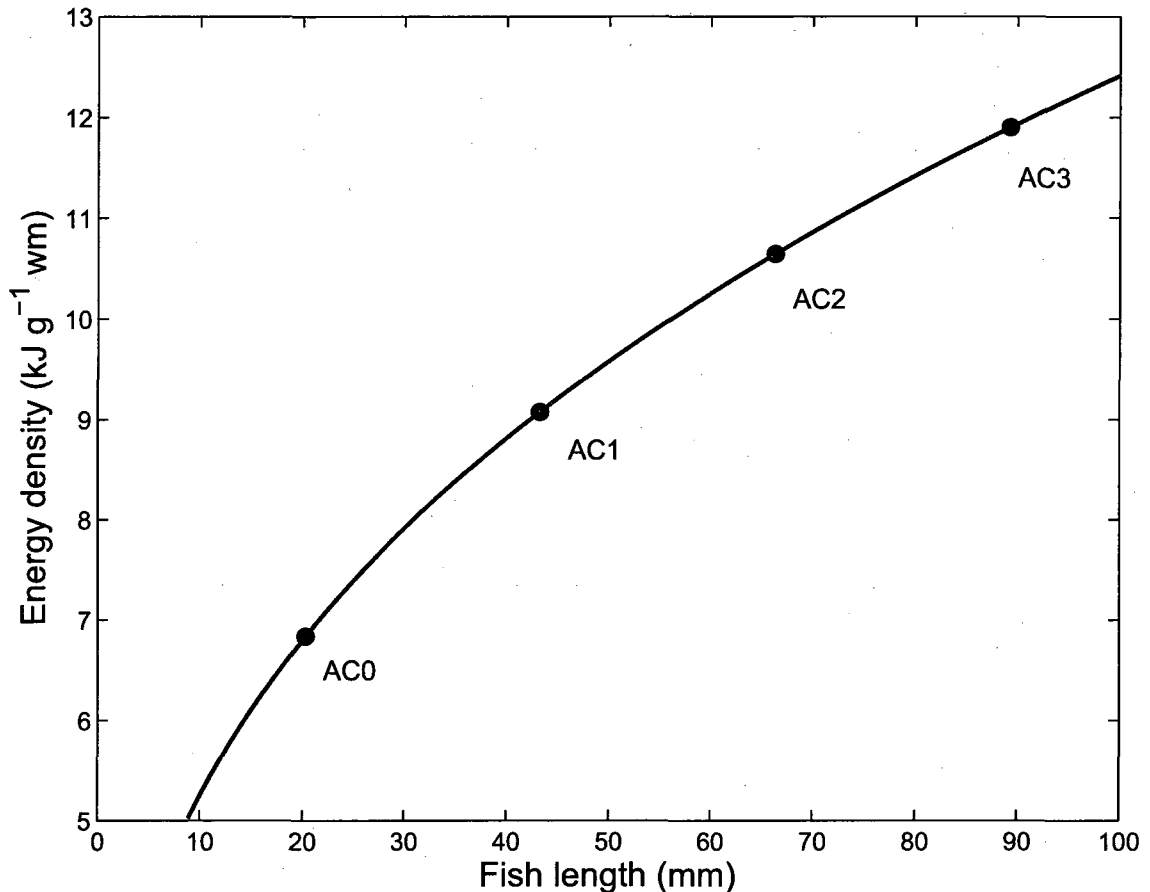


Fig. 21. The relationship between length and energy density for *Electrona antarctica* used to obtain energy density for age classes (AC) 0 to 3 years. The energy density for the mean size of AC0 through AC3 fish is indicated by filled circles.

#### IV.2.2 Altered Provisioning Schedule

##### IV.2.2.1 Increased Chick Starvation Period

The adult provisioning rate in the days prior to the starvation period provides the largest mass of food to the chick, so loss of provisioning during this time should have a substantial effect on growth. The extent of this effect was tested in simulations in which the provisioning schedule was shortened by 1 to 3 days. The potential mitigating effect of adding AC3 Antarctic silverfish to an all-krill diet as the starvation period was extended was also tested.

#### IV.2.2.2 *Reduced Chick Provisioning Rate*

The base provisioning rate used in the krill-only simulations was reduced up to 10%, for a krill-only diet and for a diet that included AC3 Antarctic silverfish. For both sets of simulations, a base provisioning rate that produced a chick of the RFM on an all-krill diet was used as a standard for comparison. The NRFM provided a measure of the effect of altered provisioning of chick fledging mass and the chick's probability of recruitment.

#### IV.2.3 *Chick Wetting*

##### IV.2.3.1 *Parameterization of Wetting Effect*

The effect of wetting on metabolism results from the influence of water on the modes of heat transfer through the skin/feather complex of the chick. Heat transfer, or the conductance of heat through the insulation provided by skin and feathers, was calculated as (Chappell and Souza, 1988)

$$C = \frac{MH}{(T_b - T_e)} \quad (20)$$

where  $C$  is the dry thermal conductance ( $\text{W kg}^{-1} \text{K}^{-1}$ ),  $MH$  ( $\text{W kg}^{-1}$ ) is the metabolic heat production or the total metabolic rate minus evaporative heat loss from respiration,  $T_b$  (K) is the body temperature of the chick, and  $T_e$  (K) is the operative temperature experienced by the chick. Chappell et al. (1990) provide a relationship to obtain the operative temperature, which is the temperature a chick experiences given an ambient temperature, solar radiation and wind speed, of the form

$$T_e = (0.69(T_a) + 0.028(Q_{sol}) - 0.0056(Q_{sol}u^{0.5}) + 1.47) + 273 \quad (21)$$

where  $T_a$  is air temperature ( $^{\circ}\text{C}$ ),  $Q_{sol}$  is incident solar radiation ( $\text{W m}^{-2}$ ), and  $u$  is wind speed ( $\text{m s}^{-1}$ ) at chick height.

Dry thermal conductance is the sum of all modes of heat loss through the skin/feather complex of the chick. Air and keratin, the protein in feather tissue, are the only insulating materials for a dry chick. The introduction of water to a chick's feathers causes mechanical disruption of the insulating structure of the feathers (removing air space) and adds water as an insulating material, increasing the rate of thermal conductance through the skin/feather complex. Evaporative heat loss from respiration is assumed not to change when a chick is wet. Therefore, any proportional change in the loss of heat from the bird due to wetting results in an increase in total metabolic rate of the same proportion. With this assumption, the effect of wetting chick down on metabolic costs is proportional to the increase in total heat loss through the skin/feather complex caused by the wetting. Total heat loss for the chick is the sum of radiative, convective, conductive heat transfer (Cena and Monteith, 1975a,b; Dawson et al., 1999), and the latent heat of evaporation (Cena and Monteith, 1975c) through a chick's skin/feather complex. These components of the heat loss for a chick are calculated as follows.

#### *IV.2.3.2 Radiative Heat Loss*

Chick down has similar structural properties to the downy adult after-feather which provides all the insulating properties for an adult penguin (Dawson et al., 1999). Therefore, the approach used by Dawson et al. (1999) for calculating radiative heat flux through adult feathers was adapted for this study. Dawson et al. (1999) calculated that the downy portion of the penguin feather created a cell of insulating air for each millimeter of its length as barbules from the feather latched onto those of neighboring feathers. Each layer was assumed to absorb radiated heat from the surface closer to the bird and radiate that heat in all directions, thereby reducing radiative heat loss by half at each layer. With these assumptions, radiative heat transfer ( $Q_r$ ,  $W\ m^{-2}$ )

Table 8. Definition, values, and sources for the constants used in the calculation of the different modes of heat transfer through the chick's skin/down complex.

Constant	Definition	Value	Heat Transfer Mode	Source
$\sigma$	Stefan-Boltzmann Constant	$5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$	Radiation	Incropera and DeWitt (1985)
$T_s$	Temperature at chick's skin	305 K	Radiation, Convection, Conduction, Evaporation	Dawson et al. (1999)
$\epsilon$	Emissivity of keratin	0.8 (unitless)	Radiation	Bejan (1993)
$n_{mm}$	Number of insulative layers per mm down	1.0 layers $mm^{-1}$	Radiation	Dawson et al. (1999)
$C_H$	Stanton number	$1.1 \times 10^{-2}$ (unitless)	Convection	Smith (1980)
$c_p$	Specific heat of water	$1.032 \text{ J g}^{-1} \text{ K}^{-1}$	Convection	Incropera and DeWitt (1985)
$dx$	Depth of chick down	8 - 27 mm	Radiation, Conduction	Taylor (1986)
$k_{water}$	Conductivity of water	$6.13 \times 10^{-1} \text{ W m}^{-2} \text{ K}^{-1}$	Conduction	Incropera and DeWitt (1985)
$k_{air}$	Conductivity of air	$2.6 \times 10^{-2} \text{ W m}^{-2} \text{ K}^{-1}$	Conduction	Incropera and DeWitt (1985)
$D$	Diffusion coefficient (Dalton's Number)	$1.5 \times 10^{-3}$ (unitless)	Evaporation	Gill (1982)
$H_{evap}$	Latent heat of evaporation	$2.5 \times 10^3$ (unitless)	Evaporation	Incropera and DeWitt (1985)

was calculated as

$$Q_r = \frac{\sigma(T_s^4 - T_e^4)}{(n+1)\left(\frac{2}{\epsilon-1}\right)} \quad (22)$$

where  $\sigma$  is the Stefan-Boltzmann constant (Table 8,  $\text{W m}^{-2} \text{ K}^{-4}$ ),  $T_s$  (K, Table 8) and  $T_e$  are the skin and operative air temperatures, respectively,  $n$  is the number of insulating layers of air, and  $\epsilon$  is the emissivity of keratin (Table 8). The value for  $T_e$  varies daily and is calculated using eq. (21). The value for  $n$  is a function of the depth of the chick down and the number of insulating layers per mm of down ( $n_{mm}$ , Table 8) which is assumed to be 1 (Dawson et al., 1999).

#### IV.2.3.3 Convective Heat Loss

Convective heat loss can occur as a result of natural and forced convection. Dawson et al. (1999) showed that natural convection is not significant through dry adult penguin feathers. Natural convection is not likely an important factor in heat loss for

dry Adélie penguin chicks because of the similarity of adult and chick down. Dawson et al. (1999) also showed that the feather structure does not allow for significant interaction between the air inside and outside of the bird's feathers, thus minimizing forced convection. This is supported by other studies (Taylor, 1986; Chappell et al., 1989) that found a minimal influence of wind on the metabolic rates of adults and chicks outside of extremely cold and windy conditions. The conditions in these studies that caused a change in metabolic rate were windier and colder than those typically observed during the nestling period on the WAP based on data used in this study (see below).

Observed or theoretical studies of the influence of wind and consequent forced convective heat loss on wet chicks have not been done. However, mechanical disruption of the chick's down by water is likely to increase convective heat loss, but behavioral responses (e.g. selection of favorable micro-habitat, huddling with other chicks, and assuming a posture that minimizes the impact of the wind) may minimize this impact under moderate wetting conditions. Forced convective heat loss was calculated using a relationship (Gill, 1982) that relates sensible heat loss ( $Q_s$ ,  $W\ m^{-2}$ ) to wind speed ( $u$ ,  $m\ s^{-1}$ ) as

$$Q_s = C_H \cdot u(T_s - T_e)\rho_a \cdot c_p \quad (23)$$

where  $C_H$  is the dimensionless Stanton number (Table 8),  $\rho_a$  is the density of air ( $g\ m^{-3}$ ), and  $c_p$  is the specific heat of water (Table 8,  $J\ g^{-1}k^{-1}$ ). The wind speed was modified to reflect the chick's ability to select an optimal habitat to minimize the effect of wind as

$$u = u_{measured} \cdot u_m \quad (24)$$

where  $u_{measured}$  is wind speed at chick height, and  $u_m$  is the reduction of wind speed by micro-habitat selection by the chick (Table 9).

Table 9. Definition and range of values for parameters that were varied in simulations assessing the influence of the wetting effect on chick metabolic costs and chick growth.

Parameter	Definition	Range	Base Value	Heat Transfer Mode
$u_m$	Modification of wind speed due to microclimate selection and physical barrier of plumage	0.1 - 1.0 (unitless)	0.4	Evaporation
$wet_{mod}$	Modification of depth of down resulting from exposure to water.	0.05 - 0.9 (unitless)	0.5	Radiation, Conduction
$p_{water}$	Percent of down complex that is water	0.1 - 20.0 %	5.0%	Conduction
$P_{wet}$	Percent of the chick that is wet	1 - 25%	5%	Radiation, Convection, Conduction, Evaporation

#### IV.2.3.4 Conductive Heat Loss

When a chick is sufficiently wet that the structural insulating properties of the feathers are lost, the conductance of the down is influenced by the relatively high thermal conductivity of water. Conductive heat loss under wet conditions was estimated from the relationship given by Incropera and DeWitt (1985)

$$Q_x = \frac{k_{down}(T_s - T_e)}{dx} \quad (25)$$

where  $Q_x$  is the rate of heat flow through the penguin's feathers ( $\text{W m}^{-2}$ ),  $k_{down}$  is the thermal conductivity of down ( $\text{W m}^{-2}$ ), and  $dx$  is the thickness of the insulating down layer (Table 8,  $m$ ).

The down depth ( $dx$ ) is modified by the presence of water as

$$dx = dx_{dry} \cdot wet_{mod} \quad (26)$$

where  $dx_{dry}$  is the dry down depth, and  $wet_{mod}$  is the modification of dry depth by the presence of water (a dry chick would have a  $wet_{mod} = 1.0$ ). Chick down depth increases with age (Taylor, 1986). In this study, down depth increases from 8 to 27

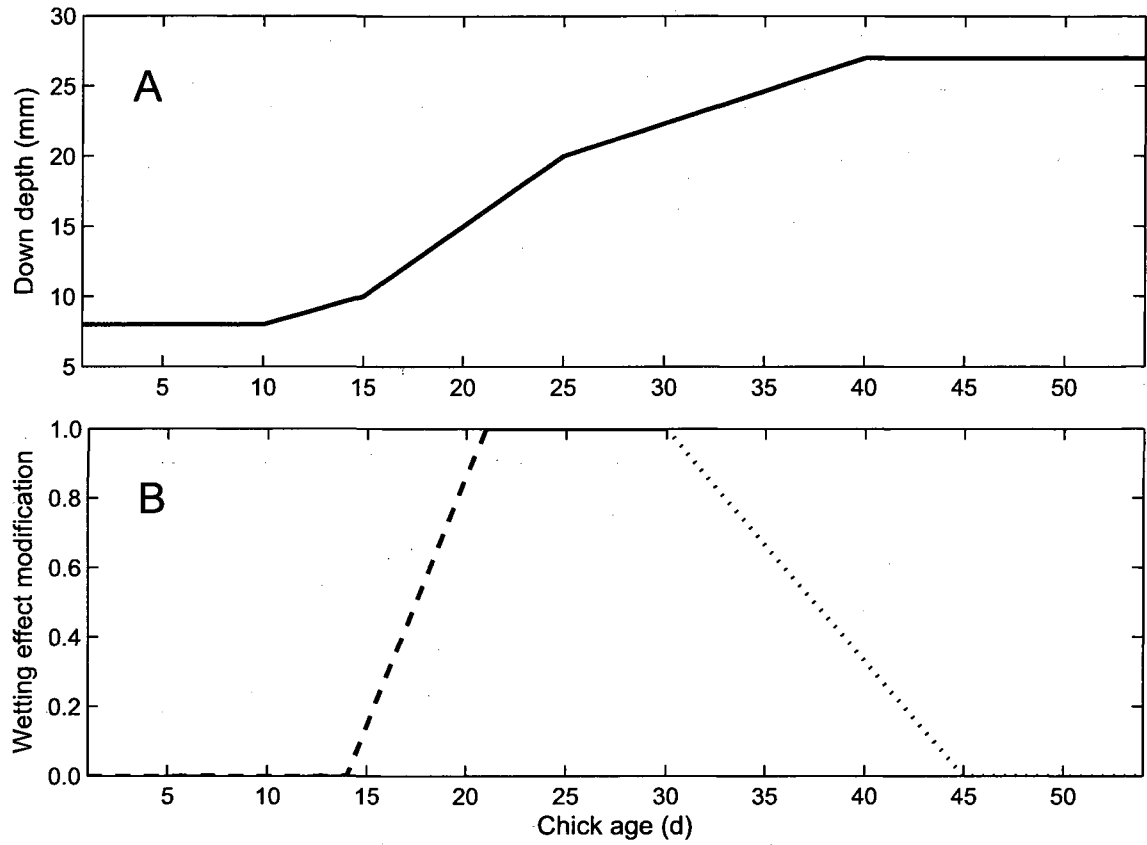


Fig. 22. A) The change in chick down depth with increasing chick age (Taylor, 1986), and B) the chick wetting effect modification that occurs as the chick ages because of decreased guarding by the parent (---) and development of fledgling down (···).

mm for chicks between the age of 10 to 40 days (Fig. 22A, Table 8).

Down thermal conductivity ( $k_{down}$ ) is the sum of the conductivity of water ( $k_{water}$ ,  $\text{W m}^{-2}\text{K}^{-1}$ ) and air  $k_{air}$  (Table 8,  $\text{W m}^{-2}\text{K}^{-1}$ ) and is calculated as

$$k_{down} = k_{water} \cdot p_{water} + k_{air}(1 - p_{water}) \quad (27)$$

where  $p_{water}$  (unitless) is the proportion of the down that is saturated with water.

#### IV.2.3.5 *Evaporative Heat Loss*

Evaporative heat loss is only important when the chick is wet. The extent to which a chick continues to become wet through contact with water (or additional precipitation) determines the potential for evaporative heat loss. Evaporative heat loss is dependent on wind speed, but this effect can be mitigated by chick behavior, as discussed previously. Evaporative heat loss as a function of wind speed is given by (Gill, 1982)

$$Q_e = \rho_a \cdot D \cdot u \frac{q_s}{q_a} H_{evap} \quad (28)$$

where  $Q_e$  is the evaporation rate ( $\text{g m}^{-2} \text{s}^{-1}$ ),  $\rho_a$  is the density of air ( $\text{g m}^{-3}$ ),  $D$  is the diffusion coefficient (Table 8),  $q_s$  and  $q_a$  are the specific humidity at the skin of the chick (assuming saturation at the skin temperature) and in the ambient air, respectively, and  $H_{evap}$  is the latent heat of evaporation (Table 8).

#### IV.2.3.6 *Calculation of Increased Thermoregulatory Cost*

The thermoregulatory cost of wetting is calculated by first determining the ratio ( $W$ ) of heat conducted through the skin/feather complex of a wet chick to that of a dry chick (eq. 29).

$$W = \frac{Q_r(wet) + Q_s(wet) + Q_x(wet) + Q_e(wet)}{Q_r(dry) + Q_s(dry) + Q_x(dry) + Q_e(dry)} - 1 \quad (29)$$

The wetting effect ( $W_{effect}$ ) is then calculated as

$$W_{effect} = P_{wet} \cdot W_m \cdot W \quad (30)$$

where  $P_{wet}$  is the percent of the chick that is wet,  $W_m$  is a wetting effect modification provided by a guarding adult or the chick's waterproof fledgling down and  $W$  scales

these effects. The wetting effect modification varies between 0 and 1 (Fig. 22B). The reduction of wetting effect by the guarding adult decreases after day 14, when the adult can no longer completely insulate the chick. The benefit from the guarding adult is gone at day 21 when the chick enters the *cr che* stage and chicks are no longer guarded by adults at the nest. The chick regains protection from wetting between days 35 and 50 as fledgling plumage develops. Thus, chicks are most vulnerable to wetting between ages 17 and 40 days (Fig. 22B). Although there may be some thermoregulatory benefit to *cr ching* behavior through huddling during this time (Lawless et al., 2001), this benefit not explicitly included in the model. Any thermoregulatory benefit gained from huddling in the *cr che* is likely to be minimal for smaller colonies where the number of huddling chicks is limited. Therefore, the model most accurately represents the wetting effect in smaller colonies.

The wetting effect obtained from eq. (30) modifies the field metabolic rate ( $MMR$ ) experienced by the chick as

$$MMR_{wet} = W_{effect} \cdot MMR \quad (31)$$

where  $MMR_{wet}$  is the increase in the total metabolic cost caused by wetting. The value for  $MMR_{wet}$  is then added to the metabolic costs otherwise experienced by the chick ( $MMR$ ). Many of the parameters used in calculating the wetting effect are poorly constrained by observations. A series of simulations were done to quantify the effect on chick fledging mass of variability among a subset of these parameters (Table 9). While the influence of variability in each parameter was tested, all other parameters were held constant (Table 9). As with the altered provisioning schedule simulations, a base provisioning rate that produced a chick of the RFM on an all-krill diet was used for the chick wetting simulations.

#### *IV.2.3.7 Data and Variables Used in Wetting Calculations*

eqs (21) to (28) require daily mean values for wind speed, ambient temperature, incident solar radiation (insolation), air density and specific humidity. Daily means of hourly values for these meteorological data during the Adélie penguin nestling period between 1995 and 2004 were obtained from the British Antarctic Survey ([www.antarctica.ac.uk/met/metlog](http://www.antarctica.ac.uk/met/metlog)). These meteorological time series were used in the simulations that explored the effect of annual variability in weather conditions on chick fledging mass.

Meteorological data were representative of conditions at colonies at ANV. With the exception of insolation, data are from Vernadsky (UKR) station which is 55 km south of Palmer Station (Prior to 1996, this was Faraday Station operated by the British Antarctic Survey, Fig. 1). Insolation data are from Rothera Station which is 360 km southwest of Palmer Station (Fig. 1). This was the closest location where insolation data were available between 1995 and 2004. Mean daily insolation data from Rothera Station between 1995 and 2004 from the chick-rearing period was only slightly higher than that measured by Chappell et al. (1990) at Palmer Station during 1986 ( $204 \text{ w m}^{-1}$  compared to  $191 \text{ w m}^{-1}$ ). Given the limited contribution that insolation makes to the calculation of the operative temperature (see eq. 21), the data from Rothera was considered appropriate to use in this study.

Increases in chick metabolic costs result when high winds and cold air temperatures occur during the time when the chick is not guarded by an adult and has not developed fledgling down (Fig. 22B). The number of days when high winds ( $> 6 \text{ m s}^{-1}$ ) and cold temperatures ( $< 0 \text{ }^{\circ}\text{C}$ ) occurred from 1995 to 2004 varied (Table 10). A relatively large number of days with high winds during the nestling period occurred during 1995, 1998, 1999, and 2001 (Table 10). During the period when chicks were most vulnerable to the wetting effect (chick ages 17-40 d), a relatively large number of days with high winds occurred in 1998, 1999, and 2001 (Table 10). Low temperatures

Table 10. The total days with high winds (mean  $> 6 \text{ m s}^{-1}$ ) and low ambient temperature (mean  $< 0 \text{ }^{\circ}\text{C}$ ) during the 54-day nestling period (19 December to 10 February) and when chicks are most vulnerable to wetting (chick age between 17 and 40 days, 4 - 17 January), a period when chicks are most vulnerable to the metabolic costs associated with the wetting effect. Mean daily wind speed and temperatures were obtained from records collected at Faraday/Vernadsky Research station from 1995 to 2004.

Year	Days with high winds		Days with low temperatures	
	Nestling period	Chick vulnerability period	Nestling period	Chick vulnerability period
1995	10	3	11	3
1996	5	3	11	4
1997	2	0	11	4
1998	10	7	7	4
1999	14	6	29	16
2000	1	0	1	0
2001	17	5	13	3
2002	2	1	1	0
2003	8	3	5	2
2004	7	1	25	12

were experienced during the nestling period for a relatively large number of days during 1999, 2001, and 2004 (Table 10). When chicks were most vulnerable to the wetting effect, a relatively large number of cold days occurred during 1999 and 2004 (Table 10).

The wind speed was measured at 10 m though winds experienced by chicks are at heights of less than 0.5 m. Therefore, the measured winds were attenuated based on an analysis of concurrent data sets collected at 10 m and at 0.35 m (the height of a large chick). Wind speeds measured at Faraday/Vernadsky Station in 1986 were compared with concurrent wind speeds measured at 0.35 m during the 1986 breeding season near Palmer Station (Chappell et al., 1990). This comparison showed that the measured winds at 10 m were 30% to 35% stronger than those measured at the height of a chick. Visual comparison between histograms of data at the height of a penguin chick (data were not available from this study for a direct correlation to

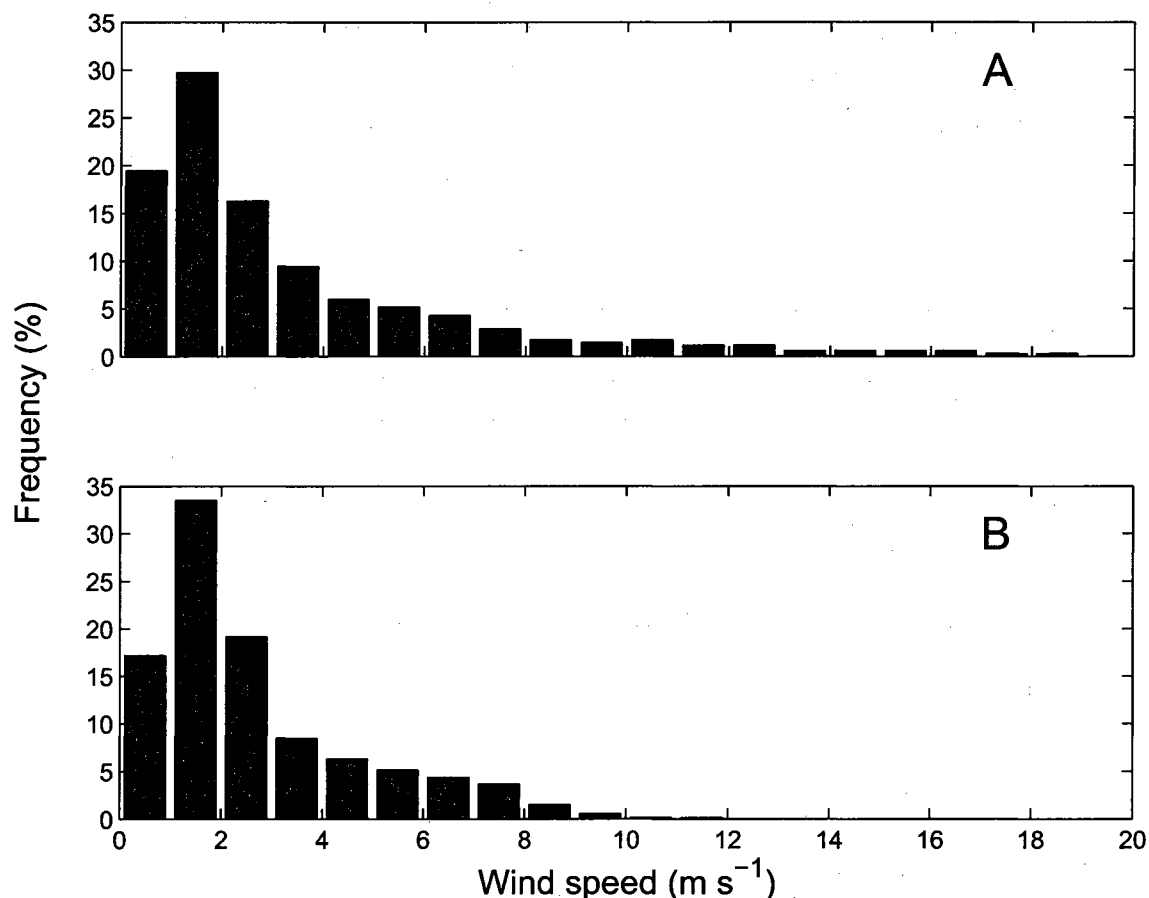


Fig. 23. A) Histogram of wind speed frequency at specific wind speeds at 0.35 m (penguin chick height) at Palmer Station (Chappell et al., 1990) and (B) that obtained from Faraday/Vernadsky and modified by a factor of 0.67 (B). Wind speed is binned at 0.5 m s<sup>-1</sup> intervals.

be calculated) and that measured at Faraday/Vernadsky and modified by a factor of 0.67 was favorable (Fig. 23). Furthermore, the mean wind measurement from both data sets (2.6 m s<sup>-1</sup>), and the proportion of measurements greater than 1 m s<sup>-1</sup> (just over 0.80 reported in Chappell et al. (1990) compared to 0.83 calculated from the Faraday/Vernadsky data) were essentially equivalent. There were more high wind speed measurements for the unmodified data from the Palmer Station study (Fig. 23), but this difference does not affect the daily mean values calculated for use in this study.

As an example, the modified wind data from 1995 (Fig. 24A) shows 6 wind events

(consisting of consecutive days with high winds) during the growth period which lasted a total of 10 days (Table 10). Two of these wind events occurred during the period when chicks are most vulnerable to the wetting effect (chick ages 17 to 40 d). The ambient temperature averaged  $1.0^{\circ}\text{C}$  during the chick growth period, ranging between  $-1.8$  and  $3.3^{\circ}\text{C}$  (Fig. 24B). Specific humidity averaged  $4.2 \times 10^{-3}$  and ranged between  $3.4 \times 10^{-3}$  and  $4.9 \times 10^{-3}$  (Fig. 24C). The 1995 weather conditions were used in the simulations that tested the effect of variability in wetting parameters (Table 9) on chick fledging mass.

Limited field and experimental data are available to validate the thermoregulatory cost of wetting in chicks obtained from eq. (29). However, it is encouraging that the mean value for the ratio of wet to dry thermal conductivity ( $W$ ) in simulations based on the 1995 meteorological data was remarkably similar to that measured in experimental studies where heat flux was measured through gentoo penguin chick down [2.5 this study and 2.7 in Kessler et al. (1967)].

## IV.3 RESULTS

### IV.3.1 Diet Complexity

#### IV.3.1.1 Antarctic Silverfish

Chicks raised on a diet consisting of AC0 or AC1 Antarctic silverfish and Antarctic krill reach a simulated fledging mass of 2.76 kg and 2.90 kg, respectively (Fig. 25). These fledging masses are less than the NRFM for chicks fed a krill-only diet. Chicks reared on AC2 Antarctic silverfish combined with Antarctic krill reached a simulated fledging mass equivalent to that obtained for a krill-only diet (Fig. 25). Adding AC3 and AC4 Antarctic silverfish to an all-krill diet increased fledging mass by 5% and 6%, respectively, to a mass above the RFM (Fig. 25).

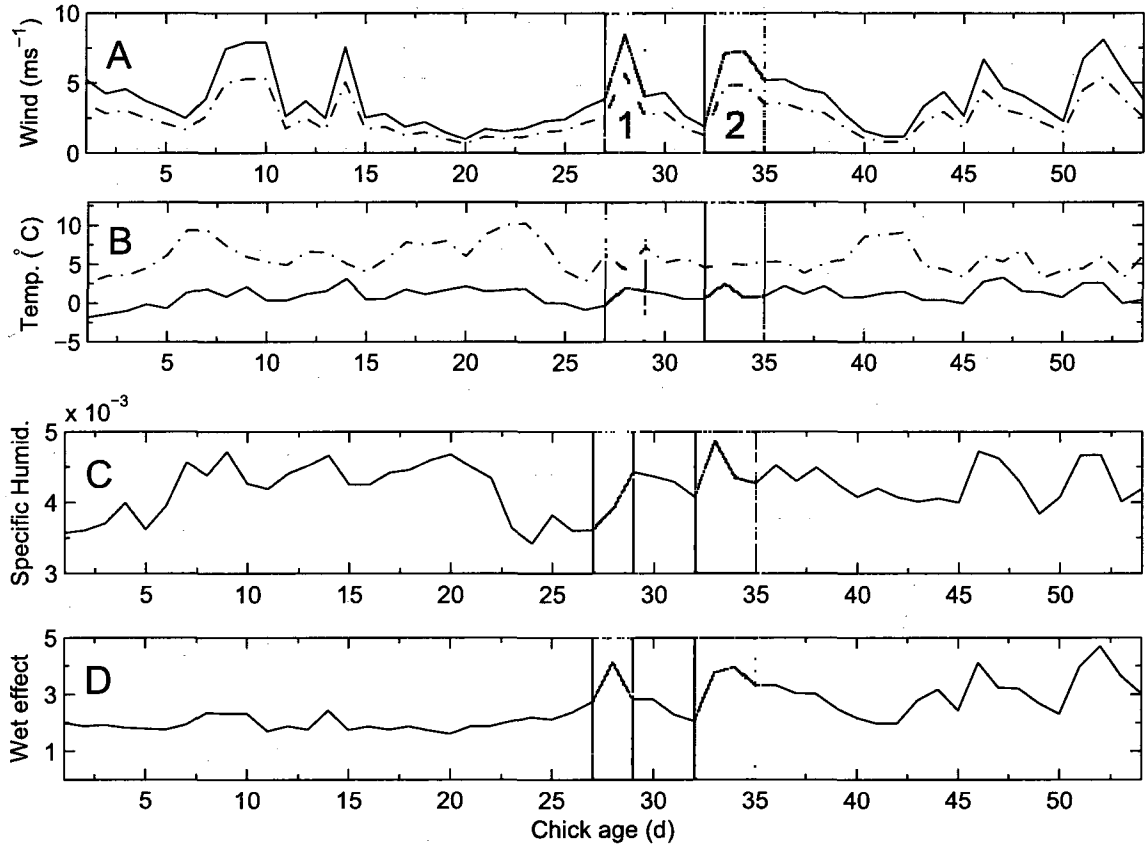


Fig. 24. Time series measured in 1995 at the Faraday (UK)/Verndadsky (UKR) meteorological station during the chick nestling period of A) wind speed ( $\text{m s}^{-1}$ ) (---) and wind speed adjusted for chick height (—), B) ambient air temperature (—) and operative temperature (---,  $T_e$ , °C), C) specific humidity (unitless), and D) calculated wet effect, or the ratio between wet and dry thermal conductance ( $W$ , unitless). The shading indicates two high wind events (daily mean wind speed  $> 6 \text{ m s}^{-1}$ ) during the nestling period when chicks are most vulnerable to the wetting effect (chick ages 17 to 40).

#### IV.3.1.2 *Electrona Antarctica*

The addition of *E. antarctica* to the all-krill chick diet yielded a simulated fledging mass that exceeded the RFM for all age classes of fish (Fig. 25). The fledging mass produced by the youngest age class (AC0) exceeded those obtained with a krill-only and AC0 Antarctic silverfish diets by 9% and 22%, respectively. Simulated fledging mass increases dramatically with *E. antarctica* age (Fig. 25). The simulated fledging mass produced by the AC3 *E. antarctica* age class exceeded that produced by the

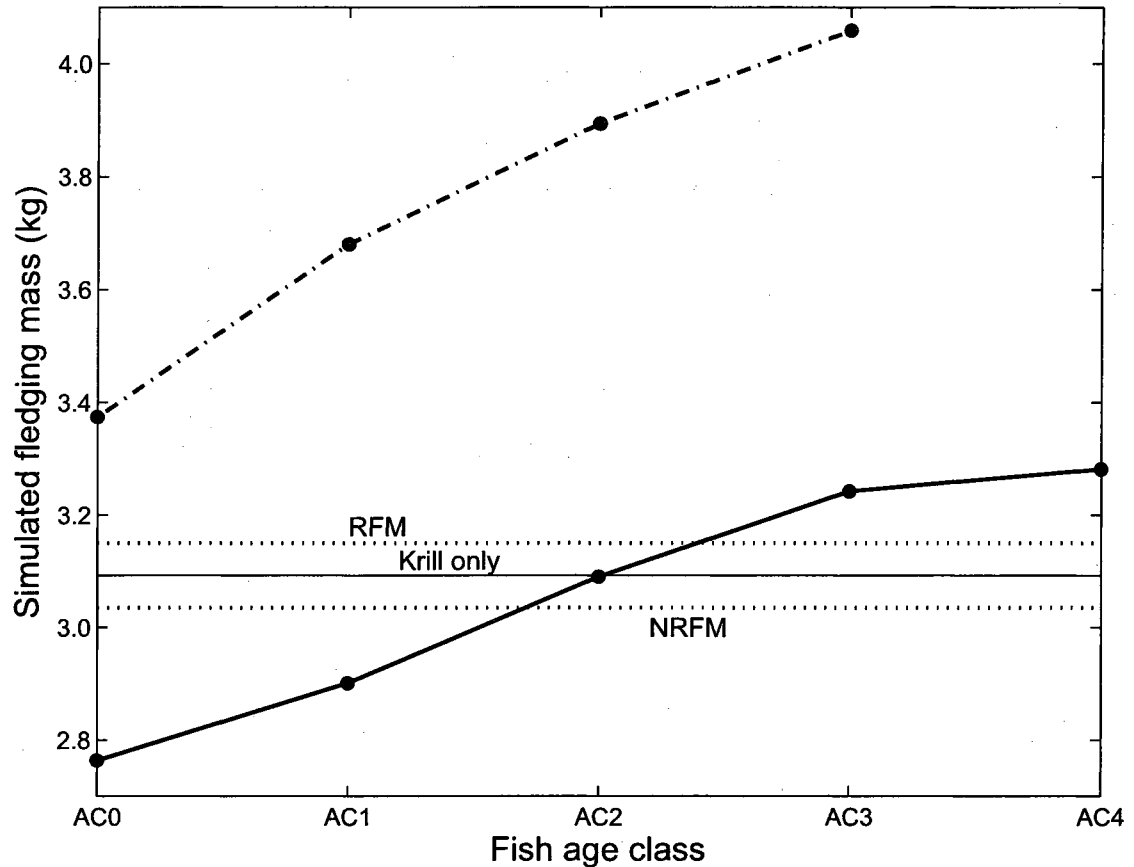


Fig. 25. Simulated fledging mass when Antarctic silverfish (—) of age classes (AC) 0 through 4 and *Electrona antarctica* (---) of age classes AC0 through AC3 are included in the Adélie penguin chick diet. The simulated fledging mass for a krill only diet (—) and the fledging mass of chicks that recruit into the breeding Adélie penguin population (RFM) and those that do not recruit (NRFM) are also indicated (···).

AC4 Antarctic silverfish age class by 23%.

#### IV.3.2 Altered Provisioning Schedule

##### IV.3.2.1 Increased Chick Starvation Period

For the krill-only diet, increased duration of the starvation period resulted in a significant decrease in chick fledging mass (Fig. 26A). Lengthening the starvation period to 3 days reduced the krill delivered to the chick by 2.52 kg. Increasing the

starvation period by more than one day decreased the simulated fledging mass below the NRFM. For the diet including Antarctic silverfish, increasing the duration of the starvation to 3 days decreased the simulated fledging mass from 3.30 kg to below the NRFM (Fig. 26A).

#### *IV.3.2.2 Reduced Chick Provisioning Rate*

Simulated fledging mass decreased proportionally from the RFM to 2.90 kg as the reduction in provisioning rate increased from 0 to 10% (Fig. 26B). With a reduction of more than 4% of the reference provisioning rate, the simulated fledging mass fell below the NRFM. For the diet including Antarctic silverfish, fledging mass decreased from 3.30 to 3.00 kg as the percentage reduction in provisioning rate increased from 0% to 10% (Fig. 26B). The simulated fledging mass fell below the NRFM when the diet was reduced by more than 8%.

#### *IV.3.3 Chick Wetting*

The calculated wet effect ( $W$ ) averaged 2.5, ranging between 1.6 and 4.7, peaking during 4 high wind events above 3.5 (Fig. 24D). Two of these events occurred when chicks are most vulnerable to the wetting effect (Fig. 24D). The wind time series were most closely correlated (11) with the ratio of wet to dry thermal conductance (Spearman's rank correlation,  $r^2 = 0.70$  p-value  $< 0.001$ ), followed by temperature experienced by the chick (spearman's rank correlation,  $r^2 = -0.31$ , p-value = 0.023) and then specific humidity (spearman's rank correlation,  $r^2 = 0.17$ , p-value = 0.21).

The simulated fledging mass obtained for environmental conditions from 1995 to 2004 for Adélie penguin chicks at Palmer Station ranged from 3.07 kg (1999) to 3.09 kg (2004), with an overall mean of 3.08 kg (Fig. 27). These years span a range of environmental conditions (Table 10), yet there was little variability among simulated fledging mass and none fell below the NRFM.

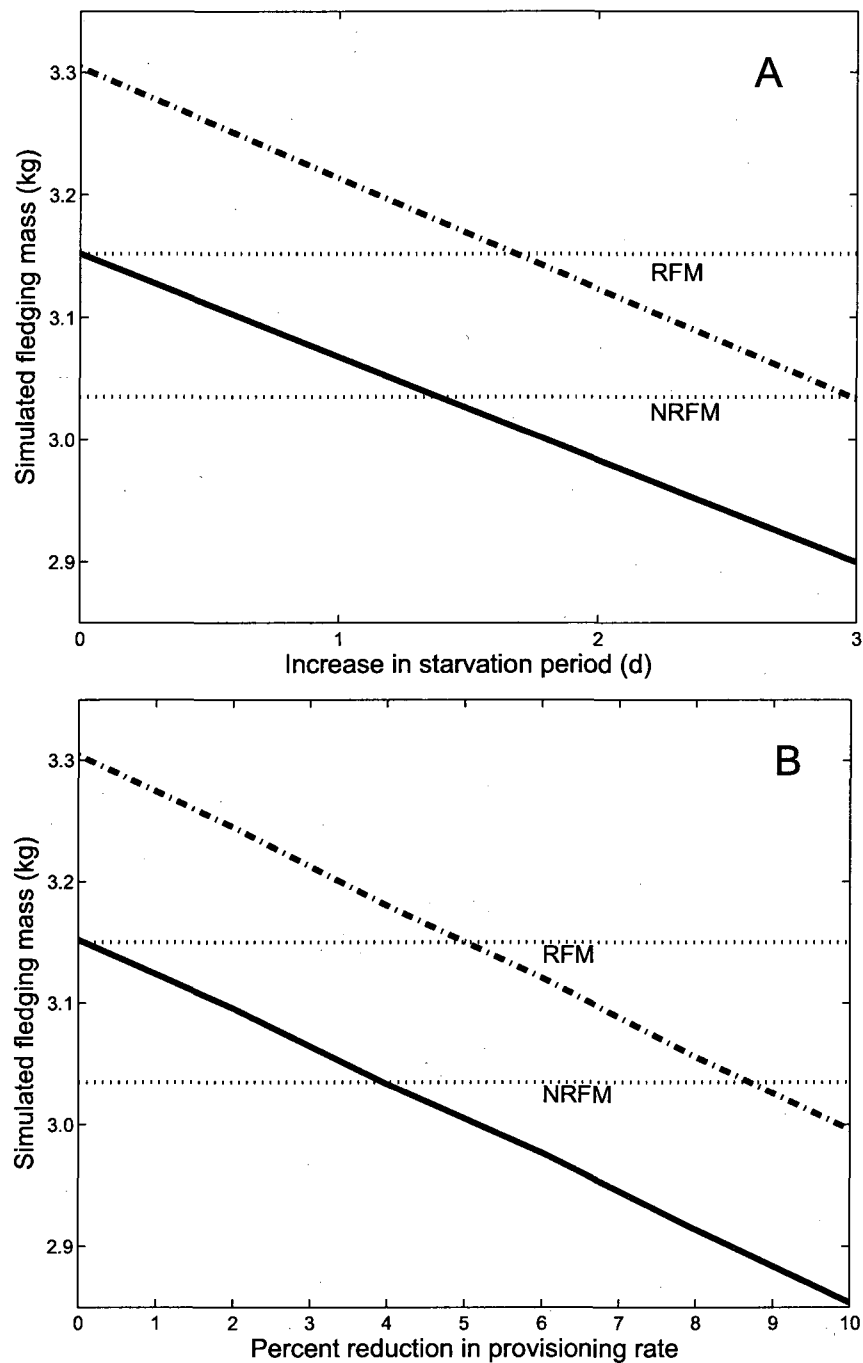


Fig. 26. Simulated chick fledging mass obtained with A) increasing length of the chick starvation period and B) variability in the chick provisioning rate. Simulated fledging mass was obtained for an all krill diet (—) and a combined diet of Antarctic krill and AC3 Antarctic silverfish (---). The mean fledging mass of tagged chicks that recruited into the breeding population at Palmer Station (RFM), and the mean mass of chicks that did not recruit (NRFM) are indicated (···).

Table 11. The range and standard deviation ( ) of the daily mean for each heat transfer mechanism and total heat flux through the penguin chick skin/down structure calculated for the each day within the 1995 nestling period.

Heat Flux ( $\text{W m}^{-2}$ )					
	Radiative	Convective	Conductive	Evaporative	Total
Dry	3.1-12.1 (3.0)	-	22.0-95.4 (24.2)	-	25.2-107.5 (27.3)
Wet	6.3-21.8 (5.3)	9.6-89.0 (21.3)	54.0-233.9 (59.4)	1.8-21.0 (3.8)	74.9-326.8 (72.6)

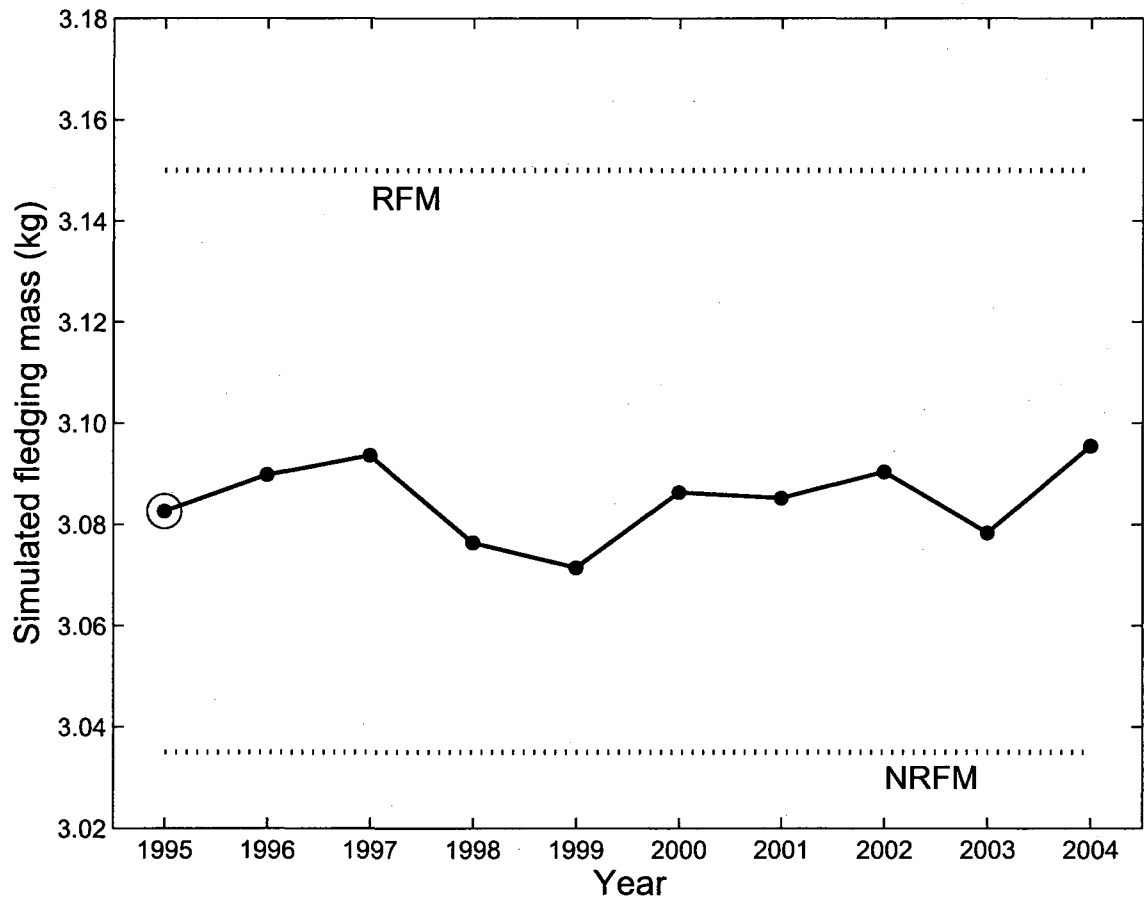


Fig. 27. Simulated fledging mass obtained using the base case wetting parameters (Table 9) and the 1995 to 2004 meteorological time series for the chick nestling periods. The 1995 fledging mass, which provides a reference simulation, is indicated (⊙). The mean fledging mass of tagged chicks that recruited into the breeding population at Palmer Station (RFM), and the mean mass of chicks that did not recruit (NRFM) are indicated (···).

Variability in simulated fledging mass was most sensitive to the number of windy and cold days during the period when chicks were most vulnerable to the wetting effect (Fig. 27 and Table 10). Specifically, fledging mass was lowest during 1999 (Fig. 27) when there were more days with high wind speeds and low temperatures during the period when chicks are most vulnerable to the thermoregulatory costs of wetting (Table 10). Wind appears to be the more important meteorological variable however, as the second lowest simulated fledging mass occurred in 1998 (Fig. 27) when there were more windy days, but a moderate number of days when temperatures were low (Table 10). The highest simulated fledging mass occurred in 2004 (Fig. 27) when there were few windy days but many cold days during the period when chicks are most vulnerable to wetting effects (Table 10).

The variability of the wetting effect during the nestling period and the wetting effect experienced by a chick is illustrated by a simulation using the 1995 conditions (Fig. 28). During this year, the wetting effect (determined by eq. 30) increased to about 0.12 on day 26 as the adult penguin provided less protection from the elements (Fig. 28). After the guard period ended and prior to the development of fledgling plumage, the extent to which wetting increased the chick's metabolic costs was determined to a large degree by local wind speed. For example, the wetting effect reached 0.21 on day 28 as a result of a high wind event (wind event 1, Fig. 22 and Fig. 28). A subsequent increase in wetting effect to 0.15 on day 33 was also associated with a wind event (wind event 2, Fig. 22 and Fig. 28). Following these wind events, the wetting effect returned to zero when the fledging plumage was fully developed.

The metabolic rate change effect for each heat loss mechanism for the 1995 nestling period (prior to modification for a guarding parent, development of fledgling plumage, or the percent of the chick that is wet) shows that the greatest heat loss is from conductive heat flux, followed by convective, latent, and then radiative heat flux (Fig. 29). There was a sharp decrease in the metabolic costs caused by wetting after

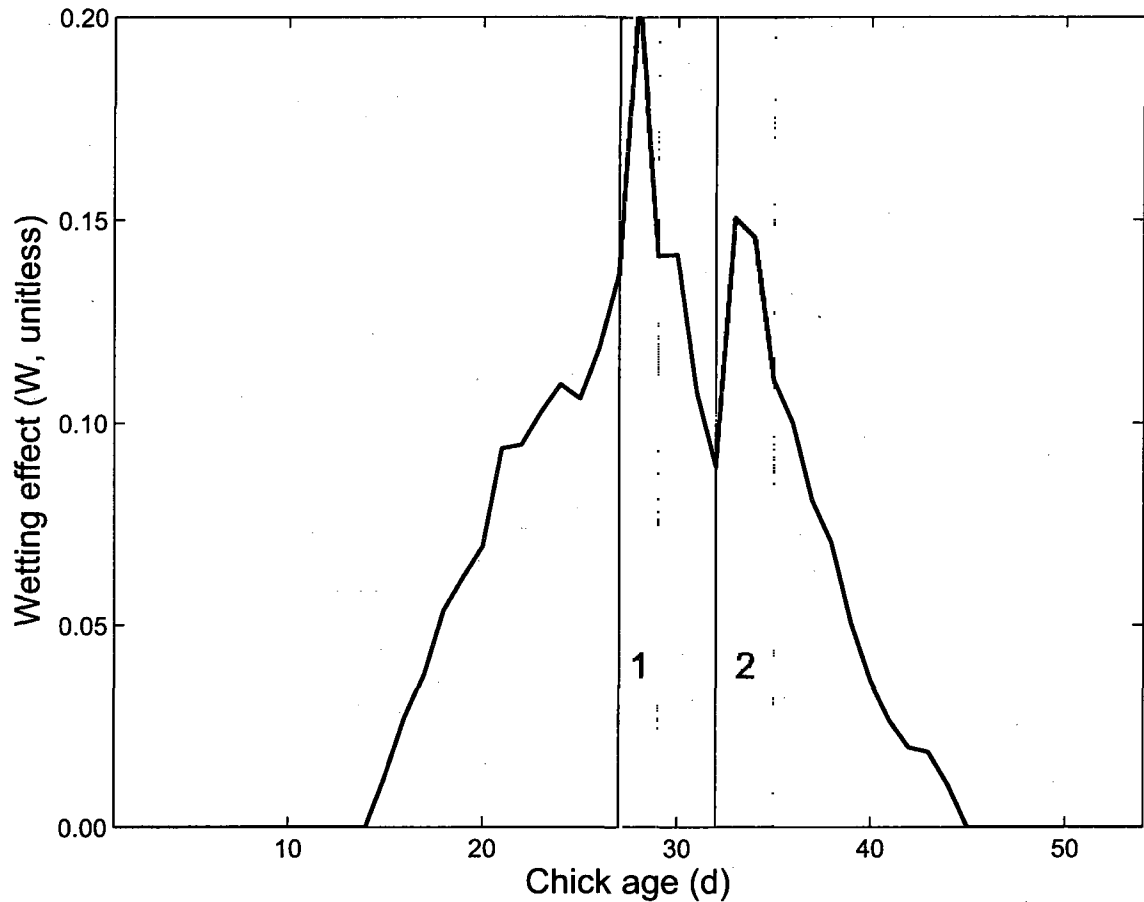


Fig. 28. The wetting effect ( $W$ ) as a function of chick age calculated using the 1995 meteorological time series for the Adélie penguin breeding season. Two wind events during the period when chicks are vulnerable to the thermoregulatory costs of wetting (chick ages 17 - 40 d) are indicated by the shading.

the guard stage (approximately chick age 21 d) as the depth of the chick's down increased. Variability in conductive heat loss was relatively high and more strongly correlated with the total increase in heat loss due to wetting than other heat loss modes. During high wind events, the heat flux due to convective heat loss surpassed that by conductive heat loss and became the mode of heat loss most responsible for the wetting effect.

Increasing the percent modification of dry down depth due to increasing presence of water resulted in decreased simulated fledging mass (Fig. 30A). Just over a 50%

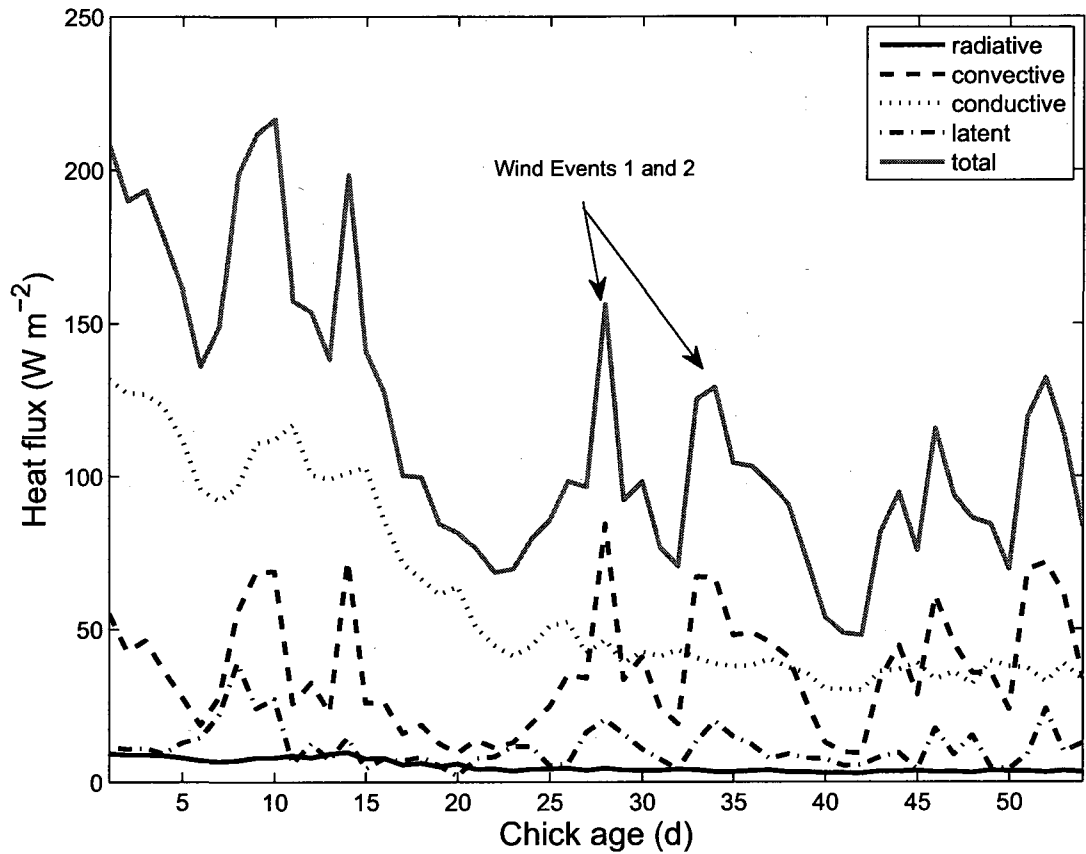


Fig. 29. The total increase in heat flux ( $\text{W m}^{-2}$ ) through the chick's skin/feather complex because of wetting and the increase for each mode of heat flux for the 1995 nestling period. The increase in heat flux is prior to modification for a guarding parent, development of fledgling plumage, or the percent of the chick that is wet. Wind events experienced by the chick during the period when it is most vulnerable to the wetting effect are indicated.

reduction in dry down depth reduced simulated fledging mass to the NRFM. As more water was retained in the chick's down (e.g. chick becomes saturated), fledging mass decreases (Fig. 30B). Wetting only 8 to 10% of the chick was sufficient to reduce the fledging mass below the NRFM (Fig. 30C).

Variability in the wind modification had less of an effect on chick fledging mass than does variability in the percent of the chick that is wet (Fig. 30D). For all effective wind speeds, chick fledging mass remained between the RFM and the NRFM. However,

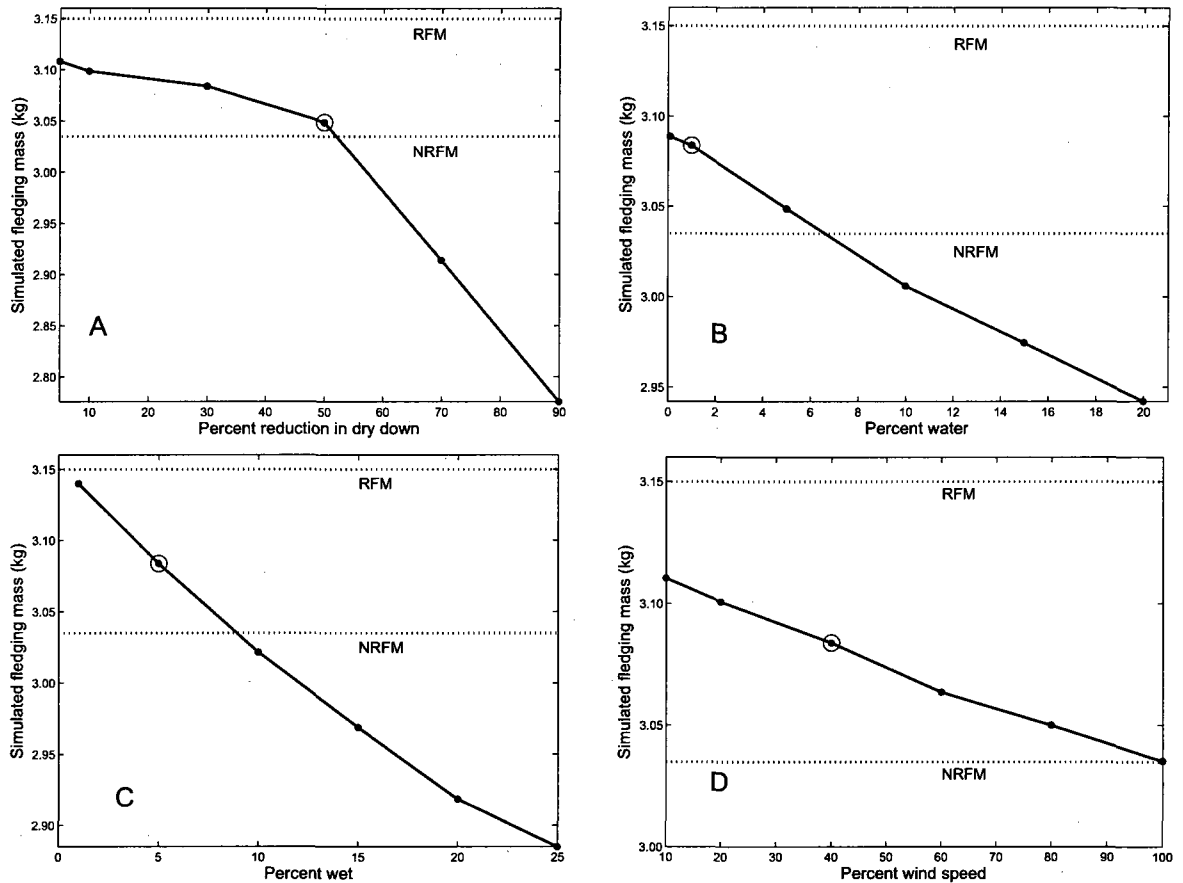


Fig. 30. Simulated fledging mass obtained from variability in A) the percent reduction in down depth by water, B) the percentage of the down structure that is composed of water, C) the percentage of the chick that is wet, and D) the percent modification of wind speed to generate the effective wind speed acting on heat transfer away from the chick. The mean fledging mass of tagged chicks that recruited into the breeding population at Palmer Station (RFM), and the mean mass of chicks that did not recruit (NRFM) are indicated ( $\cdots$ ). The parameter value used for the reference simulation (1995 conditions) is indicated ( $\odot$ ).

as discussed above, wind speed appears to be the primary meteorological variable affecting variability in simulated fledging mass (Table 10, Fig. 27). For example, two wind events during the period when chicks are most vulnerable to wetting in 1995 (Fig. 24A), had an obvious influence on the wetting effect experienced by the chick (Fig. 28). These short term increases in wetting had a slight, but noticeable effect on chick growth (Fig. 31). Growth slowed from  $101 \text{ g d}^{-1}$  to  $77 \text{ g d}^{-1}$  during wind event 1 and from  $89 \text{ g d}^{-1}$  to  $64 \text{ g d}^{-1}$  during wind event 2, which contributed to the

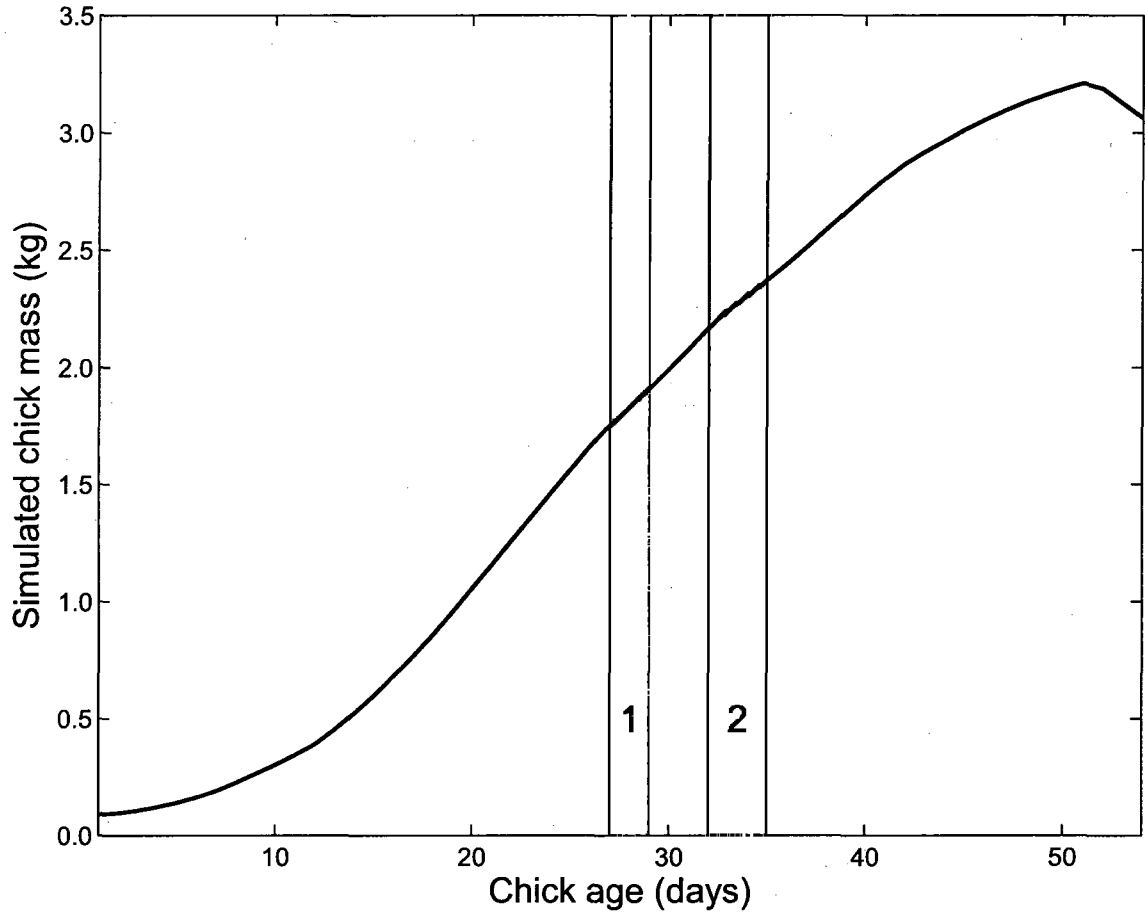


Fig. 31. Simulated chick fledging mass obtained for 1995 meteorological conditions during the chick nestling period using base values for the wetting parameters (Table 9). The two wind events that occurred during the period when chicks are most vulnerable to the wetting effect (chick ages 17 - 40 d) are indicated by shading.

overall reduction in fledging mass of 2%.

#### IV.3.4 Diet-Wetting Combined Effect

The mixed diet simulations showed that adding AC3 and older Antarctic silverfish to an all-krill diet increases chick fledging mass. Therefore, diet is one factor that can potentially offset the effects of increased thermoregulatory costs due to wetting of the chick. To test the combined effect of diet and wetting on chick growth, additional simulations were done in which the percent of the chick that is wet (0-25%) and the

percentage of the diet composed of AC3 Antarctic silverfish (0-50%) were varied.

For chicks that are less than 10% wet, simulated fledge mass that corresponded to chicks with a higher probability of survival (RFM, 3.15 kg) are obtained with a krill-only and mixed krill and Antarctic silverfish diet (Fig. 32). However, as wetting increased from 0%, a higher percent of fish in the diet was needed to compensate for thermoregulatory losses. Offsetting a 5% increase in wetting required that a chick be provided with a diet consisting of about 10% AC3 Antarctic silverfish. A chick that was 15% wet needed a diet that included almost 25% AC3 Antarctic silverfish to maintain a fledge mass of 3.15 kg (Fig. 32). Thus, switching to a more Antarctic silverfish-based diet can potentially mitigate thermoregulatory effects of increased wetting on Adélie penguin chick growth.

## IV.4 DISCUSSION

### *IV.4.1 Diet Complexity*

#### *IV.4.1.1 Antarctic Silverfish*

Given equal provisioning rates, supplementing a chick diet of Antarctic krill with Antarctic silverfish of at least AC3 produces simulated chicks that are heavier than those fed an all-krill diet. The extent to which this alternative prey source contributes to chick growth is presumably determined by environmental conditions that influence the fish's availability to the foraging adult Adélie penguin.

The environmental conditions that favor persistent availability of Antarctic silverfish are linked with aspects of the species' life history. Antarctic silverfish are long lived (about 30 year life span), grow slowly, have delayed maturation to reproductive condition, and have a high reproductive rate (Radtke et al., 1993). These characteristics, along with sluggish swimming speeds, a broad distribution, high abundance, and extensive representation in top predator diets, suggest an adaptation by Antarctic sil-

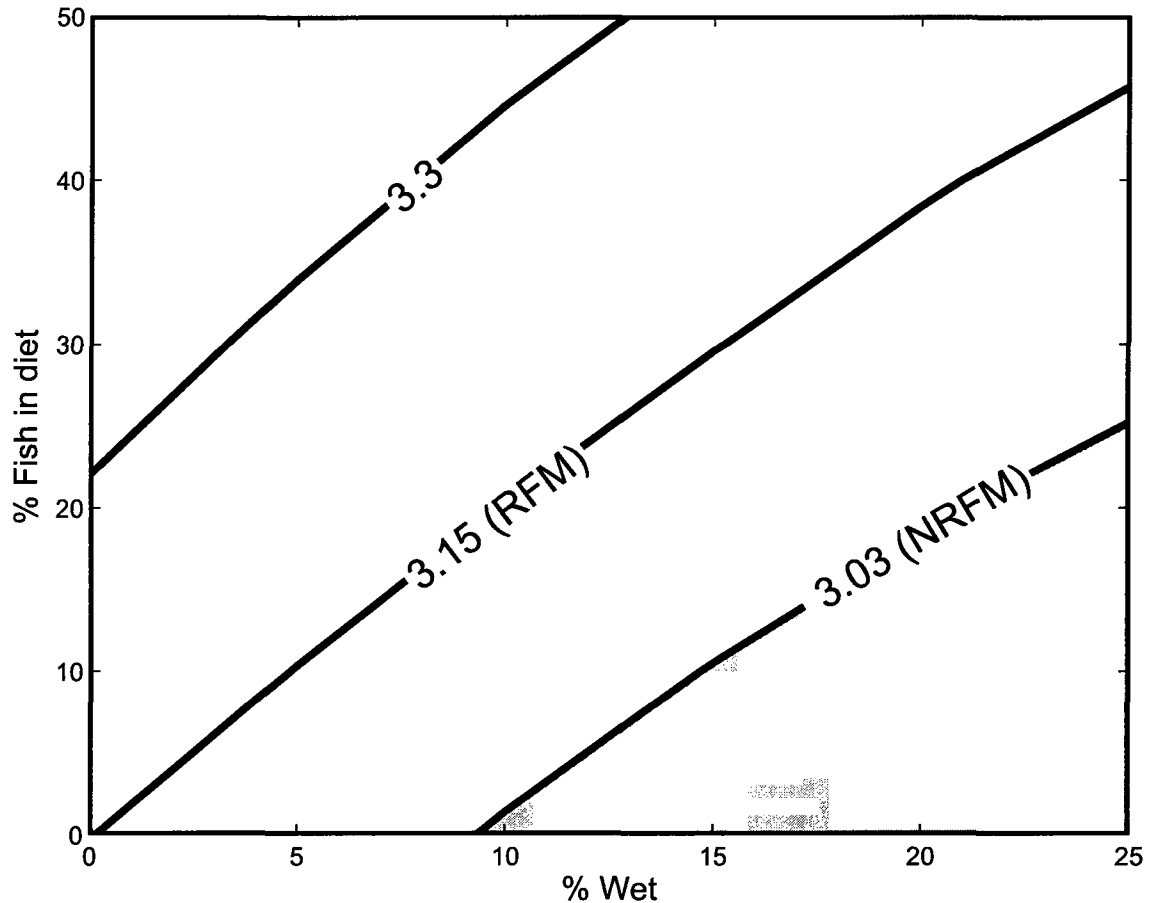


Fig. 32. Simulated chick fledging mass (kg) resulting from variability in the percent of the chick that is wet and the proportion of AC3 Antarctic silverfish in the chick diet. The simulated chick fledging mass that equals the mean mass of fledging chicks that are re-sighted (RFM, 3.15 kg) and not re-sighted and presumably do not recruit into the breeding population (NRFM, 3.03 kg) are indicated. Simulated fledging masses below the NRFM are shaded.

verfish to high predation rates (Hagen et al., 2000). Therefore, the distribution of this species is likely to be determined largely by environmental factors that influence spawning, growth, and retention of individuals rather than predation mortality.

Successful spawning of Antarctic silverfish is linked to the presence of sea ice, either as ice shelves or seasonal ice (Keller, 1983; Hubold, 1984; Kellermann, 1987; Fuiman et al., 2002). The coastal waters of the northern Bellingshausen Sea (Fig. 1), including the seasonal ice zone, were historically thought to be important spawning areas for

Antarctic silverfish (Kellermann, 1986, 1996). This region was believed to be the source for post-larval and juvenile Antarctic silverfish that were advected to the north, near the Adélie penguin populations off Anvers Island (Kellermann, 1987). Avian species distributions are sometimes limited by the diversity of food items available to them (Koenig and Haydock, 1991), presumably due to a limited ability to prey-switch when conditions are not favorable for the usual diet. The current reduction of seasonal sea-ice extent in these regions (Stammerjohn et al., 2008) may have reduced the availability of this prey item to foraging Adélie penguins that are feeding chicks in some regions off the WAP. Indeed, Antarctic silverfish have disappeared from the diets of breeding Adélie penguin diets off Anvers Island in recent years (W.R. Fraser, unpublished data). The current absence of Antarctic silverfish from Adélie penguin diets here and over the entire mid- to northern WAP (Volkman et al., 1980; Lishman, 1985; Trivelpiece et al., 1990; Fraser and Trivelpiece, 1996; Hinke et al., 2007) leaves breeding adults vulnerable to the consequences of being unable to prey-switch.

These consequences result from a dependency by breeding Adélie penguins on Antarctic krill to meet the energetic requirements of raising young. This places a larger predatory burden on Antarctic krill which, as with Antarctic silverfish, depend on the presence of sea ice for recruitment (Marr, 1962; Daly, 1990; Siegel and Loeb, 1995; Loeb et al., 1997; Quetin and Ross, 2003) and appear to be experiencing a population decline off the WAP (Atkinson et al., 2004). Therefore, environmental conditions that alter sea ice concentration and extent potentially alter the availability of two of the primary prey resources that are needed to raise Adélie penguin chicks. The dependence of breeding adult Adélie penguins on the availability of a limited number of prey species which are dependent on sea-ice conditions for recruitment and appear to be experiencing a decline in abundance, makes Adélie penguins in this region particularly vulnerable to the population effects of reduced chick growth.

Stable isotope analysis of Adélie penguin egg shells suggests that Adélie penguins

had to adjust to a diet without Antarctic silverfish about 200 years ago in several regions of the Antarctic, including some regions of the WAP (Emslie and Patterson, 2007). It has been suggested that this shift reflects a response to a krill surplus following removal of seals and baleen whales by harvesting (Emslie and Patterson, 2007). This explanation for the loss of Antarctic silverfish off the WAP is fundamentally different from that suggested by the influence of the climate-related reduction of sea-ice habitat on Antarctic silverfish (reduced populations due to reduced habitat critical to Antarctic silverfish early life-stages). According to the krill surplus theory, Antarctic silverfish should return to waters off the WAP if the marine system is able to return to its historical structure as top predator populations recover and krill populations return to historical levels. A complete discussion of these competing hypotheses is beyond the scope of this study but deserves consideration in future work. Regardless, it appears that Antarctic silverfish 95 to 117 mm in length were the most prominent fish in Adélie penguin diets off the WAP prior to 200 years ago (McDaniel and Emslie, 2002); the length of these fish corresponds to the energy-rich AC4 and older Antarctic silverfish. This loss of Antarctic silverfish from the region required some adjustment by the Adélie penguin to a lower quality diet in order to raise viable chicks. Possible adjustments might include increasing feeding rates, altering foraging behavior to focus on high energy density Antarctic krill (gravid females), or a lengthening of the nestling period. The persistence of Adélie penguins without Antarctic silverfish over the last 200 years in many of these areas suggests that Adélie penguins were able to adjust to an all-krill diet. However, a climate-driven reduction in Antarctic krill abundance and quality in recent decades may have left Adélie penguins in some of areas of the WAP unable to produce large enough chicks to recruit to the breeding population, in part, because Antarctic silverfish are no longer available in these areas to compensate for changes in the krill population.

#### IV.4.1.2 *Electrona Antarctica*

*Electrona antarctica*, one of the most lipid-rich Myctophidae (lanternfish) (van de Putte et al., 2006), is an important prey item for many top predators with a sub-Antarctic distribution, including seals (Reid and Arnould, 1996), macaroni penguins (*Eudyptes chrysolophus*), chinstrap penguins, gentoo penguins, and some flying birds (Barrera-Oro, 2002). Expansion of the range of this species to the south as conditions off the WAP trend towards warmer, sea ice free, sub-Antarctic conditions may be expected.

A diet composed of this species and krill yielded increased simulated Adélie penguin chick growth and greater fledging mass than did an all-krill or a krill and Antarctic silverfish diet. However, availability of this species to top predators appears to depend on species-specific foraging behavior. The life cycle of *Electrona antarctica* is poorly understood, but it is believed to inhabit offshore pelagic waters, with occasional intrusions inshore over the shelf (Barrera-Oro, 2002). *Electrona antarctica*'s diurnal migrations bring it from depths of 1,000 m during the day to within 200 m of the surface at night (Hulley, 1990). However, consumption by seabirds that feed primarily at the surface [e.g. gray-headed albatross (*Diomedea chrysostoma*), Antarctic tern (*Sterna vitatta*), and Wilson's petrel (*Oceanites oceanicus*) (Barrera-Oro, 2002)] suggests *E. antarctica* is also available in shallow waters at certain times. Gentoo and chinstrap penguins, which are congenitors of the Adélie penguin, are able to exploit *E. antarctica* (Ridoux, 1993). Chinstrap penguins, in particular, are known to make longer-distance overnight foraging trips during which they feed on Myctophid species, including *E. antarctica* (Jansen et al., 1998), which are detectable at night by penguins due to photophores. However, Adélie penguins are visual predators that feed primarily during daylight (Chappell et al., 1993c; Ainley et al., 1998) and have not been found to feed on *E. antarctica*. Therefore, if *E. antarctica* was to shift its distribution to higher latitudes as a result of a warming climate, Adélie penguins

would not been able to exploit this high quality prey source, although the simulations suggest this would result in viable chicks.

Thus, climate warming may shift the transfer of energy toward a top predator species assemblage that can exploit prey species that become increasingly available, such as *Electrona antarctica*, (e.g. gentoo and chinstrap penguins) and away from those that cannot (e.g. Adélie penguins). Indeed, at Anvers Island, while Adélie penguin populations have decreased, the numbers of breeding chinstrap and gentoo penguins have increased (Ducklow et al., 2007), perhaps signaling a shift in prey species available to breeding penguins in this region. These results highlight the importance of the interaction between prey availability and predator foraging behavior in determining trophic linkages that transfer energy to top predators.

#### *IV.4.2 Altered Provisioning Schedule*

Following breeding, adult Adélie penguins face the energetic cost of molting followed by the need to gain weight in preparation for reduced (and/or more patchy) prey availability during the winter (Ainley, 2002). Therefore, factors that cause a delay in the breeding schedule (e.g. delayed hatch date due to increased snowfall in colonies) may require that adults switch their efforts prematurely from chick provisioning to self-maintenance, increasing the starvation period. The simulations suggest that conditions that cause an increase in the starvation period, even of just one day, can change the amount of energy that a chick receives from the adult and compromise chick growth sufficiently to affect the probability of recruitment.

Any factor that causes even a slight reduction in provisioning rate could have a considerable impact on fledging mass and recruitment. Factors such as adult age/experience (Ainley, 2002), adult body condition (Tveraa et al., 1998), prey availability (Weimerskirch et al., 1995; Clarke et al., 2002) and increased foraging costs (Mauck and Grugg, 1995; Watanuki et al., 2002; Takahashi et al., 2003) affect the

provisioning rate of chicks by the adult. In general, adult Adélie penguins, as with other long-lived seabirds, preserve their own condition at the cost of their chicks when environmental stress occurs (Weimerskirch et al., 1995; Tveraa et al., 1998; Watanuki et al., 2002; Takahashi et al., 2003). Therefore, under environmental stress an adult is likely to partition less energy toward their chick resulting in reduced provisioning rates. One such stress may be reduced prey availability due to the added foraging pressure of other top predators (e.g. whales, seals, penguins) that have increased in abundance at Anvers Island during the nestling period (Ducklow et al., 2007). Predation pressure on the mid-trophic level has been suggested to reduce the availability of fish and krill to breeding Adélie penguin colonies (Ainley et al., 2006) and may have important implications for provisioning rate and chick growth off the WAP, but these effects are not well understood. However, the presence of older Antarctic silverfish as a prey item could compensate for environmental stressors that cause a reduction in provisioning rate.

#### *IV.4.3 Chick Wetting*

Adélie penguin chicks can maintain their body temperatures within a broad range of temperatures and wind speeds (Bucher and Bartholomew, 1986; Taylor, 1986; Chappell et al., 1989), but their ability to do so under wet conditions is unknown. Simulations suggest that the presence of water could be problematic for growth of chicks that are able to recruit into the breeding population. Therefore, environmental conditions that result in sustained or increased wetting of chick down, such as extensive snow melt or excessive rain, may adversely affect chick survivorship, potentially leading to reduced recruitment and a declining population. With increased precipitation off the WAP in recent decades (Turner et al., 2005b), chick growth in Adélie penguin colonies may have already been influenced by the wetting effect.

Simulations suggest that wind, in particular, has an important influence on the

effect of wetting on Adélie penguin chick growth. The wind speeds used in the simulations were daily averages which do not represent shorter windier events that may add to chick thermoregulatory costs and affect chick growth. As a result, the estimation of wind and wetting effects in this portion of the study is most likely a conservative estimate. Because chicks are particularly vulnerable to the effects of wetting after the guard stage and before the chick has fully formed plumage (chick ages 17 to 40 d), more frequent and/or longer duration wind events (e.g. storms) during this portion of the nestling period could potentially have an important influence on chick growth.

The effects of wetting may be particularly detrimental in smaller colonies, where the thermoregulatory benefit of huddling behavior during the cr  che stage (Lawless et al., 2001), when chicks are most vulnerable to this metabolic cost, is limited. Indeed, Ad  lie penguin colonies along the WAP where snow accumulation is highest have recently gone extinct (Fraser and Patterson, 1997; Patterson et al., 2003; Ducklow et al., 2007) possibly influenced by the wetting effect. However, little is known about the thermoregulatory effects of wetting of penguin chicks and future work should address this gap in knowledge.

#### *IV.4.4 Implications and Summary*

In general, populations at the periphery of their breeding distribution are geographically limited by some critical environmental factor and are subject to greater extinction and colonization (of individuals within the species) events than populations toward the center of their range (Mehlman, 1997; Parmesan et al., 1999). For avian species, the geographical limits to the breeding distribution can be determined by food availability, niche overlap with similar species (Gross and Price, 2000) or the diversity of available food items (Koenig and Haydock, 1991). When environmental change occurs, population and ecosystem relationships can cause a shift in biogeo-

graphical distribution as extinction events increase on one boundary and colonization events increase on another (Parmesan et al., 1999). Flightless species, such as penguins, are particularly vulnerable to environmental changes at the edge of their range as they are more constrained in their ability to track shifting favorable conditions.

Adélie penguin colonies off southwest Anvers Island are located at the northern edge of a heterogeneously distributed cluster of colonies that extends 450 km southward just beyond Avian Island. These colonies exist between the approximate northern and southern extent of the seasonal sea-ice zone off the WAP (Fig. 1). The Adélie penguin is typically associated with severe Antarctic conditions characterized by cold temperatures and the presence of sea ice (Ducklow et al., 2007). Therefore, climate warming is likely to shift environmental conditions away from those that are optimal for Adélie penguins at the northern edge of its range (Fraser and Trivelpiece, 1996); this makes the Anvers Island Adélie penguin population particularly vulnerable to any environmental change that influences breeding success. This portion of the study suggests that a reduced availability of Antarctic silverfish and Antarctic krill and the increased presence of water may have seriously reduced the ability of breeding adults to raise viable chicks near Anvers Island. These are all factors that appear to be linked with climate warming of this region. Overall, the simulations suggest the importance and complexity of the interaction between marine and terrestrial effects on chick fledging mass and recruitment. The balance of these interactions is likely to have a varied outcome with respect to chick growth in different regions of the WAP (e.g. Avian Island).

## CHAPTER V

# THE INFLUENCE OF PREY VARIABILITY AND ADULT PHYSIOLOGY ON ADÉLIE PENGUIN FORAGING AND CHICK GROWTH

### V.1 INTRODUCTION

Tracking devices and spatial analysis techniques have provided understanding and insight into seabird foraging behavior during the breeding season (Chappell et al., 1993b; Yoda et al., 1999; Lynnes et al., 2002; Ainley et al., 2004; Catry et al., 2004; Suryan et al., 2006; Weimerskirch et al., 2007, 2008). However, little is known about energetic and physiological constraints on adult seabird foraging behavior while raising chicks. These determine the adult's ability to acquire prey for provisioning chick(s), which directly affects chick growth, fledging mass, and, consequently, probability of recruitment (Perrins et al., 1973; Jarvis, 1974; Hunt et al., 1986; Golet et al., 2000; Litzow et al., 2002).

Adélie penguins are central-place foragers during the breeding season (Ainley, 2002). For this species, moderate environmental stress can result in adult behavioral changes that maintain the adult at the expense of energetic investment in offspring (Clarke, 2001; Watanuki et al., 2002; Takahashi et al., 2003). These changes limit breeding effort as well as chick growth and fledging mass. Physiological constraints such as the requirement that adults maintain their own condition (Tveraa et al., 1998) and the rate at which adults can process ingested food (Hirakawa, 1997) also affect the amount of energy that can be directed toward breeding and chick growth. Foraging Adélie penguins off the WAP encounter seasonal and inter-annual variability in prey density, distribution relative to the breeding colony, and composition (Reid et al., 1996; Brierley et al., 1999; Reid et al., 2002, 1999; Ainley et al., 2003; Fraser and Hofmann, 2003; Quetin and Ross, 2003; Siegel, 2005). These variations, coupled with individ-

ual variability due to digestion rate and appropriation of energy to self-maintenance, directly affect the ability of an adult to raise a viable chick.

The objective of this chapter is to investigate the limitations imposed by these factors on the ability of an adult Adélie penguin to raise viable chick(s) in breeding colonies near Anvers Island off the WAP. This objective was addressed using an individual-based model (IBM) to simulate the energetics of an adult Adélie penguin. The model is a spatially-explicit Lagrangian foraging model that includes adult condition (mass) and is coupled with the chick-growth IBM used previously in this study.

The chronology of chick growth in the breeding colony and how this relates to adult foraging are given in the next section. This information provides the framework for the chick-growth model and the adult-foraging model, which are described next. The simulations that address the limitations of environmental variability and adult physiological constraints are then described, followed by a discussion of results in the context of the current understanding of Adélie penguin foraging behavior.

## V.2 METHODS

### *V.2.1 Adélie Penguin Foraging Behavior*

Foraging behavior of breeding adults is characterized by foraging trip duration (FTD) and nest cycle duration (NCD). The former is the time between an adult leaving and returning to the nest. The latter is the time between consecutive foraging departures. The NCD includes both time spent away from the nest during the foraging trip and time attending the nest prior to departing on a subsequent foraging trip.

For breeding Adélie penguins in a colony near Anvers Island (Fig. 1), annual mean FTD and NCD were determined by tagging 30 to 40 individuals that were provisioning chicks between 1991 and 2005. An equal number of male and female adults were tagged. Only one individual from a breeding pair was tagged and included

in the study. Foraging trip durations were obtained using an automatic data logger positioned in the colony that recorded the presence or absence of each tagged bird every 20 min. The FTD was assumed to be the period during which penguins were absent from the colony and the NCD was calculated as the time elapsed between the departure time for consecutive foraging trips. The ratio of the FTD to NCD is the fraction of the total time that an adult bird spends away from the colony. Chick developmental stage can influence foraging behavior (Lishman, 1985); to minimize this effect, mean annual FTD, NCD, and percent time spent at sea were calculated for a 10-day period beginning when the chicks were approximately 25 days old. This period was identified by back-calculating from the date of peak fledging (the date when the largest number of chicks fledge). Assuming that all chicks fledge 54 days after hatching, a chick age was assigned for each day prior to peak fledging.

Foraging trips shorter than 3 hours were not considered, as birds are not likely to complete a foraging trip in such a short time (Fraser and Trivelpiece, 1996). For 1991-2005, mean FTD was 10.8 h (range 5.8-19.9h, Fig. 33A), mean NCD was 23 h (range 18-35.3 h, Fig. 33A), and mean percent time at sea was 48% (range 25-73%, Fig. 33B).

At colonies near Palmer Station (Fig. 1), adult foragers travel an estimated 10 km from the colony when foraging during the guard and crèche stages (Chappell et al., 1993c). At many locations, including the WAP (Trivelpiece et al., 1987b), adult Adélie penguins from the same colony appear to return repeatedly to the same general area to forage, presumably where prey are predictably found (Watanuki et al., 1997; Ainley et al., 2004; Ropert-Coudert et al., 2004).

During foraging, adults spend time swimming toward a foraging area, searching for prey, hunting, resting on sea ice or at the ocean surface, and returning to the nest (Chappell et al., 1993c; Wilson et al., 1993; Wilson and Wilson, 1995; Wilson and Peters, 1999). Hunting behavior consists of foraging dives and recovery periods

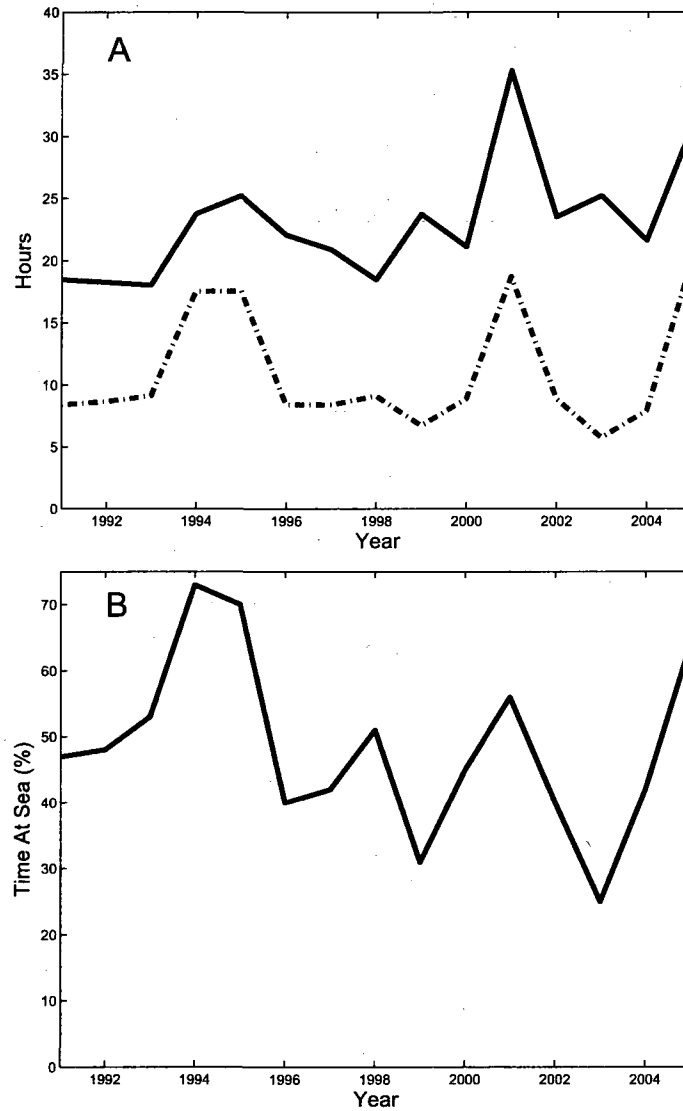


Fig. 33. Estimated A) foraging trip duration (FTD, ---) and nest cycle duration (NCD, —) and B) the percent time spent at sea ( $\text{FTD}/\text{NCD} \times 100$ ) of tagged Adélie penguins at a colony off Anvers Island between 1991 and 2005.

between dives spent at the surface restoring oxygen reserves (Chappell et al., 1993b). While hunting, adults ingest and digest prey. The amount of food in the gut is a function of the difference between prey ingestion and digestion rates and the time spent foraging. Adélie digestion rate is variable, and adults are able to stop digestion to preserve a meal for their chick(s) when they stop hunting and return to the colony (Gauthier-Clerc et al., 2000).

During the nestling period (the time between chick hatching and fledging), adults may either maintain their mass or lose up to  $19 \text{ g d}^{-1}$  (Watanuki et al., 2002). While foraging, adults must acquire sufficient food to meet the energetic requirements of both self-maintenance (replace lost energy reserves and cover metabolic costs) and of their chick(s).

### *V.2.2 Adélie Penguin Chick Attendance and Growth*

One or two chicks hatch from each Adélie penguin nest in late December off the WAP (Culik et al., 1990; Culik, 1994). For the first 16-34 days (average of 22) during the guard stage, one adult attends the nest at all times while the second member of the breeding pair forages (Taylor, 1962; Davis, 1982). During this period, each adult may only forage about 50% of the time, spending the balance of time at the colony guarding the chick(s). After the guard stage, chicks form crèches, loose groups in the colony, and adults no longer need to attend the nest and can forage for longer periods. During the crèche period, chicks grow rapidly and their energetic requirements increase (Lishman, 1985; Culik et al., 1990; Salihoglu et al., 2001).

The energy demand for a single chick is approximately half that for two chicks. Typically, chicks from single-chick nests receive a higher provisioning rate and thus fledge at a higher mass than those from 2-chick nests (Ainley and Schlatter, 1972). When chicks are between 47 and 51 days old, adults cease to feed them (Trivelpiece et al., 1987a; Ainley, 2002). The brief starvation period between the end of provisioning and the start of self-feeding stimulates fledging, which occurs when the chicks are about 54 days old (Culik et al., 1990; Culik, 1994). The mass at which chicks enter the water for the first time is the fledging mass, about 3.00 kg (Ainley, 2002). After fledging, chicks are no longer attended by adults and must feed themselves.

### V.2.3 Model Overview

The adult-foraging model simulates adult foraging behavior and mass change. It is coupled to a chick-growth model through provisioning of food to the chick by the adult (Fig. 5). The foraging model is a state-based model in which behavior is determined by a decision framework that assesses state variables at each time step (Houston and McNamara, 1999). The foraging adult steps through a series of consecutive nest cycles between chick hatching and fledging in the model.

During each nest cycle, the adult proceeds through a sequence of behaviors, beginning with leaving the colony and moving toward prey (Fig. 34). The adult behavior is assigned at the beginning of each time step. Behavior of the adult forager depends on its state which is characterized by a number of state variables. After the behavior is determined, the state variables are re-calculated and the next time step begins (Fig. 34). A decision framework outlines the criteria (adult state) used to determine the behavior of the adult forager.

State variables consist of those associated with the adult and those that represent the energetic goals (self-maintenance and chick growth) of the foraging trip (Fig. 34). An important characteristic of the decision framework is that the adult must first meet its own energy requirements before attempting to meet those of its chick(s). The adult *attempts* to recover a portion of the energy reserves lost during activity; this amount is assigned prior to a simulation. The adult may or may not be able to recover this amount of energy reserves during the nest cycle, so the adult mass is not determined prior to a simulation. The energy required by the chick(s) is that which is sufficient to raise a chick that fledges at a mass allowing survival, about 3.15 kg (see Section V.2.7). If the adult is not able to meet this goal, a chick that is not full-sized is fledged. The state variable calculations and the decision framework are described below.

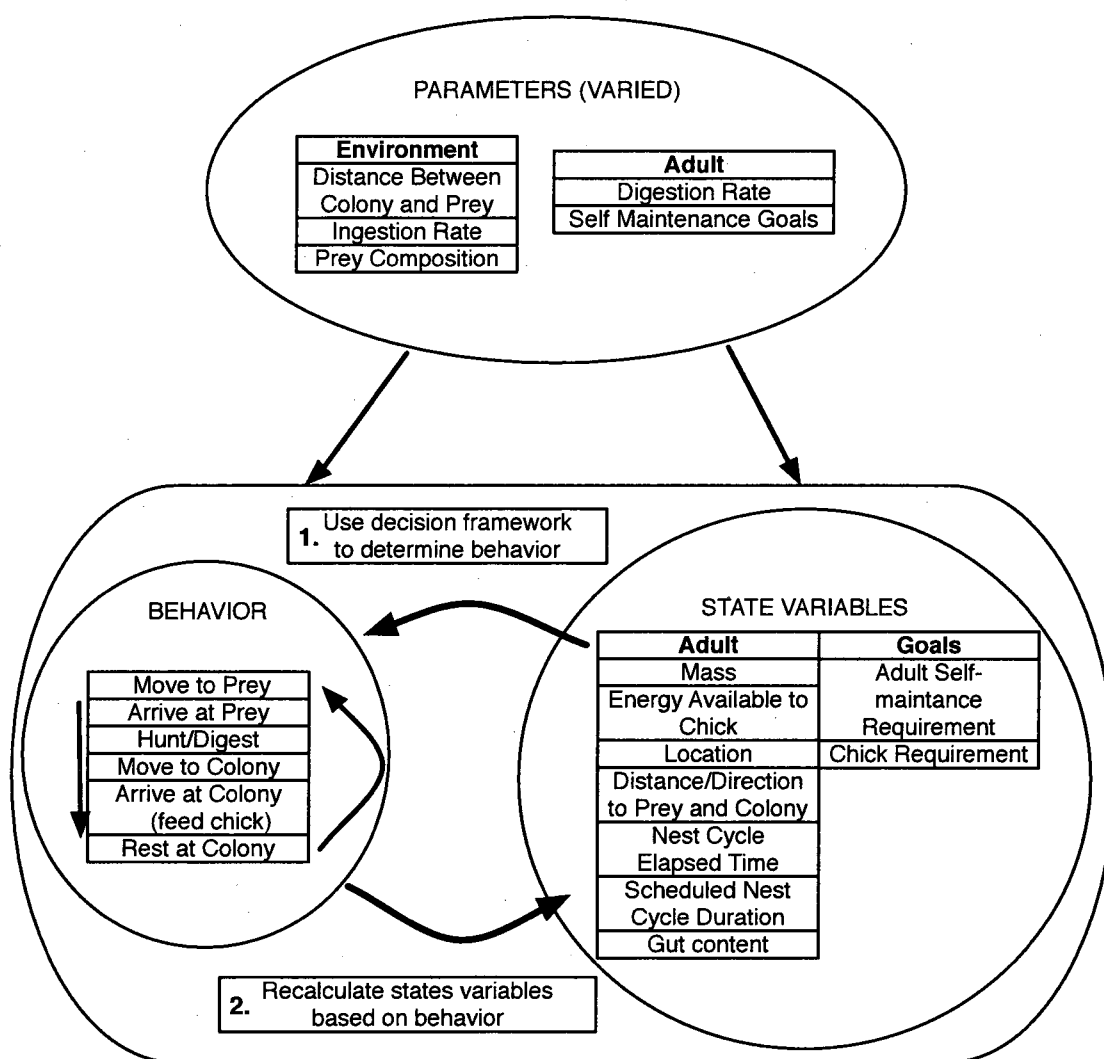


Fig. 34. [A schematic of the interaction between states variables and adult behaviors in the adult-foraging model. The parameters that are varied in simulations that influence this interaction and ultimately determine the amount of food provisioned to chicks are also indicated.]

Table 12. Parameters, values, and sources used in the adult Adélie penguin foraging model.

Parameter	Name	Value	Source(s)
Minimum NCD	Minimum nest cycle duration	15 h	This study
Maximum NCD	Maximum nest cycle duration	38.3 h	This study
$ED_{ar}$	Energy density of adult reserves (lipid)	$1.38 \times 10^4 \text{ kJ kg}^{-1}$	Schmidt-Nielsen (1983); Cherel et al. (1993)
$AE_a$	Adult assimilation efficiency	0.72, unitless	Chappell et al. (1993c)
$BMR$	Basal metabolic rate	$313 \text{ kJ kg d}^{-1} \times \text{mean adult mass during nestling period (kg)}$	Chappell and Souza (1988)
$DR$	Dive recovery factor	0.5, unitless	Chappell et al. (1993c)
$IAM$	Initial Adult Mass	4.05 kg	Ainley (2002)
$E_{chick-req}$	Energy required by a chick fledging at 3.15 kg	see Fig. 35	This study
Lower FTD	Lower foraging trip duration limit	14.0 h	This study
Upper FTD	Upper foraging trip duration limit	37.3 h	This study
$G_{max}$	Maximum gut capacity	1.0 kg	Clarke et al. (2002)
$G_{room}$	Gut capacity that allows an adult forager to resume feeding	0.9 kg	Estimate
$K_{ed}$	Krill wet-mass energy density (50% female)	$4.51 - 4.82 \text{ kJ g}^{-1} \text{ wm}$	See references in Chapter III
$GK_{ed}$	Krill wet-mass energy density (100% female)	$4.73 - 5.02 \text{ kJ g}^{-1} \text{ wm}$	See references in Chapter III
$KAS_{ed}$	Krill and Antarctic Silverfish diet energy density	$5.49 - 5.61 \text{ kJ g}^{-1} \text{ wm}$	See references in Chapter IV

#### V.2.4 State Variable Calculations

The scheduled NCD (SNCD) (Table 13) is the time assigned duration of the current nest cycle. The SNCD determines the amount of energy required for self-maintenance and chick growth during the nest cycle. The SNCD is initially set at the minimum NCD but can be increased to the maximum NCD if additional foraging time is needed to meet. The values for minimum and maximum NCD are 3 h below and above the minimum and maximum annual mean NCD between 1991 and 2005 in order to reflect the broader range of observed NCDs among individual birds. Three hours was the mean standard deviation of NCD's for all individuals during each year of the time-series.

The governing equation for adult mass (eq. 32) assumes that change in adult mass ( $AM$ , Table 13) over time ( $t$ ) is the difference between ingested energy available for production ( $E_{ap}$ , Table 13) and energy lost to metabolic costs ( $E_{mmc}$ , Table 13),

Table 13. List of variables calculated in the adult-foraging model. State variables are underlined.

Variable	Name
<u>SNCD</u>	Scheduled nest cycle duration (d)
<u>AM</u>	Adult mass (kg)
$E_{ap}$	Energy available for adult production (kJ)
$E_{mmc}$	Mean metabolic cost of adult forager (kJ)
$E_{ing}$	Energy ingested by the adult (kJ)
$ED_p$	Energy density of prey (kJ kg <sup>-1</sup> )
$CA$	Chick age (d)
<u>AM<sub>target</sub></u>	Target adult mass (kg)
<u>E<sub>chick</sub></u>	Energy available for chick(s) (kJ)
<u>x<sub>loc</sub></u>	Adult forager location (x coordinate, km)
<u>y<sub>loc</sub></u>	Adult forager location (y coordinate, km)
<u>dis<sub>col</sub></u>	Distance to colony (km)
<u>dir<sub>col</sub></u>	Direction to colony (degrees)
<u>dis<sub>prey</sub></u>	Distance to prey (km)
<u>dir<sub>prey</sub></u>	Direction to prey (degrees)
<u>NCET</u>	Nest cycle elapsed time (h)
$E_{prov}$	Energy required by chick during a nest cycle (kJ)
$t_{ncs}$	Nest cycle start time (d)
$t_{nce}$	Nest cycle end time (d)
<u>G</u>	Gut content (kg)

scaled by the energy density of the adult's energy reserves ( $ED_{ar}$ , Table 12).

$$\frac{dAM}{dt} = \frac{1}{ED_{ar}}(E_{ap} - E_{mmc}) \quad (32)$$

Energy available for production is calculated according to

$$E_{ap} = E_{ing} \cdot AE_a \quad (33)$$

where  $E_{ing}$  (Table 12) is the energy ingested by the adult and  $AE_a$  is the adult assimilation efficiency (Table 12).

Energy ingested by the adult ( $E_{ing}$ ) is given as

$$E_{ing} = (I \cdot ED_p)dt \quad (34)$$

where  $I$  (Table 14) is the rate of prey ingestion while the adult is hunting and  $ED_p$  (Table 13) is the wet-mass energy density of ingested prey. The value of  $ED_p$  is determined by the composition of the prey consumed by the foraging adult (Section

Table 14. Parameter names, ranges, reference values, and sources used in the adult-foraging model that are varied in simulations.

Variable	Name	Range (reference value)	Source(s)
<i>I</i>	Ingestion rate (kg h <sup>-1</sup> )	0.17 - 0.50 (0.25)	Chappell et al. (1993c)
<i>DP</i>	Distance between colony and prey (km)	10 - 30 (10)	Chappell et al. (1993c)
<i>TML</i>	Target adult mass loss rate (kg d <sup>-1</sup> )	-0.018 - 0.00 (-0.010)	Chappell et al. (1993c); Watanuki et al. (2002)
<i>D</i>	Digestion rate (g h <sup>-1</sup> )	55 - 80 (55)	Davies (1956); Copestake et al. (1983)
<i>PF</i>	% female krill ingested	50 - 100 (50)	Croxall et al. (1999); Endo et al. (2002)
<i>PAS</i>	% Antarctic silverfish	0 - 60 (0)	Volkman et al. (1980); Lishman (1985); Trivelpiece et al. (1990); Ainley (2002); Endo et al. (2002); Ainley et al. (2003)

V.2.6). The metabolic loss,  $E_{mmc}$ , is calculated as a function of the adult's behavior (Table 15) and basal metabolic rate ( $BMR$ , Table 12).

When the adult is not foraging, eq. (32) results in a loss of mass. While foraging, the adult must recover some of this loss and therefore allocates energy toward growth. The allocation toward growth is directed by the requirement that the adult attempt to have its mass ( $AM$ ) equal to a target mass ( $AM_{target}$ , Table 13). The  $AM_{target}$  is calculated as

$$AM_{target} = IAM - (TML \cdot CA) \quad (35)$$

where  $IAM$  is the adult's initial mass when the chick is hatched (Table 14),  $TML$  is the adult's target mass loss rate (Table 14), and  $CA$  (Table 13) is the chick age. All ingested energy is allocated to metabolic costs incurred while hunting and to growth until the adult reaches the  $AM_{target}$ . Any remaining energy is allocated to the chick ( $E_{chick}$ , Table 13).

The Lagrangian portion of the adult model simulates forager movement in 2 dimensions ( $x_{loc}$  and  $y_{loc}$ , Table 13) and is calculated based on the speed and direction associated with the behavior (Table 15). The distance and direction to prey ( $dis_{prey}$ ,  $dir_{prey}$ , Table 13) and to the colony ( $dis_{col}$ ,  $dir_{col}$ , Table 13) are calculated at the

Table 15. A list of adult behaviors and their assigned parameter values.

Behavior	Speed (m s <sup>-1</sup> )	Direction	Metabolic Cost (× BMR) (Chappell et al., 1993c)	Ingestion (kg h <sup>-1</sup> )
Move to prey	2.0 (Culik and Wilson, 1991)	Toward prey	8.20	-
Arrive at prey	-	Toward prey	8.20	-
Hunt	0.4	Random	5.00	<i>I</i>
Digest	0.0	-	1.33	-
Move to colony	2.0 (Culik and Wilson, 1991)	Toward colony	8.20	-
Arrive at colony	-	Toward colony	8.20	-
Rest at colony	0.0	-	1.33	-

beginning of each time step. The nest cycle elapsed time (*NCET*, Table 13) is also calculated at the beginning of the time step. A provisioning schedule sufficient to raise a 3.15 kg chick ( $E_{chick-req}$ , kJ, Fig. 35) is used to calculate the energy requirement of the chick. Based on this schedule, the amount of energy required by the chick for each nest cycle ( $E_{prov}$ , Table 13) is calculated as

$$E_{prov} = \sum_{t=t_{ncs}}^{t_{nce}} E_{chick-req} \quad (36)$$

where  $t_{ncs}$  and  $t_{nce}$  (Table 13) are the start and end time of the nest cycle. When the SNCD is extended beyond the minimum value in order to allow the adult more time to meet its total energy requirements, the  $t_{nce}$  is delayed and  $E_{prov}$  must be re-calculated. Because each adult shares the energetic requirements of raising young with another adult, for a 2-chick nest, the adult must provide enough food to meet the energetic requirements of a single chick while for a single-chick nest, the adult must supply the energy requirement of half of a full-sized chick.

The decision framework requires calculation of two limits on the FTD. The lower FTD (Table 12) allows the adult to return to the nest 1 hour prior to the end of the minimum NCD. The upper FTD (Table 12) allows the adult to arrive at the colony 1 hour prior to the end of the maximum NCD. The adult must return 1 hour prior to the end of the SNCD to have sufficient time to feed the chick(s).

A component of the decision framework requires the adult to haul out on sea ice to

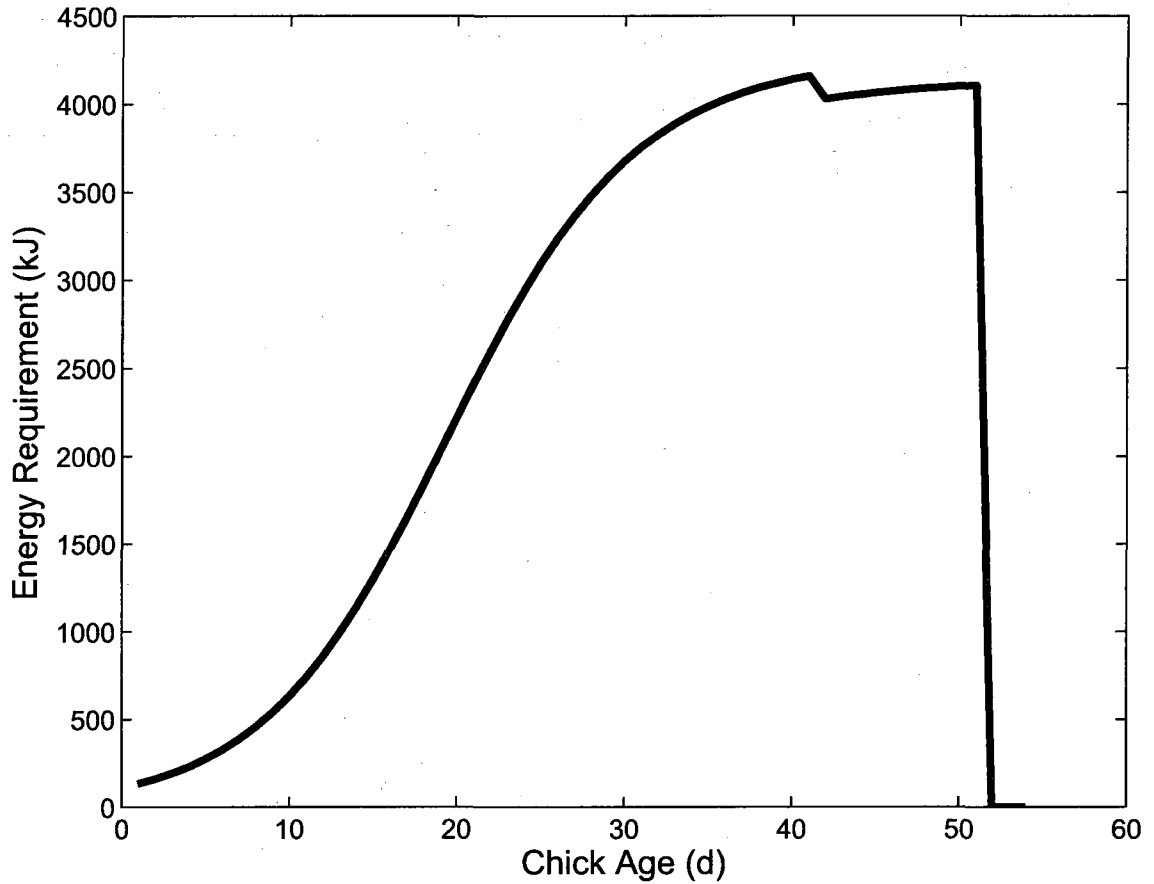


Fig. 35. Time history of the simulated energy requirements needed to raise a 3.15 kg chick on a 50% female, all-Antarctic krill diet ( $E_{chick-req}$ ). The energy requirement was obtained from a model developed to simulate the growth of an Adélie penguin chick (see Chapter III).

digest if its gut reaches its maximum capacity. The change in the amount of prey in the penguin's gut ( $G$ , Table 13) is calculated as

$$\frac{dG}{dt} = I - D \quad (37)$$

where  $I$  (Table 14) is the prey ingestion rate, and  $D$  (gastric emptying rate, Table 14) is the digestion rate. The upper limit on gut mass is set by a maximum gut content ( $G_{max}$ , Table 12). For this study,  $G_{max}$  was slightly greater than the largest reported mean difference in mass between adult Adélie penguins arriving at a colony

and leaving it after provisioning chick(s) (0.94 kg, Clarke et al. (2002)). If an adult reaches the maximum gut content while foraging, it is assumed that the adult is able to rest on sea ice while it digests. It will continue digesting until the gut content falls below a value sufficient to allow room for the adult to ingest additional prey ( $G_{room}$ , Table 12). While digesting, the adult does not move and has the metabolic cost of a penguin resting on land (Table 15). In order to preserve prey for the chicks, digestion does not continue after the adult begins its return to the nest. Upon arriving at the nest, the adult feeds the chick, and any remaining prey in its gut is assumed to be digested prior to leaving for the next nest cycle. Thus, there is no food in the foraging adult's gut at the beginning of each foraging trip.

#### *V.2.5 Nest Cycle Behavior and The Foraging Decision Framework*

Each adult forager behavior is characterized by swim speed, direction, metabolic cost, and ingestion rate (Table 15). The adult begins a nest cycle by departing the nest and moving toward prey (Fig. 36). The adult continues to move toward the prey until it is within the distance it covers while swimming directionally during a single time step. At such time, the adult continues to move toward prey but its speed is adjusted so that the adult arrives at the prey location. Once the adult arrives at prey, it begins hunting. A hunting adult moves in a random direction at a speed that is modified by a scaling factor ( $DR$ , Table 12) that accounts for time the adult spends at the surface recovering its oxygen supply between dives.

After hunting during a time step, the adult returns to the colony if it has reached its target mass and has ingested enough energy to meet the chick's energy requirements for the nest cycle (Fig. 37). If the adult has not met these requirements and its gut has reached its maximum capacity, then the adult hauls out on ice to digest. If the gut has not reached its maximum capacity and the elapsed time during the nest cycle is less than the lower FTD, the adult continues to hunt. If the elapsed time during

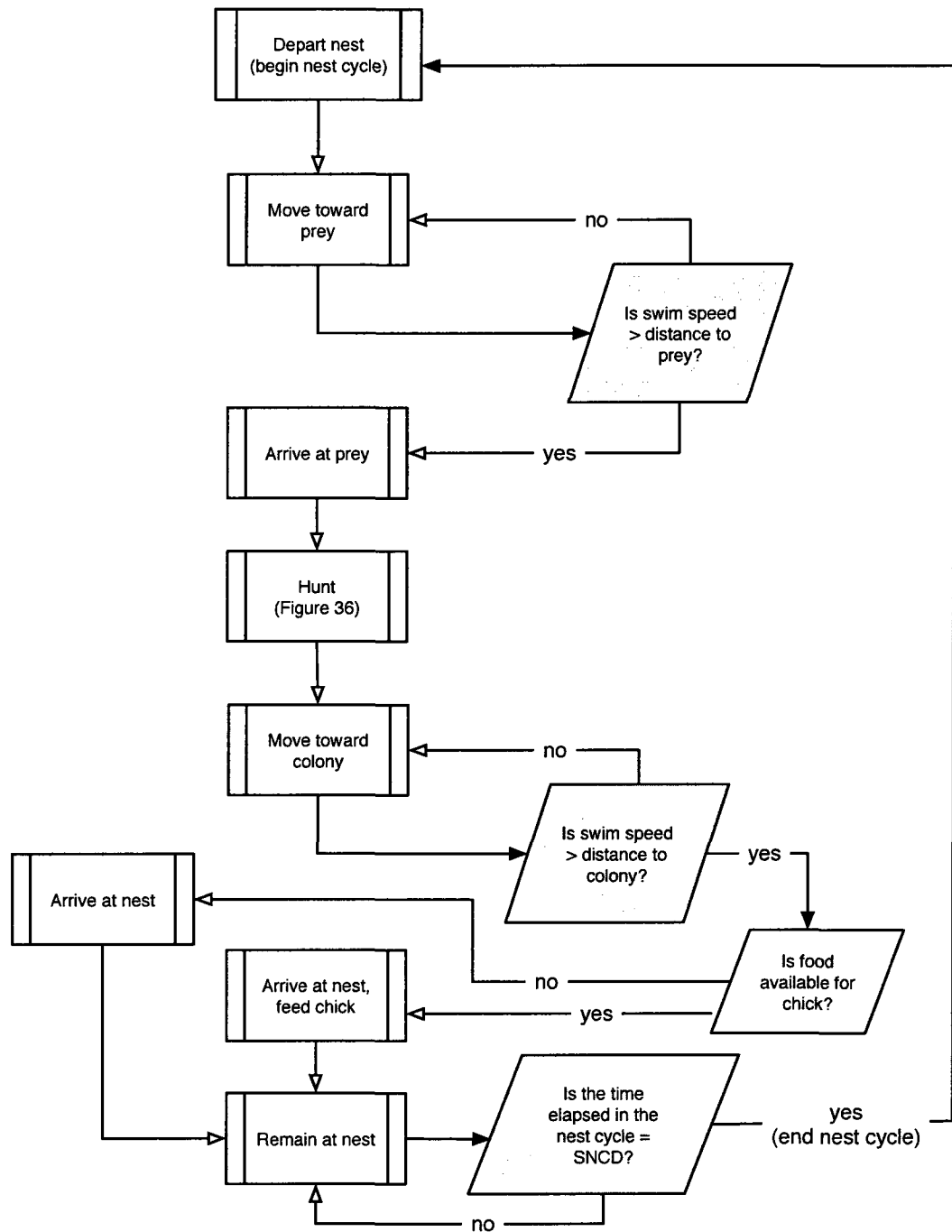


Fig. 36. A schematic of the decision framework that guides adult foraging behavior during a nest cycle. White boxes are behaviors and shaded boxes indicate the state variable criteria used to determine a new behavior.

the nest cycle is beyond the lower FTD and less than the upper FTD, the SNCD is extended an additional time step and the adult continues to hunt. If the adult has reached the upper FTD, then the adult must return to the colony.

After the adult spends a time step digesting, the adult continues to digest on the ice if it has not reached the Upper FTD and there is sufficient room in the gut to allow ingestion of additional prey. If at this time there is enough space in the adult gut to allow prey ingestion, the adult resumes hunting. If the elapsed time is greater than the Lower FTD and less than the Upper FTD and there is not sufficient space in the gut to allow hunting, the SNCD is extended and the adult continues to digest. If at this time there is sufficient room in the gut, the SNCD is extended and the adult resumes hunting. If after the adult spends a time step digesting the elapsed time during the nest cycle is greater than the Upper FTD the adult must return to the colony.

When returning from foraging, the adult continues to move toward the colony until it is within the distance covered over a single time step. If the returning adult is within this distance of the colony and has food available for the chick, it arrives at the nest and feeds the chick. The energy provided to the chick by an adult during a nest cycle is converted to a daily provisioning rate which is passed to the chick-growth model. Details of the chick-growth model are provided in Chapter III. If the adult does not have food for the chick, the adult arrives at the nest and the chick is not provisioned. After arriving at the nest, the adult remains at the nest until the time elapsed during the nest cycle is equal to the, when it departs the nest and begins the next nest cycle.

#### *V.2.6 Prey Energy Density*

For this study, it was assumed that a foraging adult encounters prey consisting of either Antarctic krill (*Euphausia superba*) or both Antarctic krill and Antarctic

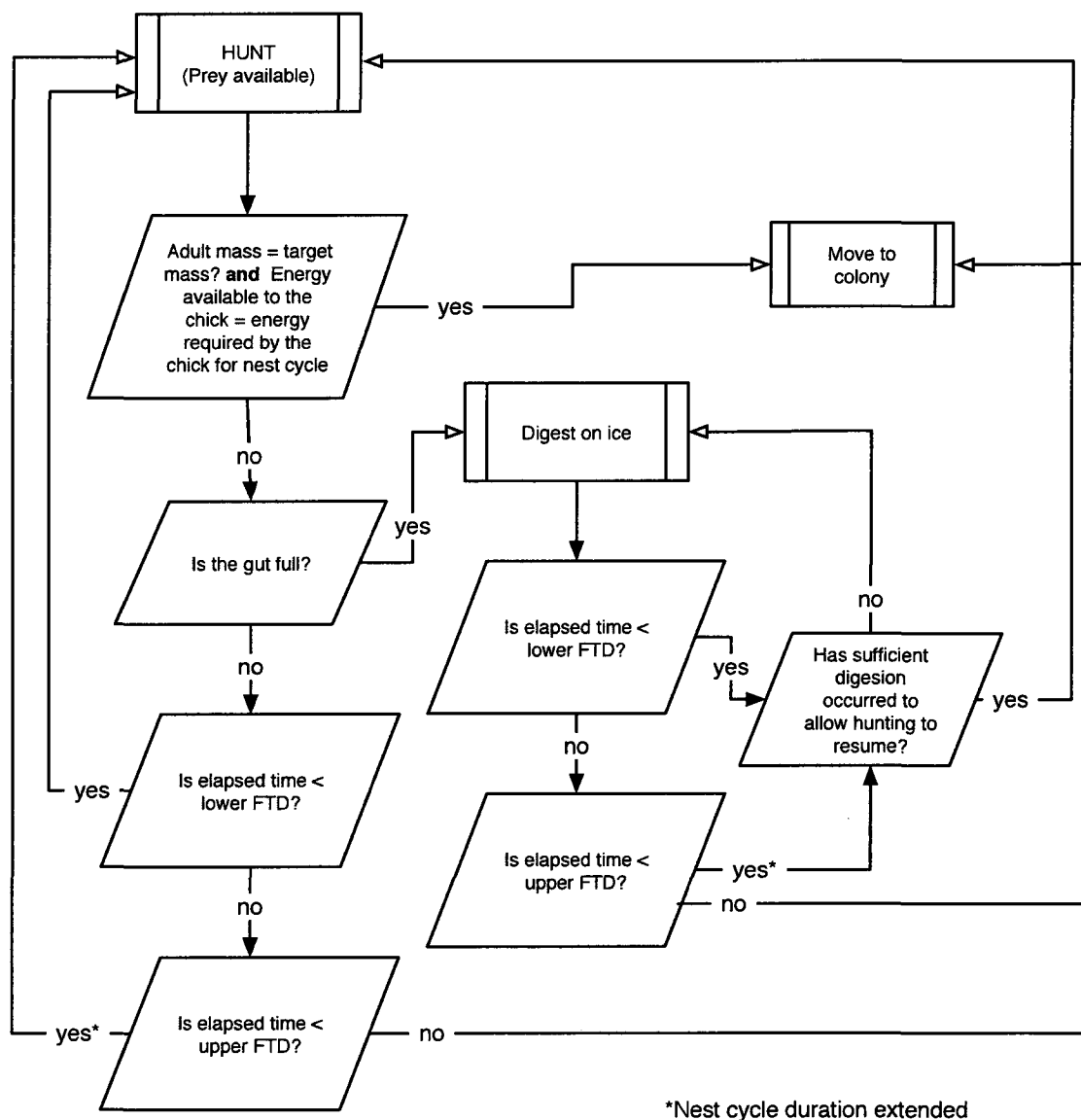


Fig. 37. A schematic of the decision framework that guides adult behavior after reaching prey and before returning to the colony to attend the nest. White boxes are behaviors and shaded boxes indicate the state variable criteria used to determine a new behavior.

silverfish (*Pleuragramma antarcticum*). Antarctic krill wet mass energy density is a function of lipid content, which varies with sex/maturity stage. The latter is assumed to increase over the 54-day chick growth period as the krill within the adult foraging area ingest food and accumulate lipid. The energy density of Antarctic krill is estimated using techniques outlined in Chapter III for populations consisting of 50% female ( $K_{ed}$ , Table 12, when  $PF=50\%$ , Table 14), and 100% female ( $GK_{ed}$ , Table 12, when  $PF=100\%$ , Table 14). Antarctic krill size-distribution ingested by the foraging adult is based on Adélie penguin diet sampling during the 1995 chick provisioning period, a year when the krill population consisted of a relatively even distribution of size classes (see Chapter III).

The addition of Antarctic silverfish to the diet required estimating the energy density for this species. The energy density for age class 3 years (AC3) Antarctic silverfish, the size class that was historically available to Adélie penguins off the WAP (McDaniel and Emslie, 2002), was obtained from size and lipid-content data, biochemical composition estimates, and a growth relationship for this species (see Chapter IV).

#### V.2.7 Model Implementation and Simulations

The adult mass and Lagrangian foraging models were implemented using an Eulerian integration scheme. The models used a 20-minute time step, which is sufficient to resolve variability in behavior during foraging trips which can be as short as 3 hours. The integration scheme for the chick-growth model is described in Chapter III. Both models were used to establish reference simulation using mean conditions (Tables 14 and 16) measured for Adélie penguin chicks at Anvers Island. Subsequent simulations assessed the influence on adult-foraging behavior, chick growth, and fledging mass of variability in a subset of parameters, as described below.

Simulations were done to assess the influence on adult foraging energetics and

Table 16. Identification of the parameters varied in each simulation set.

Simulation set	Parameter(s) varied
Prey distribution and abundance	Distance to prey ( $DP$ ) and ingestion rate ( $I$ )
Self-maintenance	Adult mass change ( $ML$ ), distance to prey ( $DP$ ), and Ingestion Rate ( $I$ )
Digestion	Digestion rate ( $D$ ), distance to prey ( $DP$ ), and Ingestion Rate ( $I$ )
Selection of female krill	Percent female krill in diet ( $PF$ ), distance to prey ( $DP$ ), and Ingestion Rate ( $I$ )
Selection of Antarctic silverfish	Percent Antarctic silverfish in diet ( $PAS$ ), distance to prey ( $DP$ ), and Ingestion Rate ( $I$ )

chick growth of varying ingestion rate, distance between colony and prey, adult mass loss rate, digestion rate, percent female krill and addition of Antarctic silverfish to the adult forager diet (Table 16). The results were evaluated by comparisons with observed maximum meal size and percent time adults must spend at the colony during the guard stage. Maximum meal sizes should match observation and the adult should attend the nest about 50% of the time to meet the behavioral requirement of chick attendance during the guard stage. A nest attendance of 40% was considered plausible, assuming that chicks move into the crèche prior to 21 days of age.

Simulated chick fledging mass provided an assessment of the foraging adult's reproductive effort. It was compared with measurements of weighed and banded fledging chicks near Palmer Station (see Chapter III for methods). Once again, the RFM and the NRFM provided reference values against which the influence of simulated fledging mass on recruitment was assessed. A simulated fledging mass below the NRFM indicated a reduction in fledging mass sufficient to affect the chick's probability of recruitment. It is not possible, however, to quantify the effect of simulated fledging mass on the chick's probability of recruitment. The lightest chick to be resighted in the banding study was 2.7 kg, and this value was used as a minimum simulated fledging mass for a chick to recruit into the breeding population.

Table 17. Values of diagnostics obtained from simulations with variable hunting ingestion rate for all-Antarctic krill prey 10 km from the colony.

Diagnostics Value	1 Chick	2 Chicks
Mean NCD (h)	15.5	23.7
Mean FTD (h)	8.6	19.0
Mean % time at-sea	55	80
Mean FE	1.63	2.34
Total Ingestion (kg)	93.4	92.4
Total Ingestion (MJ)	436.6	432.0
Adult Maintenance (MJ)	369.9	344.9
Chick Growth (MJ)	66.7	87.1
Simulated Fledging Mass (kg)	3.15	1.87
Mean Guard Stage Time at Nest (%)	56	48
Mean FTD (days 25-35, h)	7.6	32.4
Mean NCD (days 25-35, h)	15.0	34.7
Mean % time at-sea (days 25-35, %)	61	98

## V.3 RESULTS

### V.3.1 Reference Simulations

Adult ingestion rate while hunting and distance between colony and prey (Table 14) are from a previous study of Adélie penguins at Palmer Station (Chappell et al., 1993c). The rate of digestion of foraging penguins is unknown, but this rate has been measured in resting penguins ( $0.055 \text{ kg h}^{-1}$  Davies (1956); Copestake et al. (1983)), which was taken as the initial rate. The initial adult mass (*IAM*, Table 14) for the foraging adult was a typical mass for male Adélie penguins entering the nestling period which are slightly heavier than the mass female penguins (Ainley, 2002). The minimum NCD during the first 21 days of the simulation was increased from 15 to 16 h, which maintained adult attendance at the nest for 50% of the guard stage.

The range of simulated meal sizes provided by the adult over the chick growth period (Fig. 38) was similar to the range of estimated meal sizes provisioned to chicks at Palmer Station (Salihoglu et al., 2001). Large meal sizes were provisioned in the 2-chick reference simulation after day 22 (Fig. 38) when the adult extended the nest cycle duration in an attempt to meet the increasing energy requirement of its chicks (Fig. 35). The simulated foraging adults used 85% and 80% of the ingested energy to cover their own metabolic costs when raising 1 and 2 chicks, respectively. These

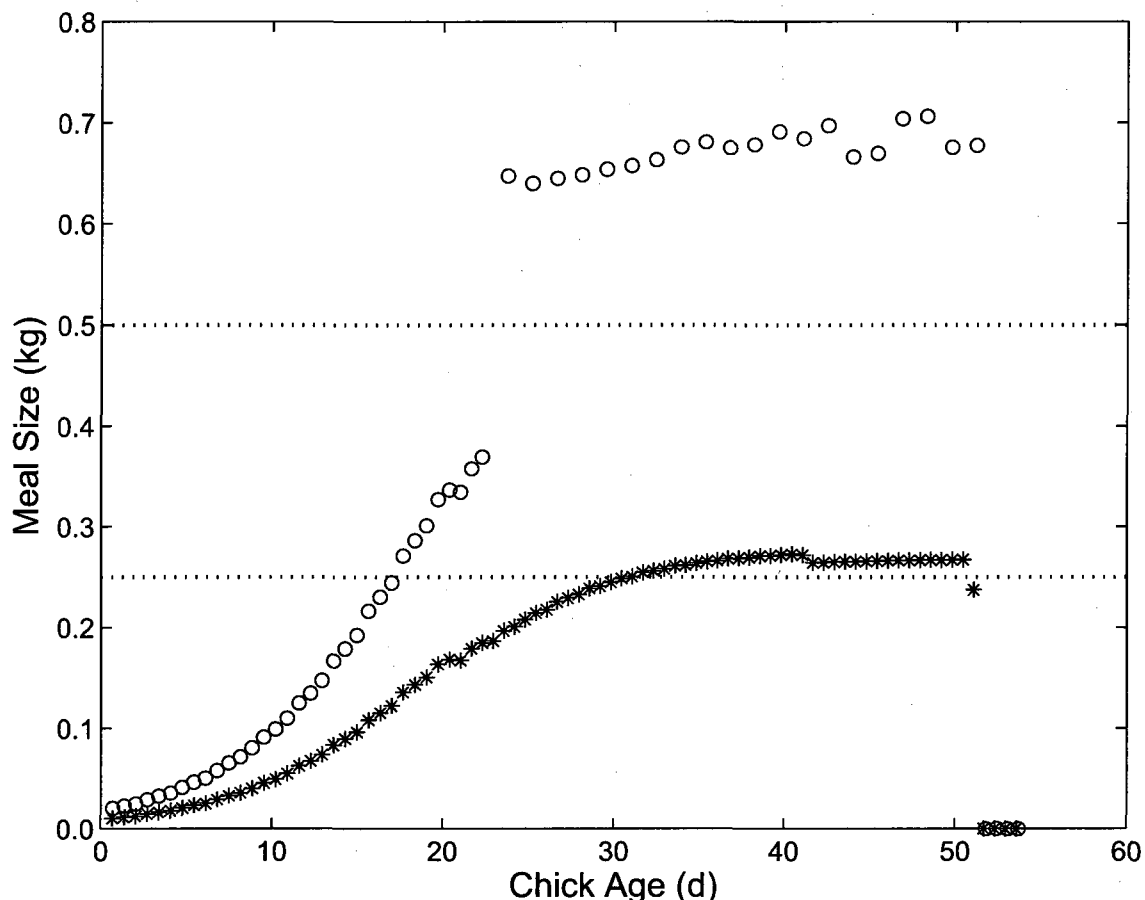


Fig. 38. Simulated meal sizes provisioned by the foraging adult to nests with 1 (\*) and 2 chicks (○). The increase in meal sizes provisioned at the 2-chick nest at about a chick age of 23 days occurred when the foraging adult extended its nest cycle duration. The range (within one standard deviation of the mean) of observed Adélie penguin stomach content mass at Palmer Station (Salihoglu et al., 2001) is indicated (···).

values are consistent with the range observed during a study of foraging energetics of breeding Adélie penguins near Palmer Station (Chappell et al., 1993c). In the reference simulations, 133 MJ were required to raise a full-sized chick, which is within the range estimated both from field (162 MJ, Janes (1997)) and modeling (98 MJ, Salihoglu et al. (2001)) studies.

The reference conditions resulted in an adult raising a full-sized chick (fledging at 3.15 kg) for a 1-chick nest and low fledging mass chicks (1.87 kg) for a 2-chick

nest (Table 17). The mass of the chicks fledged from the 2-chick nest was below the minimum mass of a chick that was subsequently observed to recruit into the breeding population (2.7 kg). Raising a single chick allowed the foraging adult to spend 6% less time hunting and 21% more time resting at the nest relative to raising 2 chicks (Table 17 and Fig. 39). The adult raising 2 chicks rested on sea ice in order to digest, while the adult raising 1 chick did not (Fig. 39). This resulted from adults having to ingest more food to raise a 2-chick rather than a 1-chick nest. Whether raising 1 or 2 chicks, the foraging adult was able to maintain its condition based on the assigned mass loss rate over the nestling period (Fig. 40A and B). In both cases, adult mass had short time-period fluctuations that were associated with mass losses and gains while foraging (Fig. 40A and B). After about day 22, when the adult raising 2-chicks extended its SNCD to meet its energetic requirements, adult mass became less variable (Fig. 40B) but still declined at the assigned mass loss rate.

### *V.3.2 Prey Distribution and Abundance*

Ingestion rate is determined by the adult penguin's ability to capture and handle (swallow) prey in combination with prey density, distribution, size, and behavior down to 100 m, the maximum depth observed for foraging penguins off Anvers Island (Chappell et al., 1993b). Distance between the colony and prey represents variability in both the distance between colony and a single, large prey patch as well as the size and distance between prey patches. For example, when small patches are dispersed over a large area, adults assume additional energetic costs while swimming between patches much as they would if a large, single prey patch was located further away. Thus, distance between prey and colony and ingestion rate are the two variables that, together, determine prey availability for foraging adult Adélie penguins. Scenarios for different distances between colony and prey were conducted at variable ingestion rates in order to assess the effects of a broad range of prey-availability characteristics.

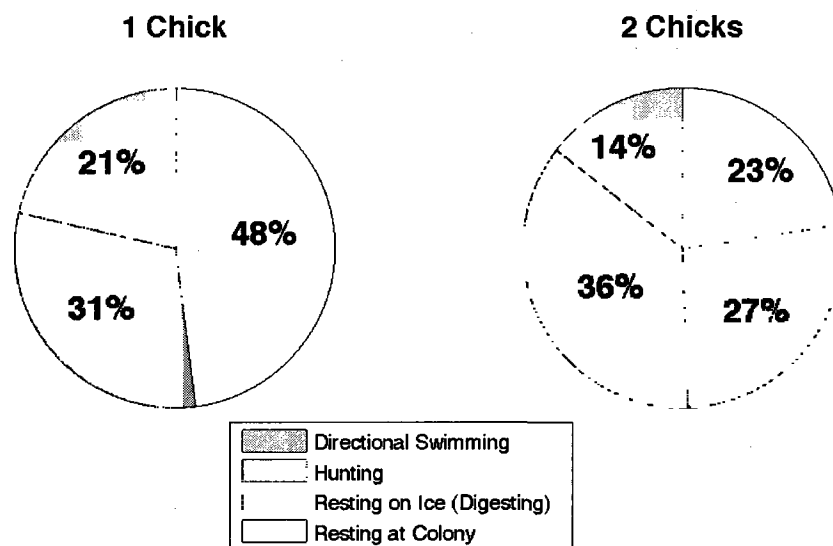


Fig. 39. The simulated proportion of time the adult forager spent swimming between the colony and prey, hunting, resting on ice (digesting), and resting at the colony, obtained from the reference simulations for raising 1 and 2 chicks.

The range of ingestion rates and distances between colony and prey that allowed adults to raise full-sized chicks (3.15 kg) were considered the range of prey-availability characteristics allowing viable chick production.

Simulated fledging mass increased with increasing hunting ingestion rate and decreased with distance between the colony and prey for both 1- and 2-chick nests (Fig. 41A and B). Raising a single viable chick required a hunting ingestion rate in excess of  $0.25 \text{ kg h}^{-1}$  and prey within 24 km of the colony. Lower ingestion rates and more distant prey resulted in chick fledging masses below the NRFM (3.03 kg). A 2-chick nest affords a foraging adult a much more restricted range of prey-availability characteristics that allow growth of full-sized chicks (Fig. 41A). Specifically, ingestion rate

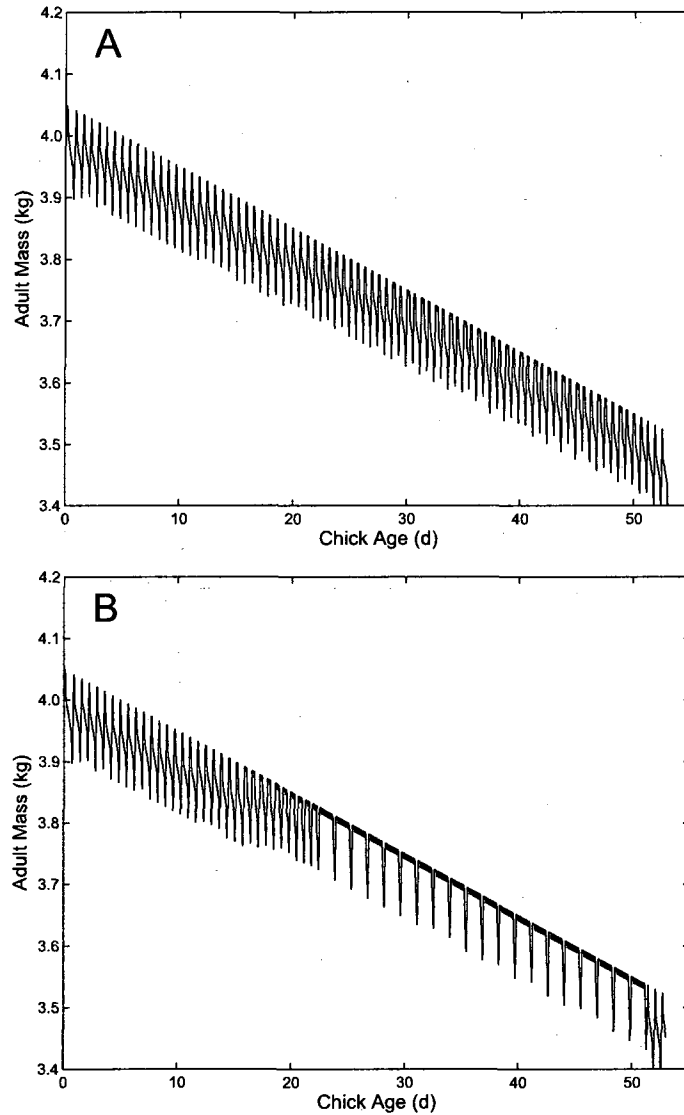


Fig. 40. Change in simulated adult mass obtained from the reference simulations for raising A) 1 chick and B) 2 chicks. For the 2-chick nest, the adult extended its nest cycle near day 22 in an attempt to meet its own and the chick's energy requirement.

must be above  $0.4 \text{ kg h}^{-1}$  and prey within 15 km of the colony for an adult to raise 2 viable chicks (Fig. 41B).

The average meal size provided to a chick is directly related to the chick's eventual fledge mass. For a 1-chick nest, regardless of ingestion rate, maximum meal size increased with increasing distance to prey until it reached a maximum value, after which it decreased (Fig. 41C). At ingestion rates above  $0.3 \text{ kg h}^{-1}$ , the same pattern

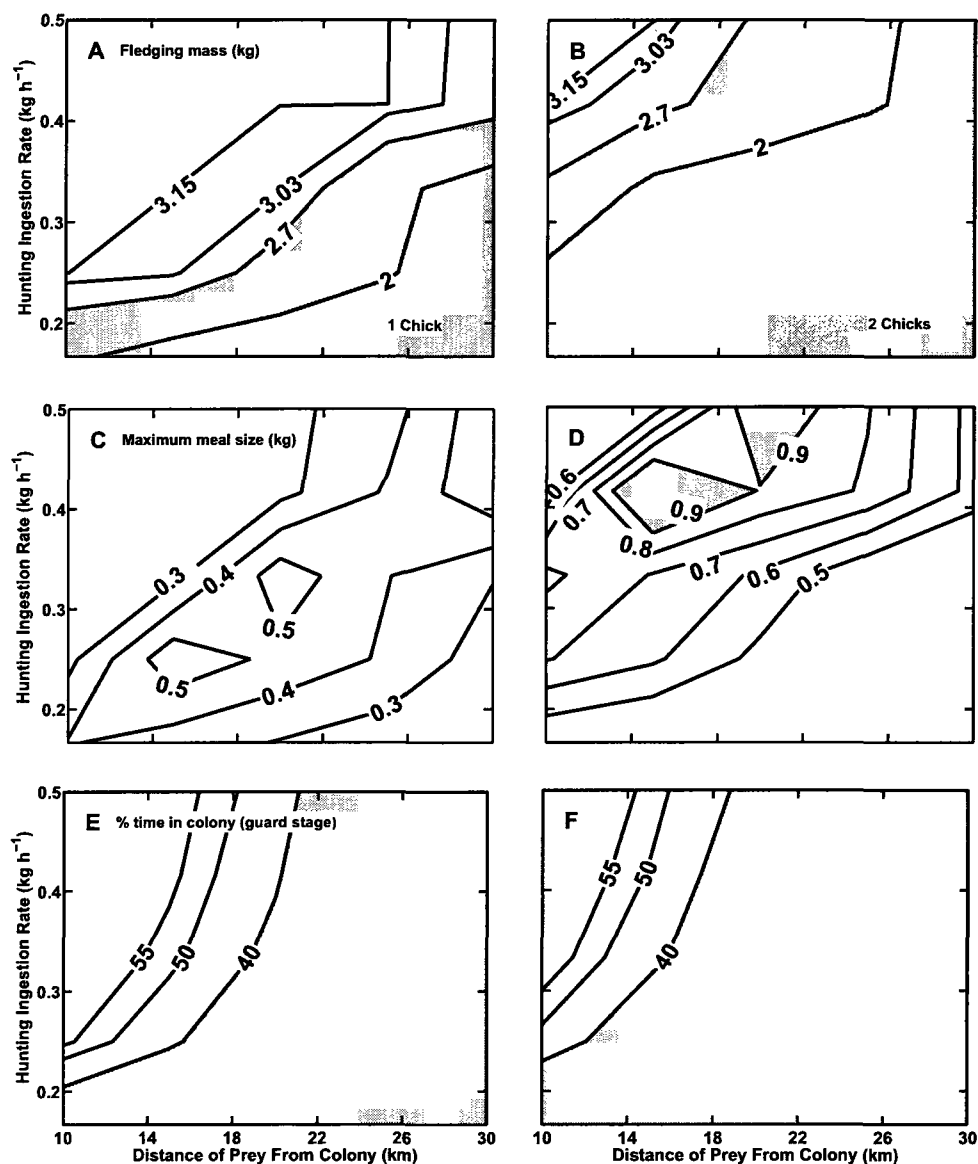


Fig. 41. Adélie penguin simulated fledging mass (kg, A and B), maximum meal sized delivered to the nest (kg, C and D), and percent time spent at colony during guard stage (% E and F) as a function of hunting ingestion rate and distance of prey from the colony. The left panels are for a 1-chick nest; the right panels are for a 2-chick nest. Contour lines indicating prey availability that produced chicks fledging at 3.15 kg (RFM) and 3.03 kg (NRFM) are shown. Shading indicates a simulated fledging mass below 2.7 kg (A and B), the minimum mass of tagged Adélie penguin fledglings later observed to recruit into the breeding population; a maximum meal size above 0.9 kg (C and D), which is at the upper range of observed meal sizes for Adélie penguins; and the percent time spent at the colony that was below 40% during the guard stage (E and F), when the adult was not likely to be able to attend the nest sufficiently during this period. Foraging adults ingested an all-Antarctic krill diet.

was observed for a 2-chick nest (Fig. 41D). In each case, the maximum meal size occurred at greater prey distances as ingestion rate increased (Fig. 41C and D). At ingestion rates lower than  $0.3 \text{ kg h}^{-1}$  for a 2-chick nest, maximum meal size decreased with increasing prey distance. The maximum meal size for 1- and 2-chick nests coincided with the transition in fledge mass from the NRFM (3.03 kg) to the minimum fledge mass observed for a recruiting chick (2.70 kg). Hence, maximum meal size was not necessarily correlated with fledge mass of viable chicks. For single-chick nests maximum meal sizes were provided under two scenarios; when ingestion rate was  $0.25 \text{ kg h}^{-1}$  and prey was 15 km from the colony and when ingestion rate was  $0.3 \text{ kg h}^{-1}$  and prey was 20 km from the colony (Fig. 41C). For a 2-chick nest, meal sizes were higher than those provided to a 1-chick nest, with maximum values at similar distance between the colony and prey, but at higher ingestion rates. The simulated maximum meal size provided to the chick over all simulations is slightly lower than the largest reported mean value for male Adélie penguins, 0.92 kg vs 0.94 kg (Clarke et al., 2002).

Prey distance from the colony had a stronger influence on the amount of time that an adult guarded the nest than did ingestion rate (Fig. 41E and F). Once prey distance exceeded 16 to 18 km, adult attendance at the nest was less than 50% of the time, even for the highest ingestion rates for both 1- and 2-chick nests (Fig. 41E and F). For a 1-chick nest, viable chicks were produced for prey located at greater distances (20 - 25 km), even when adult nest attendance was less than the minimum (40%, Fig. 41A and E). This is in contrast to a 2-chick nest, in which a viable chick results only when adults were able to attend the nest for at least 50% of the time during the guard stage (Fig. 41B and F).

The amount of time spent foraging by the adult penguin is directly related to the length of NCDs. As the adult is required to travel further to acquire prey, it spends more time at sea (Fig. 42A and B), which requires longer NCDs (Fig. 42C and D)

for both 1- and 2-chick nests. For 1- and 2-chick nests, 50 to 60% time spent at sea and 16 h nest cycles coincided with ingestion rates and prey distances that produced viable chicks (Fig. 41A and B). The time spent hunting decreased with increasing prey ingestion rate and was not greatly affected by the distance between the colony and prey (Fig. 42E and F). This response was essentially independent of the number of chicks being raised.

For 1- and 2-chick nests, adult foraging efficiency (the ratio of metabolizable energy captured to energy expended hunting and swimming) ranged between 0.8 and 2.4, increasing with ingestion rate and decreasing with distance of prey from the colony (Fig. 43A and B). Foraging efficiency was higher for 2-chick nests, particularly at high ingestion rates and at shorter distances between prey and the colony (Fig. 43A and B).

The energy ingested by a foraging adult differed in amount and pattern for raising 1 versus 2 chicks (Fig. 43C and D). For a 1-chick nest, regardless of ingestion rate, total ingested energy increased with increasing distance to prey until it reached a maximum value, after which it decreased (Fig. 43C). The maximum total ingested energy occurred at greater distances between colony and prey as ingestion rate increased (Fig. 43C). For a 2-chick nest, the total ingested energy was less variable and remained near 430 MJ over most of the simulated prey-availability characteristics (Fig. 43D). The highest values of total ingested energy for a 2-chick nest were at the highest ingestion rates and the shortest distances between the colony and prey (Fig. 43D). The maxima in total ingested energy occurred at ingestion rates and prey locations that coincided with the values that allowed production of viable chicks (Fig. 41A and B).

The adult allocated an increasing percent of all ingested energy to self-maintenance with increasing distance of prey from the colony and with decreasing ingestion rate (Fig. 43E and F). For equivalent prey-availability characteristics, the adult raising 2 chicks allocated a slightly lower percent of the total ingested energy to self-

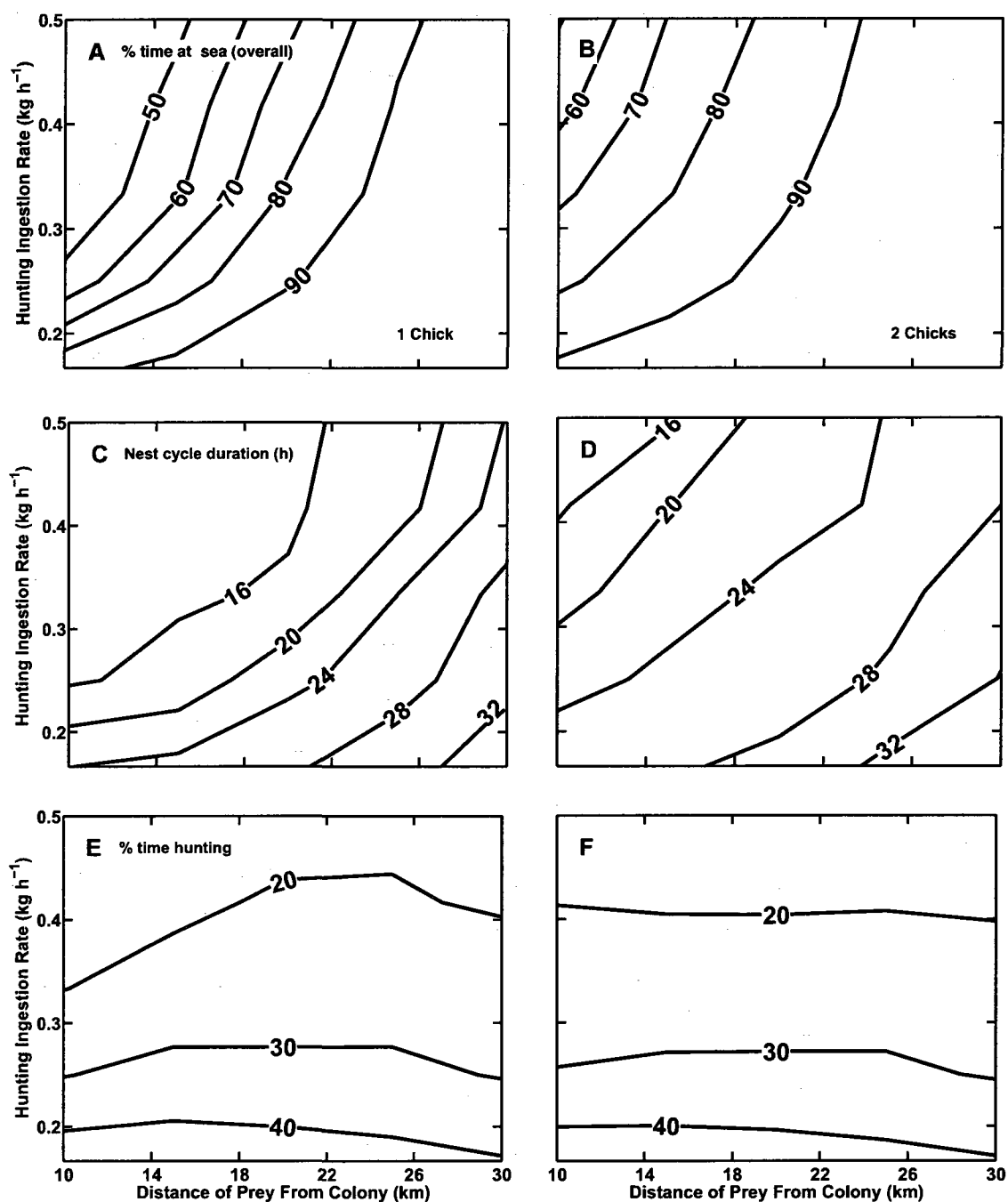


Fig. 42. Simulated Adélie penguin overall time spent at sea (%; A and B), mean nest cycle time (h; C and D), and time spent hunting (%; E and F) as a function of adult forager ingestion rate and distance of prey from the colony. The left panels are for a 1-chick nest; the right panels are for a 2-chick nest. Foraging adults ingested an all-Antarctic krill diet.

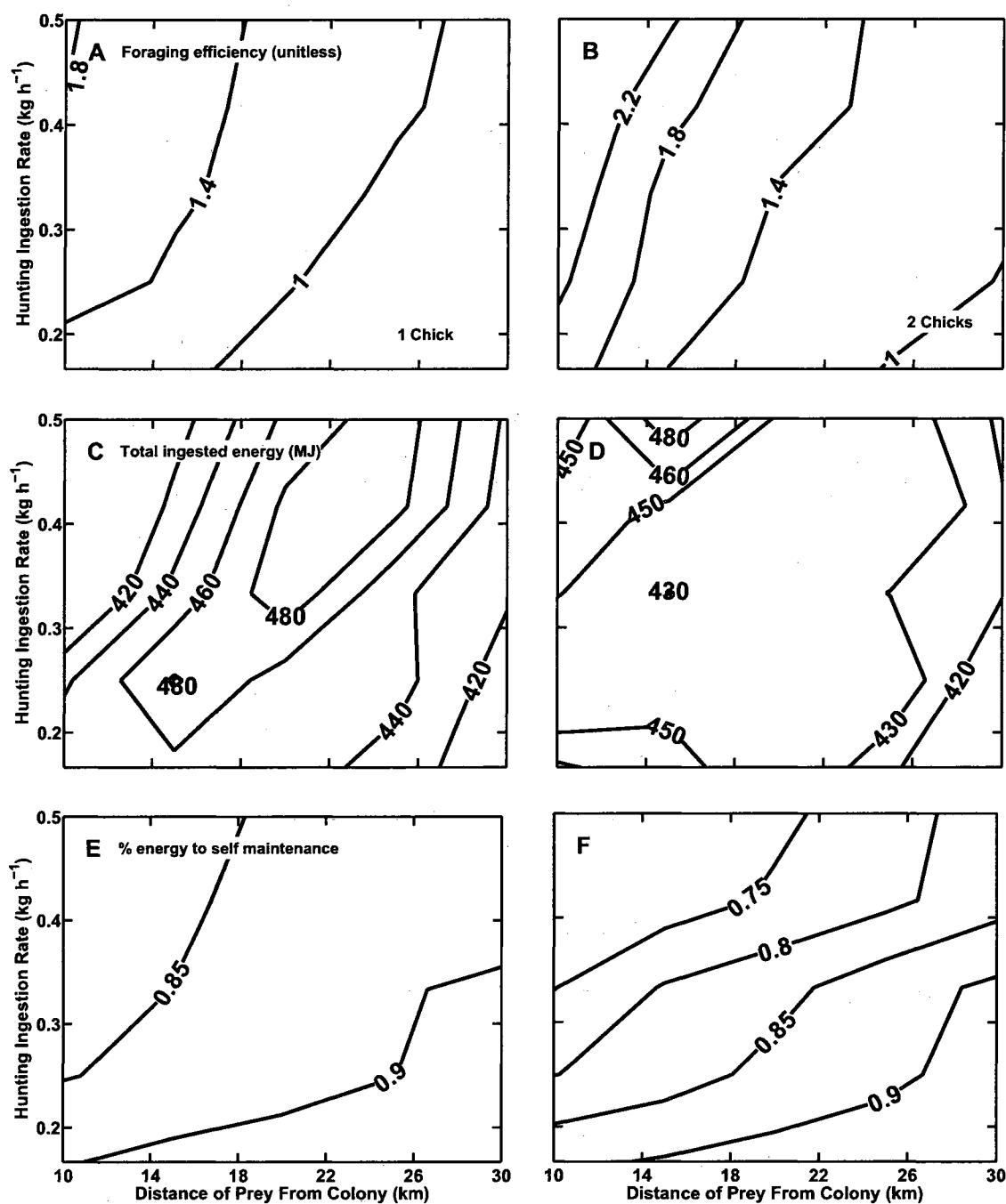


Fig. 43. Simulated Adélie penguin foraging efficiency (unitless, A and B), total ingested energy (MJ, C and D), and proportion of ingested energy apportioned to self maintenance (unitless, E and F) as a function of adult forager ingestion rate and distance of prey from colony. The left panels are for a 1-chick nest; the right panels are for a 2-chick nest. Foraging adults ingested an all-Antarctic krill diet.

maintenance. The minimum in allocation to self-maintenance coincided with the range of prey-availability characteristics that resulted in two viable chicks (Fig. 43F and Fig. 41B).

### *V.3.3 Adult Forager Variability*

An important determinant of chick growth and fledging mass is how the adult partitions energy between self-maintenance and chick growth. In simulations, the rate at which adults lose mass was used as a parameter related to the extent to which adults partition energy toward self-maintenance. Simulated chick fledging mass is related to the amount of mass that an adult loses during the simulation. Increasing the mass loss rate to  $0.018 \text{ kg d}^{-1}$ , an 80% increase from the reference simulation value and the maximum rate reported in a published study (Watanuki et al., 2002), meant that the adult was able to use more of its energy reserves in place of ingested energy to meet its metabolic costs. This increase in adult mass-loss rate had a minimal effect on fledging mass (Fig. 44A and B compared to Fig. 41A and B), though adults raising 1 chick were able to raise full-sized (at least 3.15 kg) chicks over a slightly broader range prey-availability characteristics (Fig. 44A). Requiring that the adult maintain its mass throughout the provisioning period (no mass loss) necessitated greater investment in restoring lost adult energy reserves, but also had little influence on the range of prey-availability characteristics that produced full-sized chicks (Fig. 44C and D compared to Fig. 41A and B).

An important determinant of the amount of ingested energy available for chick growth was the rate at which food is digested, which determined the percent of time allocated to digestion. A high degree of plasticity has been observed in the digestion rate among Adélie penguins (Gauthier-Clerc et al., 2000), suggesting that this species may be able to significantly increase this rate from that measured in resting birds. In simulations, increasing digestion rate expanded the range of prey-

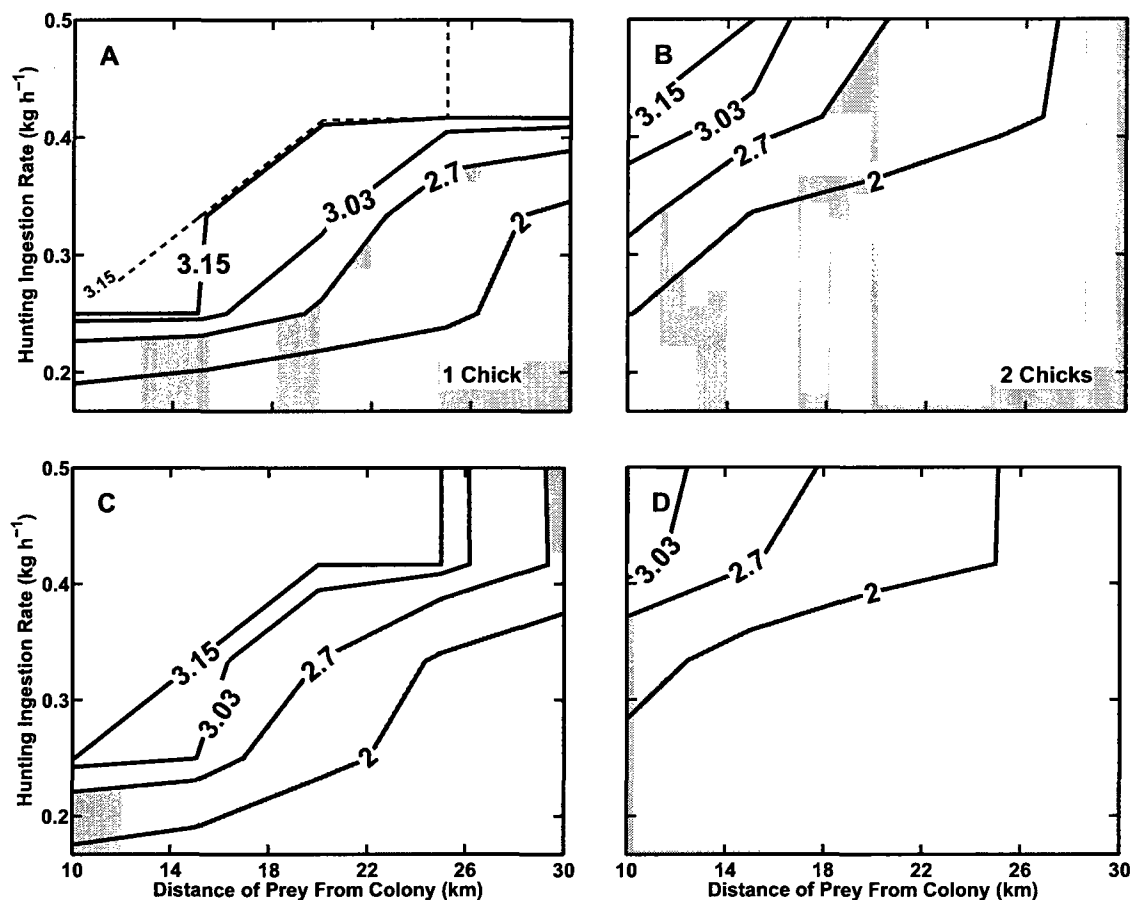


Fig. 44. Simulated chick fledging mass obtained for an adult forager with increased mass loss rate ( $ML = 0.018 \text{ kg d}^{-1}$ ) (A and B) and decreased loss rate ( $ML = 0.0 \text{ kg d}^{-1}$ ) (C and D) as a function of adult forager ingestion rate and distance of prey from the colony. The left panels are for a 1-chick nest; the right panels are for a 2-chick nest. Contour lines indicating prey availability that produced chicks fledging at 3.15 kg (RFM) and 3.03 kg (NRFM) are shown. Foraging adults ingested an all-Antarctic krill diet. Shading indicates simulated fledging mass below 2.7 kg, the minimum mass of tagged Adélie penguin fledglings later observed to recruit into the breeding population. The dashed line indicates simulated fledging mass for chick(s) of a simulated foraging adult at the reference mass loss rate ( $ML = 0.010 \text{ kg d}^{-1}$ ). The reference simulated fledging mass is only provided where results from these simulations were significantly different from those generated in the reference simulations (A).

availability characteristics that allowed an adult to raise a full-sized offspring in 1- and 2-chick nests (Fig. 45A and B). Time spent by the adult hauled out on ice digesting increased with increasing distance between the colony and prey (Fig. 45C and D). Increasing the digestion rate from its reference value decreased the percent of time spent digesting by the foraging adult at a given combination of distance between the colony and prey and ingestion rate for both 1- and 2-chick nests (Fig. 45C and D).

#### *V.3.4 Prey Composition*

The quality and composition of the diet available to the foraging adult is an important factor influencing the ability of the forager to raise a viable chick. The energy density of krill varies considerably with krill sex/maturity stage and season. Spawning females have the highest lipid content [see citations in Chapter III] and large females often dominate penguin diets (Hill et al., 1996; Endo et al., 2002; Reid et al., 1996). Increasing the percent of female krill is one way of enhancing the diet of the adult (and, consequently, the chick) because gravid females provide a high-lipid food source (see Chapter III). Increasing the percent of females in the diet from 50% to 100% allowed the adult to forage over larger distances and at lower ingestion rates and still produce viable chicks (Fig. 46A and B). Antarctic silverfish are a second primary prey item often included in the diets of breeding Adélie penguins (Ainley, 2002; Endo et al., 2002; Ainley et al., 2003). Supplementing the diet with AC3 Antarctic silverfish, which are rich in lipids, significantly extended the range of prey-availability characteristics, relative to the reference simulations, that allowed the foraging adult to produce viable chicks (Fig. 46C and D).

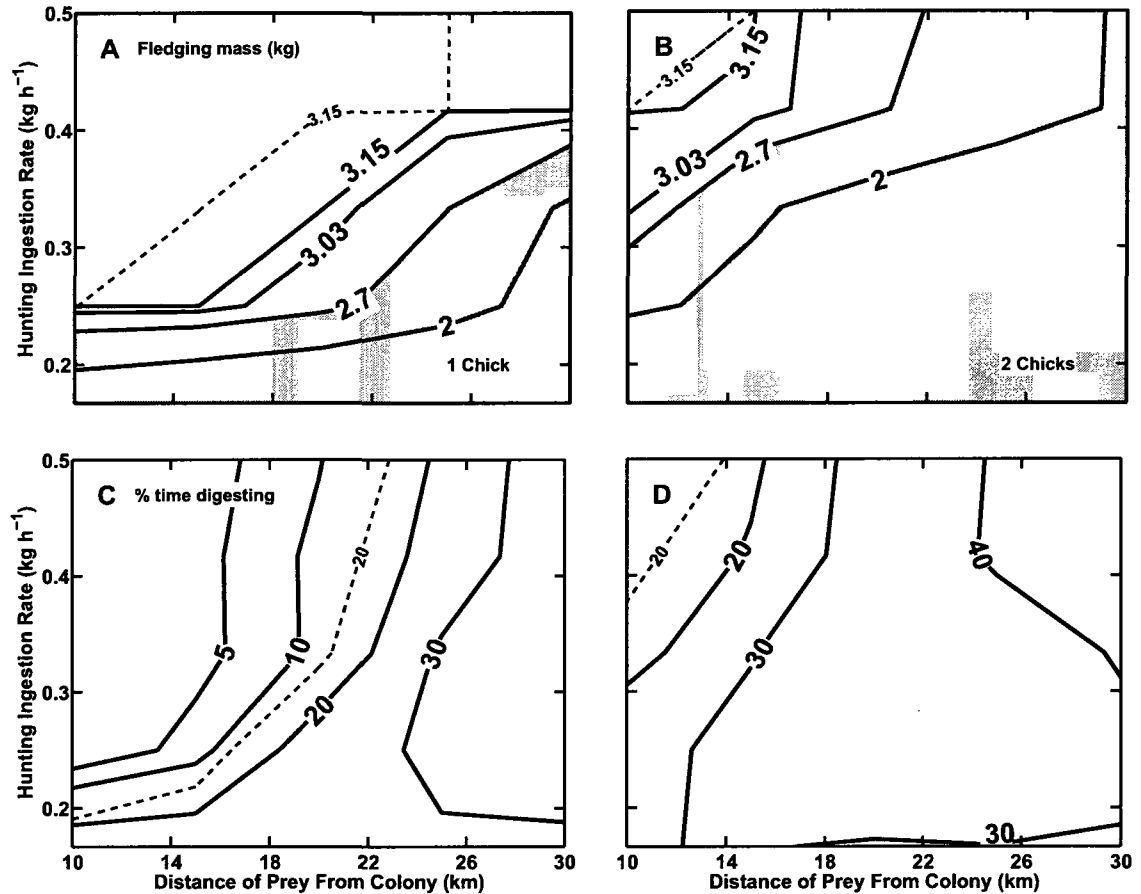


Fig. 45. Simulated Adélie penguin fledging mass (kg, A and B) and time spent foraging (% , C and D) obtained for chick(s) of an adult forager with digestion rate increased from the reference digestion rate (80 vs 55 g h<sup>-1</sup>) as a function of adult forager ingestion rate and distance of prey from the colony. The left panels are for a 1-chick nest; the right panels are for a 2-chick nest. Foraging adults ingested an all-Antarctic krill diet. Contour lines indicating prey availability that produced chicks fledging at 3.15 kg (RFM) and 3.03 kg (NRFM) are shown. Shading indicates simulated fledging mass below 2.7 kg, the minimum mass of tagged Adélie penguin fledglings later observed to recruit into the breeding population. For comparison, the dashed-line indicates the corresponding values for a simulated foraging adult at the reference digestion rate.

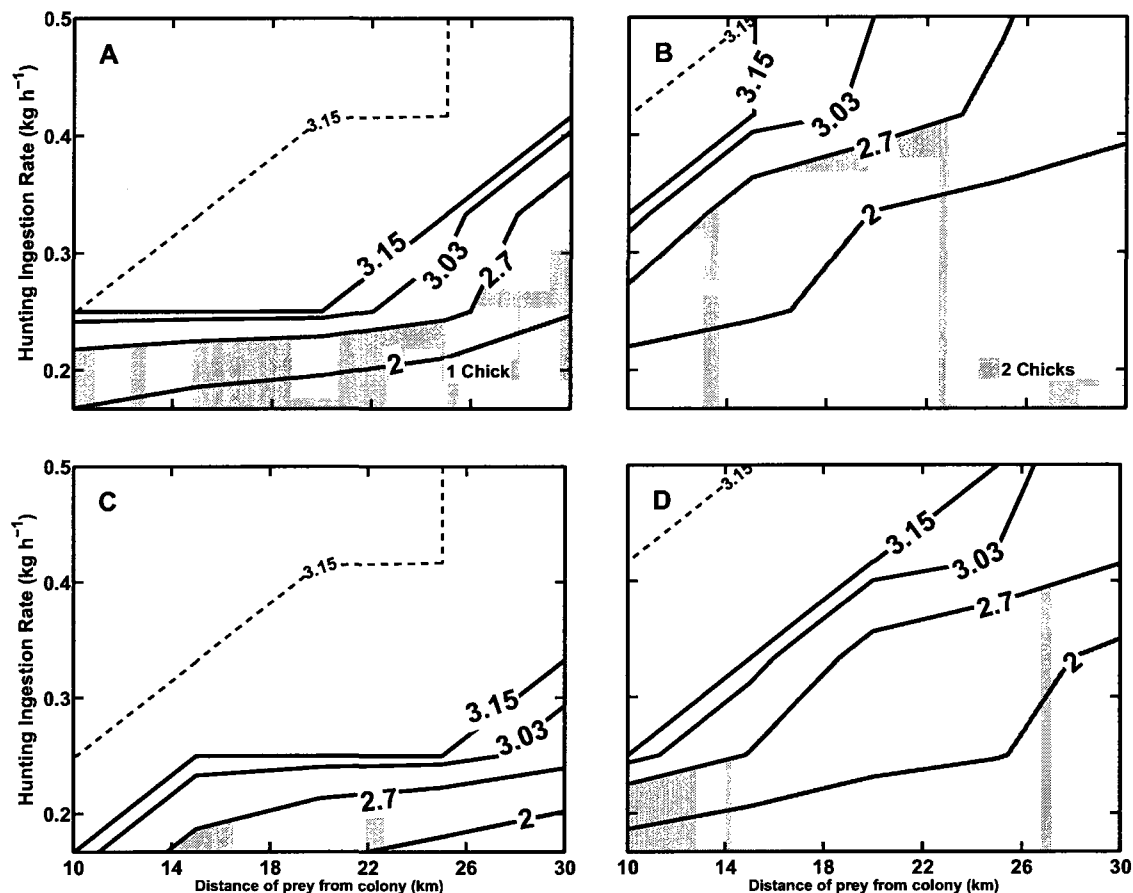


Fig. 46. Simulated Adélie penguin fledging mass of chick(s) for adults feeding on 100% female Antarctic krill (kg, A and B) and a diet consisting of both Antarctic silverfish and krill (kg, C and D) as a function of adult forager ingestion rate and distance of prey from colony. The left panels are for a 1-chick nest; the right panels are for a 2-chick nest. Contour lines indicating prey availability that produced chicks fledging at 3.15 kg (RFM) and 3.03 kg (NRFM) are shown. Shading indicates simulated fledging mass below 2.7 kg, the minimum mass of tagged Adélie penguin fledglings later observed to recruit into the breeding population. For comparison, the dashed line indicates the corresponding values for a simulated foraging adult at the reference digestion rate.

## V.4 DISCUSSION

### *V.4.1 Prey-availability Characteristics, Adult Foraging, and Chick Growth*

The simulations demonstrate the importance of prey-availability characteristics, defined by ingestion rate and distance between colony and prey, in determining the ability of adult foragers to raise viable chicks. These components of prey-availability characteristics vary inter-annually, seasonally, and in response to the presence of other top predators.

The availability and density of Antarctic krill, the primary prey of Adélie penguins in WAP waters, have considerable inter-annual variability (Loeb et al., 1997; Siegel et al., 2002), which presumably influences foraging by adult Adélie penguins. Low prey availability has been observed to increase foraging trip duration (Fraser and Hofmann, 2003) and to decrease the amount of food provisioned to chicks, thus reducing breeding success (Croxall et al., 1999). The simulations reproduce these observations, suggesting that low ingestion rates and extended travel distances are possible mechanisms that limit the ability of adults to adequately provision chick(s). Therefore, environmental conditions that alter ingestion rate and foraging distance may constrain the breeding success of adult foragers.

Superimposed on inter-annual variability are seasonal changes in krill abundance (Lascara et al., 1999) and distribution of size classes (Siegel, 1988; Siegel et al., 2002), which alter prey availability to foraging adults. For example, larger Antarctic krill (> 40 mm) appear to move offshore toward the shelf break on the WAP during the austral summer (Lascara et al., 1999), which places them outside the range of foraging penguins (a distance of approximately 150 km). Neither the timing of this offshore movement with respect to the Adélie penguin provisioning period (and the response of foraging adults to this movement) nor the influence of climate variability on this process are known. However, simulations show that prey proximity is a primary

determinant of the adult's ability to raise a viable chick(s). Thus, changes in the prey distribution that result in longer foraging trips, even for good-quality food (e.g. large, gravid female krill or Antarctic silverfish), potentially affect chick fledging mass and eventually recruitment.

The presence of other top predators in the foraging region during the chick provisioning period can potentially alter adult ingestion rate and foraging distance. For example, removal of prey by whales in the Ross Sea is believed to force Adélie penguins to forage further from colonies (Ainley et al., 2006). Whether the change in Adélie penguin foraging behavior is due to a local reduction in prey densities near colonies due to foraging whales and penguins, movement of krill away from colonies, or a change in behavior of krill populations in the presence of whales (i.e. breaking up into smaller swarms) is not known. However, results from these simulations suggest that inter-species interactions that influence prey availability, consequently affecting ingestion rate and distance traveled to reach prey, will impact Adélie penguin foraging energetics and possibly chick growth.

For the Anvers Island region, competitors of Adélie penguins include gentoo (*Pygoscelis papua*) and chinstrap (*Pygoscelis antarctica*) penguins whose nesting cycles (and consequently, the energetic requirements of provisioning chicks) lag behind, but still overlap in time, those of the relatively early breeding Adélie penguin. Marine mammals such as fin whales (*Balaenoptera physalus*), humpback whales (*Megaptera novaeangliae*), and fur seals (*Arctocephalus gazella*) are also present in the region during the chick provisioning period (Ducklow et al., 2007). Populations of gentoo and chinstrap penguins have increased off Anvers Island (Ducklow et al., 2007); thus, food resources that these penguin species share with Adélie penguins (e.g. Antarctic krill) may be altered, reducing Adélie penguin adult ingestion rate and increasing foraging distances and consequently decreasing chick fledging mass.

The influence of prey-availability characteristics on Adélie penguin foraging success

deserves attention in future field studies. Antarctic krill ingestion rate has been estimated indirectly through a combination of observed and estimated parameters and as a result is uncertain (Chappell et al., 1993c). Ingestion rate for Adélie penguins foraging on fish populations has not been estimated. Antarctic silverfish consumed by Adélie penguins can be over 100 mm long (McDaniel and Emslie, 2002) and are significantly larger and heavier than krill, so it is likely that ingestion rates for Antarctic silverfish differ from that for krill. The distributions of Antarctic krill and Antarctic silverfish within the water column and the Adélie penguins foraging range are also poorly understood and are likely to be different. Therefore, prey choice may affect ingestion rate, distance required to capture food, and hunting energy cost. Although limited observations suggest that Adélie penguin foraging behavior does not differ when foraging on Antarctic silverfish or krill during the breeding season (Ropert-Coudert et al., 2002), the influence of Antarctic silverfish on Adélie penguin foraging energetics deserves further study. More direct estimates of hunting ingestion rates may be possible through combined laboratory, mesocosm, and/or field studies focused on measuring the effect of variable prey types and densities on foraging energetics similar to approaches used for Arctic avian benthivores (Lovvorn and Gillingham, 1996).

#### *V.4.2 Adult Forager Variability*

##### *V.4.2.1 Variable Self-maintenance Goals*

Provisioning of seabird chicks increases significantly when adults are in better condition (greater mass) heading into the breeding period (Tveraa et al., 1998). However, result suggested that when an adult is allowed to lose considerable mass during the chick-growth period (a possible consequence of an adult entering the the nestling period in good condition) chick fledging mass is only slightly improved. This discrepancy between observation and model results suggests that the improved ability of larger adult foragers to raise larger chicks may be the consequence of factors that are not

included in the model. For example, larger adults may produce larger chicks because they are better foragers (e.g. find and ingest food faster and at a lower metabolic cost) than smaller adults.

#### *V.4.2.2 Variable Digestion Rate*

Energy intake can be limited by a digestive constraint (the rate of gastric emptying) rather than abundance (Hirakawa, 1997). Simulations showed that increased digestion rate broadens the range of environmental conditions that allow adults to fledge viable chicks. Because digestion rate is presumably genetically determined, natural selection should favor high digestion rate which is likely to be maximized among Adélie penguins (and other penguins) to a physiological limit. The degree to which digestion rate limits the ability of penguins to fully use prey resources is not well understood. The rate of digestion is known to vary with prey type among resting penguins (Wilson et al., 1985), and Adélie and other penguins can control the rate of digestion (Gauthier-Clerc et al., 2000). Beyond this information, little is known about this rate and its variability. Therefore, measurement of digestion rate for foraging penguins, though problematic, deserves consideration in future field studies.

Underestimation of digestion rate while foraging may, in part, be responsible for the inability of the model to capture viable chick production when prey is located further than 30 km from the colony. The foraging model used here was developed using data collected for Adélie penguins at Anvers Island where adults typically forage within 10 km of a colony (Chappell et al., 1993c). At other locations, however, Adélie penguins provision nests while traveling to prey up to 120 km from the colony (Lishman, 1985; Clarke et al., 2006). No combination of parameters or environmental conditions used in this study allowed for an adult to raise a full-sized chick when foraging over such a large distance. This suggests the possibility of a wider range of variability in the model

parameters than is suggested by available data. For example, increased digestion rate combined with lower field metabolic rate, higher swim speed (at the same or lower metabolic rate), or a high energy density diet would allow viable chicks to be raised over a more extensive foraging range. Alternatively, this suggests that Adélie penguins at Anvers Island may have a limited range of responses to environmental variability.

The physiological limits of digestion may also influence the cost of foraging by requiring adults to stop foraging in order to process food. Studies of penguin foraging behavior have found that adult penguins periodically rest on ice floes or land during periods of intense hunting activity (Wilson et al., 1993; Wilson and Wilson, 1995; Wilson and Peters, 1999) which led to the speculation that these represented periods when the adults were digesting food. This pattern emerged from the simulations as a result of the physiological requirement that adult's must digest food when their gut is full.

The digestion requirement may cause additional energetic costs for foraging Adélie penguins where sea ice is not available. For the foraging model, it was assumed that Adélie penguins were able to rest on sea ice when digesting. The Anvers Island Adélie penguin colonies are in a region where sea ice is declining (Jacobs and Comiso, 1997; Smith and Stammerjohn, 2001; Kwok and Comiso, 2002; Liu et al., 2004; Stammerjohn et al., 2008) and is less available within the penguin foraging range. This may be particularly problematic when adults are required to rest and digest because the metabolic cost of resting on water has been estimated to be 2.2 times that of resting on land or sea ice (Culik and Wilson, 1991). As a result, the energetic cost of foraging may increase dramatically when sea ice is not available to provide a lower-energy cost behavior during digestion.

### *V.4.3 Diet Composition*

Analysis of diet samples from several penguin species suggest that large, female Antarctic krill dominate penguin diets during the nestling period (Hill et al., 1996; Reid et al., 1996). Similar results have been obtained for Adélie penguins in particular (Endo et al., 2002). Furthermore, analysis of net tows collected coincident with Adélie penguin diet sampling showed the presence of significantly smaller krill with a higher proportion of males in waters adjacent to colonies compared with krill ingested by penguins provisioning chicks (Hill et al., 1996; Endo et al., 2002). These patterns suggest that Adélie penguins either select large, mature female krill within swarms or forage in areas where this sex/maturity stage dominates. Simulations suggest that this strategy results in a reduction in the energetic costs of foraging and an increase in the range of prey ingestion rates and distances between colony and prey that allow for full-sized chicks to be fledged. However, environmental conditions or behavioral factors (e.g. seasonal migration) that result in gravid krill females being located further from colonies could reduce the ability of adults to provision sufficiently.

In simulations, the addition of Antarctic silverfish to the Adélie penguin diet increased the range of prey-availability characteristics that allow adults to raise one or two full-sized chicks. Diet switching has been observed in chinstrap penguins, which take longer foraging trips when only small krill are available in order to feed on more energy-rich fish species (in this case, Myctophids) (Miller and Trivelpiece, 2008). The simulations showed that a similar extension in foraging range might be possible for Adélie penguins when an energy-rich diet is available.

Off the WAP, Antarctic silverfish were once a prominent component of the Adélie penguin diet during breeding (McDaniel and Emslie, 2002; Emslie and Patterson, 2007). However, the availability of Antarctic silverfish to Adélie penguins depends on environmental conditions that influence sea ice extent and concentration, as this fish species requires heavy sea ice conditions for recruitment and spawning (Kellermann,

1987; Keller, 1983; Hubold, 1984; Fuiman et al., 2002). Therefore, climate change that influences sea ice patterns is likely to have a strong influence on Antarctic silverfish distribution. Hence, the current reduction of seasonal sea-ice extent in the WAP region (Stammerjohn et al., 2008) may reduce the availability of Antarctic silverfish to foraging Adélie penguins. The simulation results indicated that reduction or loss of Antarctic silverfish in the Adélie penguin diet would limit the range of prey-availability characteristics that allow adults to raise full-sized chicks.

#### *V.4.4 1- and 2-Chick Nests*

The number of chicks that fledge per nest in a penguin colony exhibits significant inter-annual variability, with fewer chicks per nest fledged during years when prey is less available to foraging adults (Ainley, 2002). Some nests raise two chicks, and among those that do, one chick may be significantly larger than the other because adults may actively favor provisioning of one chick, particularly when prey availability is low (Bustamante et al., 1992). The relatively broad range of ingestion rates and prey distances that allowed adults to raise one versus two full-sized chicks in the simulations supports the broadly accepted notion that raising one chick is a better choice when environmental conditions are not favorable, such as when prey abundance is reduced.

#### *V.4.5 Importance of the Guard Stage*

In many of the simulations, even when foraging adults were able to raise full-sized chicks, the time required to attend the nest during the guard stage was not met. Though chick energy requirements were low, the simulation results suggested that adults may have a difficult time meeting both the behavioral (guarding) and energetic requirements during the guard stage. Increasing the NCD allowed the adult to attend the nest longer after feeding the chick. However, this increased the energetic

requirements of the chick and the metabolic costs of the adult during each nest cycle. The adult then needed to ingest more prey during the next foraging trip and provide a larger meal to the chick (which may be limited by the young chick's small gut capacity). This places a limit on the amount of time that the NCD can be extended.

Alternatively, the adult may focus less on self-maintenance during the guard stage and forego time spent foraging to meet its own energetic needs to allow more time to attend the nest. Indeed, male Adélie penguins were observed to lose over  $0.035 \text{ kg d}^{-1}$  while females lost over  $0.017 \text{ kg d}^{-1}$  during the guard stage (Clarke, 2001) while both sexes maintained their mass during the crèche stage despite the high chick energy requirement during this time (Clarke, 2001). This suggests greater partitioning of energy towards the chick(s) than to self-maintenance during the guard stage, perhaps in an attempt to allow adults the flexibility to attend the nest 50% of the time during the guard stage. It is also possible that one adult may attend the nest more of the time, allowing the second adult additional foraging time to meet its own energetic requirements.

Conditions that prevent adults from attending the nest 50% of the time later in the guard stage may lead to earlier transition to the crèche stage, which would still allow for provisioning adequate to support the growth of full-sized chicks. However, early entry to the crèche would presumably increase chick thermoregulatory costs and exposure of chicks to predation while they are unattended by the adult, which could reduce survival and growth of the chick. Nevertheless, the adult does appear to have some options that may allow it to meet behavioral (guarding) and energetic requirements under sub-optimal conditions during the first stage of chick-rearing.

#### *V.4.6 Implications and Summary*

Results from this portion of the study highlighted several poorly understood processes associated with foraging adult Adélie penguins that influence the ability of

adults to raise viable chicks. In particular, prey ingestion rate (and its inter-annual and seasonal variability) and the adult digestion rate while foraging are poorly constrained by observational data but have an important influence on foraging energetics and chick growth. Simulation results also showed that the availability of high-quality prey, such as Antarctic silverfish and gravid female Antarctic krill, can expand the range of spatial prey distributions that allow adults to raise viable chicks. Moreover, simulation results support the suggestion that loss of Antarctic silverfish from the diets of Adélie penguins (reducing prey quality) and reduced abundance of Antarctic krill (reducing prey ingestion rate and increasing the required distance of travel to reach prey) off the WAP are limiting the ability foraging adults to maintain their own energetic needs while raising full-sized chicks.

## CHAPTER VI

### SUMMARY

#### VI.1 RESEARCH QUESTIONS

This study used a framework of individually-based models of chick growth and adult foraging to explore factors that influence Adélie penguin chick growth off the WAP. Results and conclusions with respect to the research questions of this study obtained from these coupled models are outlined below.

*Research Question 1: How does variability in physical and biological variables associated with the marine and terrestrial environment influence Adélie penguin chick growth at colonies off the WAP?*

Simulations found that when varied independently, the timing and duration of spawning, krill size-class distribution, and sex-ratio all influence the lipid content of Antarctic krill ingested by Adélie penguin chicks and, consequently, chick fledging mass. Specifically, earlier spawning, longer spawning duration, and the availability of large, female krill to foraging adults improved chick fledging mass. The variability in the timing of krill spawning was shown to have the greatest influence on predicted Adélie penguin fledging mass. The effect of this variability was sufficient to influence the probability of recruitment for fledging chicks. Simulations varying the timing of krill spawning suggest that any alteration of the timing of krill spawning and accumulation of lipid may influence chick growth by altering the quality of prey available to breeding Adélie penguins. This suggests a possible link between climate variability, a shifting phenology of seasonal biological events, and the transfer of energy through the marine system to top predators.

Further simulations with the chick-growth model suggest the importance of availability of high lipid-content gravid females to foraging Adélie penguins for chick growth and fledging mass. Therefore, environmental variability that causes a shift

in the distribution of krill spawning areas away from Adélie penguin foraging areas during the chick provisioning period would have a negative influence on chick growth and recruitment of penguin chicks by limiting the access of foraging adults to gravid females. Results from this portion of the study underscore the importance of developing field studies that will improve our understanding of environmental control of lipid accumulation in the krill population and the timing and distribution of spawning among Antarctic krill.

Additional simulations using the chick-growth model assessed the influence on chick growth of diet complexity, alteration of the chick provisioning schedule, and wetting of chicks at nests due to increased precipitation and snow melt in colonies. Results showed that addition of 17% (averaged over the nestling period) of AC3 Antarctic silverfish to the all-Antarctic krill diet improved chick fledging mass by 5%. Antarctic silverfish distribution and spawning has been linked with ice shelves and the presence of seasonal ice (Keller, 1983; Hubold, 1984; Kellermann, 1987; Fuiman et al., 2002). Therefore, reduced annual sea ice coverage due to climate warming off the WAP may have limited the distribution of Antarctic silverfish, thus reducing the energy density of prey available to foraging Adélie penguins and the ability of adult penguins to raise full-sized chicks.

Addition of a 17% (averaged over the nestling period) of AC3 *Electrona antarctica* to the all-krill diet improved chick fledging mass by 33%. A shift in environmental conditions that increases the distribution of this species within the foraging range of Adélie penguins would not, however, benefit chick growth because Adélie penguins do not feed on this prey item. However, chinstrap and gentoo penguins, congenitors of the Adélie penguin with a more sub-Antarctic distribution, do feed on *Electrona antarctica* and would be able to capitalize on increased availability of this high-energy prey type. This underscores the importance of predator-prey relationships in ecosystem adjustment to climate-induced environmental change.

Increasing the starvation period of the chick by a single day or reducing the provisioning rate by 4% was enough to reduce chick growth sufficiently to affect chick recruitment. This highlights the vulnerability of Adélie penguins to environmental changes that cause even slight changes to the provisioning schedule.

An approach for describing and parameterizing the cost of wetting on chick metabolic costs was developed. Results from simulations varying parameters used in this portion of the model found that the combination of wind and water in colonies could reduce recruitment of chicks when just 10% of the chick is wet. However, results also found that the negative effects of wetting as well as those caused by a reduced provisioning rate could be compensated for by an increase in the amount of AC3 Antarctic silverfish in the chick diet. This result implies that chick growth is the product of a complex interaction between land- and ocean-environmental conditions.

*Research Question 2: How does variability in environmental and internal factors influence adult Adélie penguin foraging energetics and chick growth during breeding at colonies off the WAP?*

The simulations showed that environmental change that reduces the prey density (reducing hunting ingestion rate) or increases the distance required to reach prey limits the ability of adults to adequately provision chick(s). These results suggest that the reduction in abundance of Antarctic krill off the WAP, which has been linked with climate warming in the region (Loeb et al., 1997; Atkinson et al., 2004), could be limiting the ability of breeding adult Adélie penguins to raise full-sized chicks by reducing prey ingestion rate and increasing the distance required to travel to reach patches of krill. Furthermore, the increase in chinstrap and gentoo penguins and fur seals off the WAP may have altered prey availability, reducing prey ingestion rate and increasing the distance required to capture prey, similarly reducing Adélie penguin foraging success and chick growth.

Simulations varying self-maintenance goals and digestion rate showed that phys-

iological variability of foraging penguins could also influence the potential range of ingestion rate and distance to prey that allows adults to raise full-sized chicks. Increased appropriation of energy to self-maintenance only slightly decreased the range of environmental conditions that allowed foragers to raise full-sized chicks. Increasing the hunting digestion rate, however, significantly broadened the environmental conditions that allowed for successful adult foraging and viable chick production.

Finally, selection of female Antarctic krill or AC3 Antarctic silverfish increased the quality of prey ingested by foragers and expanded the range of prey-availability characteristics that allowed foragers to raise full-sized chicks. As a result, environmental conditions that lead to a decreased availability of these high-energy prey would limit the ability of foraging adult Adélie penguins to adjust to other environmental stresses that limit chick growth.

## VI.2 CONCLUSIONS

Overall, results demonstrate the complexity of both marine and terrestrial factors that influence chick growth, fledging mass, and recruitment of Adélie penguins. Adélie penguins breeding off Anvers Island may be experiencing cumulative energetic stresses associated with reduced availability and quality of Antarctic krill and Antarctic silverfish (due to reduced seasonal ice coverage) in addition to an increased cost of wetting at the nest (due to increased snowfall). This may be particularly troublesome because colonies near Anvers Island are at the northern edge of a regional cluster of breeding colonies and are particularly vulnerable to a local shift away from optimal environmental conditions in response to climate warming. The combined effect at Anvers Island may leave breeding Adélie penguins with a limited ability to raise more viable chicks compared to colonies further to the south. Sustained unfavorable conditions may ultimately result, or may have already resulted, in an Adélie penguin population at Anvers Island that is no longer self-sustaining.

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### Publications

Chapman, E.W., W.R. Fraser, E.E. Hofmann and D.L. Patterson, (in press).

Variability in sex/maturity stage and demography among Antarctic krill (*Euphausia superba*) on Adélie Penguin (*Pygoscelis adeliae*) chick growth: A modeling study, Deep-Sea Research II.

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