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

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ABSTRACT

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

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1. Introduction

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

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

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

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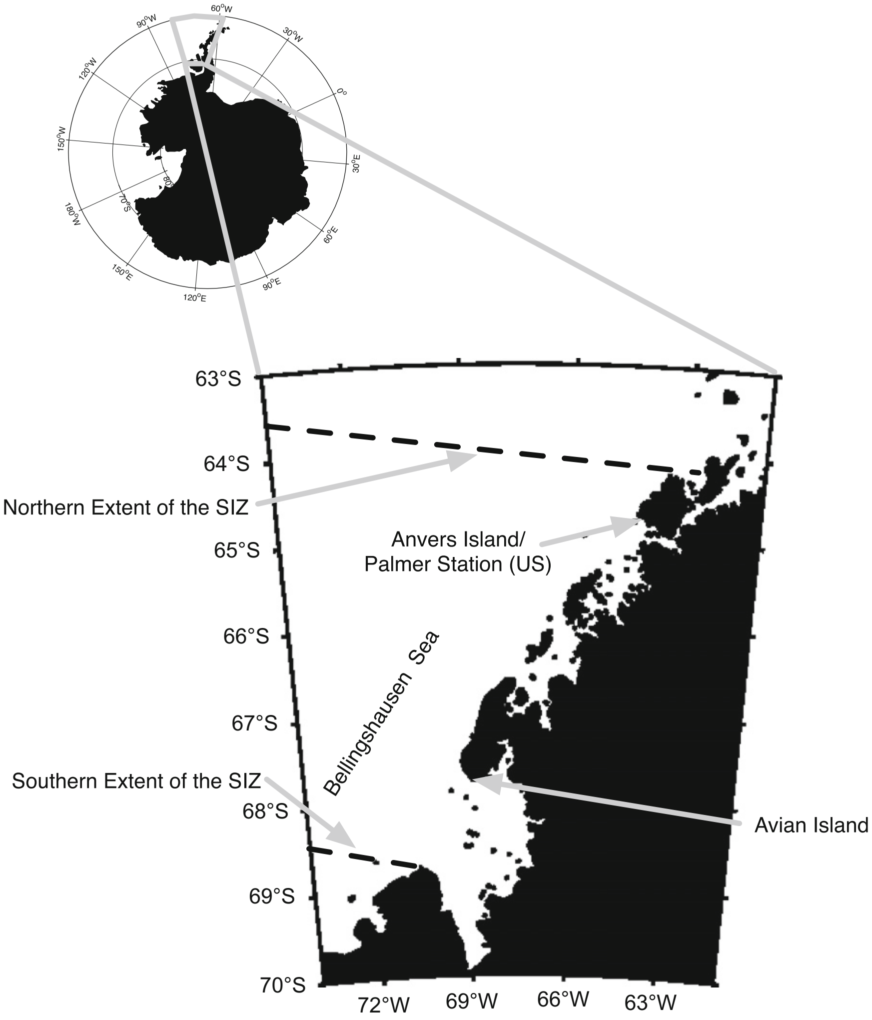

Fig. 1. Map of the western Antarctic Peninsula showing locations of Adélie penguin breeding colonies at Anvers Island (ANV) and the location of Palmer Station (US). Also shown are the northern and southern extent of the seasonal ice zone, adapted from Jacobs and Comiso (1997).

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

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

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

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

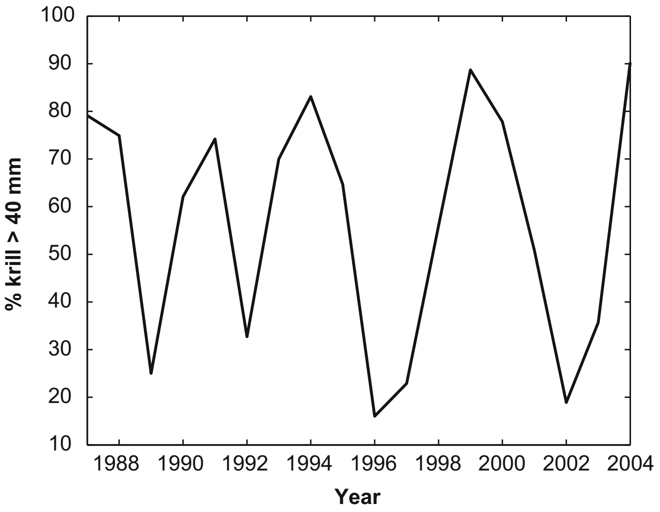

Fig. 2. The variability in the percentage of krill larger than 40 mm (> 2 years old) in diet samples obtained from penguins provisioning chicks in colonies near Palmer Station between 1987 and 2004.

2. Methods

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) increase dramatically until both adults must forage simultaneously, ending the guard stage. At this time, unattended chicks gather in wandering groups called créches. 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., 1987; Ainley, 2002), resulting in a brief starvation period during which the chicks lose about 50 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.

2.1.1. 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 5422 fledglings were weighed during this time period (285 ± 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. 3). 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 ± 0.352 kg at fledging (resighted fledge mass (RFM)), while birds that were not resighted (n=2030) averaged 3.035 ± 0.258 kg (not resighted fledge mass (NRFM)) (Fig. 3). The difference between these two means, 0.117 kg, is statistically significant (t-test, p-value < 0.001).

2.2. Model structure and governing equation

Chick growth is expressed as the change over time (t) in chick mass (M, kg) according to

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

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 (kJ kg^{-1}) (Fig. 4). The latter term converts tissue to energy.

The energy production available to the chick is calculated as

$$E_p = ED_{kwm}PAE \tag{2}$$

where ED_{kwm} is the prey wet-mass energy density (kJ kg^{-1}), P is the amount of prey provisioned to a chick (kg), and AE is the assimilation efficiency (unitless), or proportion 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 2.4.

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

$$E_u = PED_{kwm}(1 - AE) \tag{3}$$

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

$$E_i = PED_{kwm}. \tag{4}$$

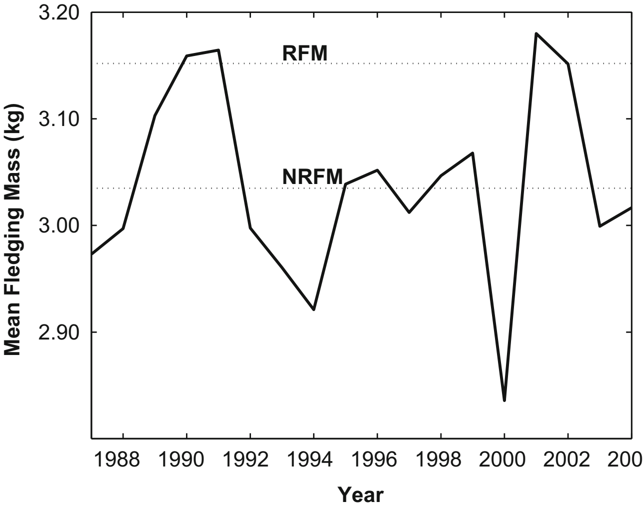

Fig. 3. Mean fledging mass measured for Adélie penguin chicks leaving Humble Island, near Palmer Station for each year between 1987 and 2004. The mean fledging mass of banded chicks that were resighted (RFM) and the mean fledging mass of chicks that were not resighted (NRFM) are indicated. See text for details.

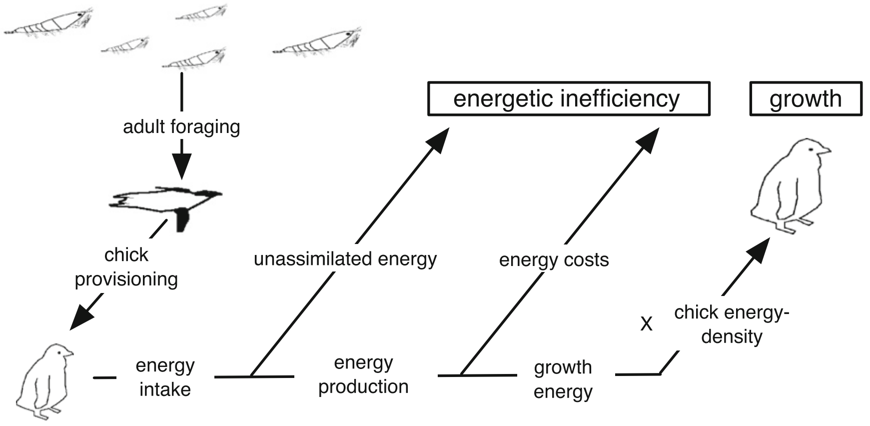

Fig. 4. Schematic representation of the energy flow that is included in the Adélie penguin chick growth model. See text for details.

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

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

where $Prov_{max}$ is the maximum feeding rate (kg d^{-1}), $Prov_0$ is the feeding rate at time zero (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 hatching, increased to 0.80 at day 40, and declined to 0.76 at fledging (Cooper, 1977; Heath and Randall, 1985; Janes, 1997) (Fig. 5A). 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

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

where *MMR* is the mean metabolic rate (kJ d^{-1}) and *TR* is the energy needed to convert chick tissue to the new energy density (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

$$MMR = aM \qquad (7)$$

where a was initially set to 910 kJ d^{-1} 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 kJ d^{-1} kg^{-1} (Janes, 1997). The conversion to the new energy density (*TR*) was calculated as

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

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

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

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

where ED_{cdm} is the dry-mass energy density of the chick (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 to 0.0273 kJ kg^{-1} as the chicks grow from 0.09 to 2.40 kg (Fig. 5B). As chicks continue to grow, chick dry mass energy density begins to decrease (Myrcha and Kaminski, 1982) (Fig. 5B). 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 kJ kg^{-1}) on day 54 (Myrcha and Kaminski, 1982) (Fig. 5B). The proportion of water in chick tissue (WC_c) declines from an initial value of 85–67% at fledging (Myrcha and Kaminski, 1982; Konarzewski et al., 1998) (Fig. 5C).

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 kJ kg^{-1}) was substituted for the chick's wet-mass energy density (ED_{cdm}).

2.3. Calculation of Antarctic krill energy density

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. 6). 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

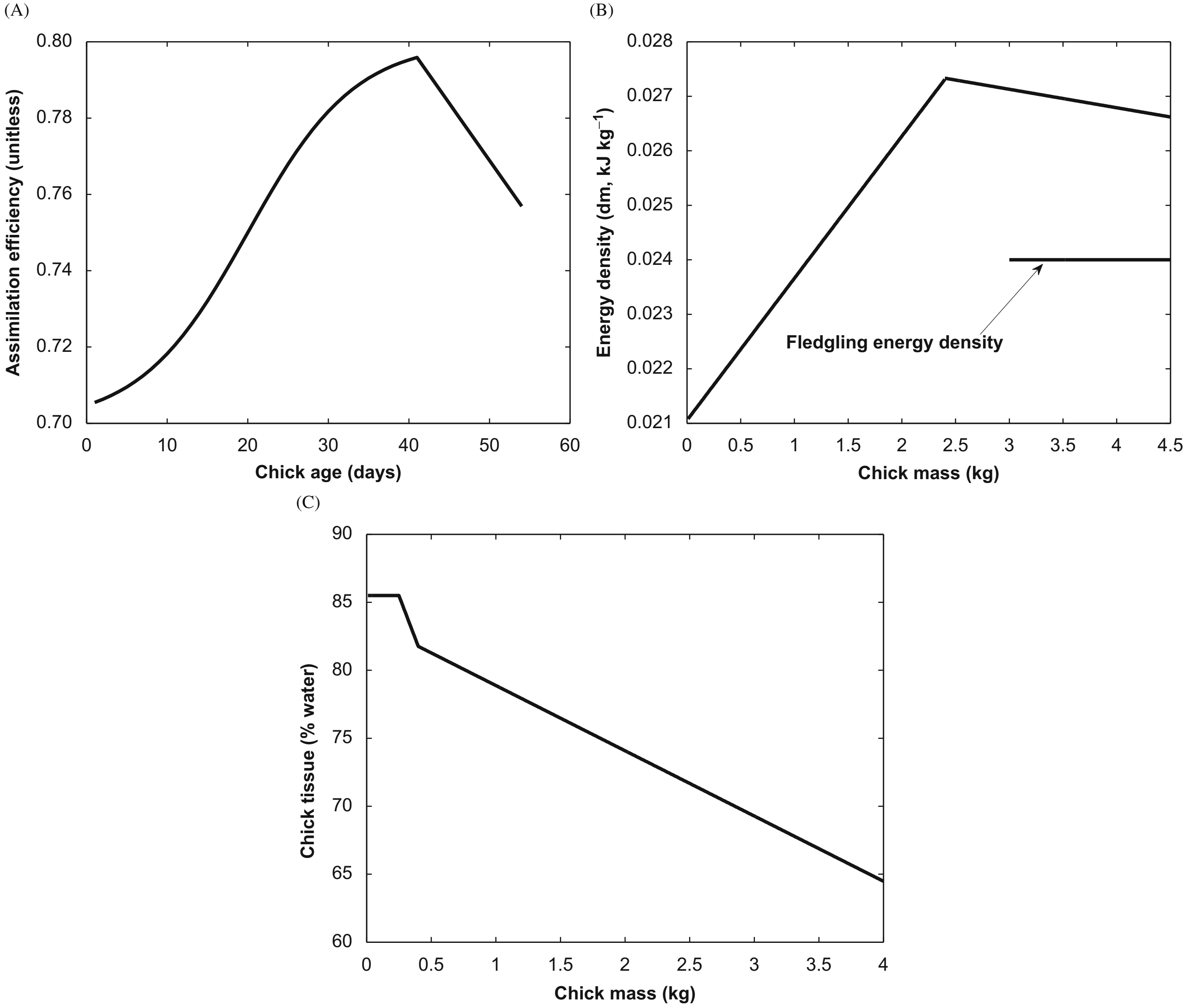

Fig. 5. Dependency on chick mass of relationships used in the chick-growth model to describe (A) chick assimilation efficiency as a function of chick age, (B) chick dry-mass energy density as a function of chick mass (fledgling energy density also shown), and (C) percent of chick somatic tissue that is water. See text for details.

Table 1
Ratios and energy density of Antarctic krill biochemical components calcu991 lated from Clark (1980). The lipid proportion is calculated for the Antarctic krill population as described in Section 2.4.

Biochemical component	Ratio	Dry mass energy density (kJ kg^{-1})
Lipid	Calculated	0.0395
Protein	10.0	0.0236
Carbohydrate	0.5	0.0172
Chitin	2.0	0.0171
Ash	3.0	0.0

produce a sex/maturity stage distribution (Fig. 6). The proportion of gravid and spent females was allowed to vary relative to spawning. 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. 6).

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

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

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. 7A and B).

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

$$T_{m/f} = \sum_{1}^{N} p_{m/f,n} R_{m/f} SC_n \tag{11}$$

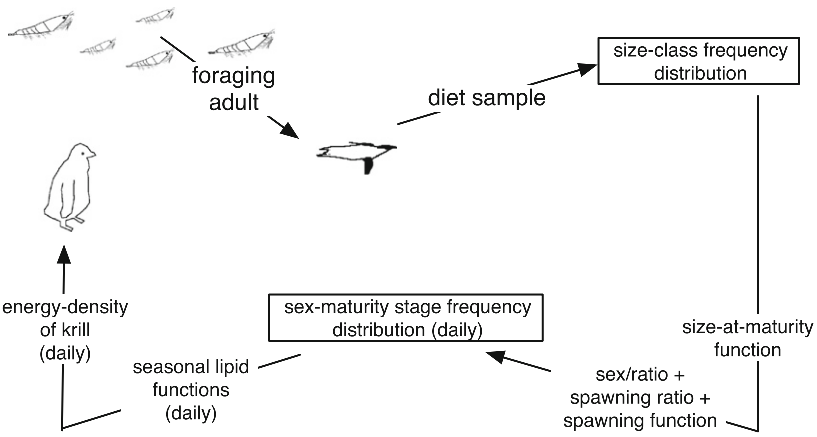

Fig. 6. Schematic representation of the calculation of energy-density of Antarctic krill ingested by Adélie penguin chicks.

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

$$SP_{m/f} = T_{m/f}sp_{m/f} \tag{12}$$

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 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

$$P_{gravid}(t) = T_f\, e^{(t-S_{pk})^2/S_{dur}} \tag{13}$$

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. 7C). 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. 8A–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. 8A–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. 8A) is more than mature male krill (Fig. 8B) or spent females (Fig. 8C), but less than gravid females (Fig. 8C).

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

$$E_{kdm}(t) = \sum_{1}^{n} p_{ms}(t)L_{ms}(t)LED \tag{14}$$

where E_{kdm} is the dry-mass energy density of the krill population (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)

$$E_{kwm}(t) = \frac{E_{kdm}(t)}{0.216}. \tag{15}$$

2.4. 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

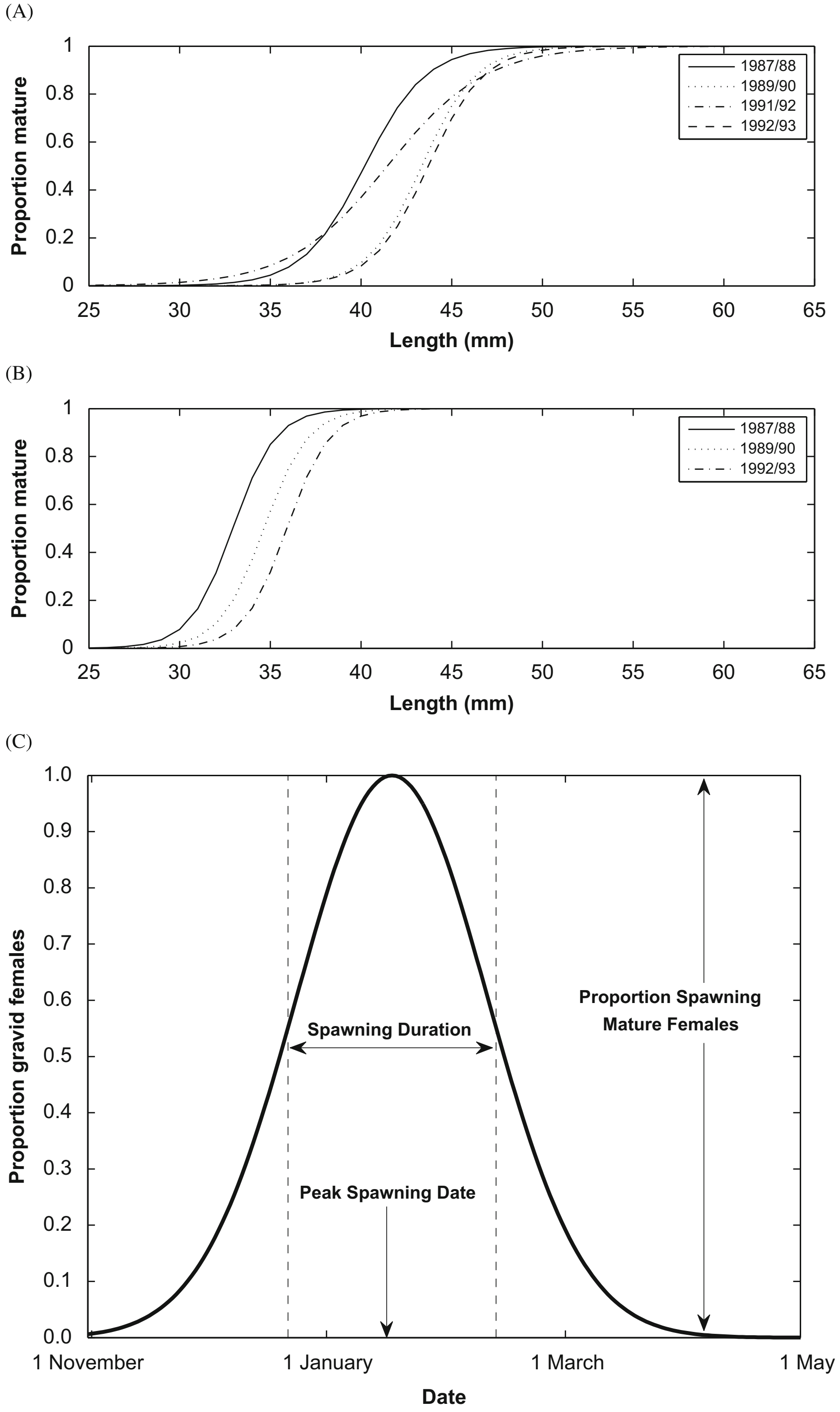

Fig. 7. Length-at-maturity functions from Siegel and Loeb (1995) for (A) male and (B) female Antarctic krill used to calculate the proportion of mature (potentially spawning) males and females from size-class distributions obtained from Adélie penguin diet samples collected at Palmer Station, and (C) 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.

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 3A and B) and

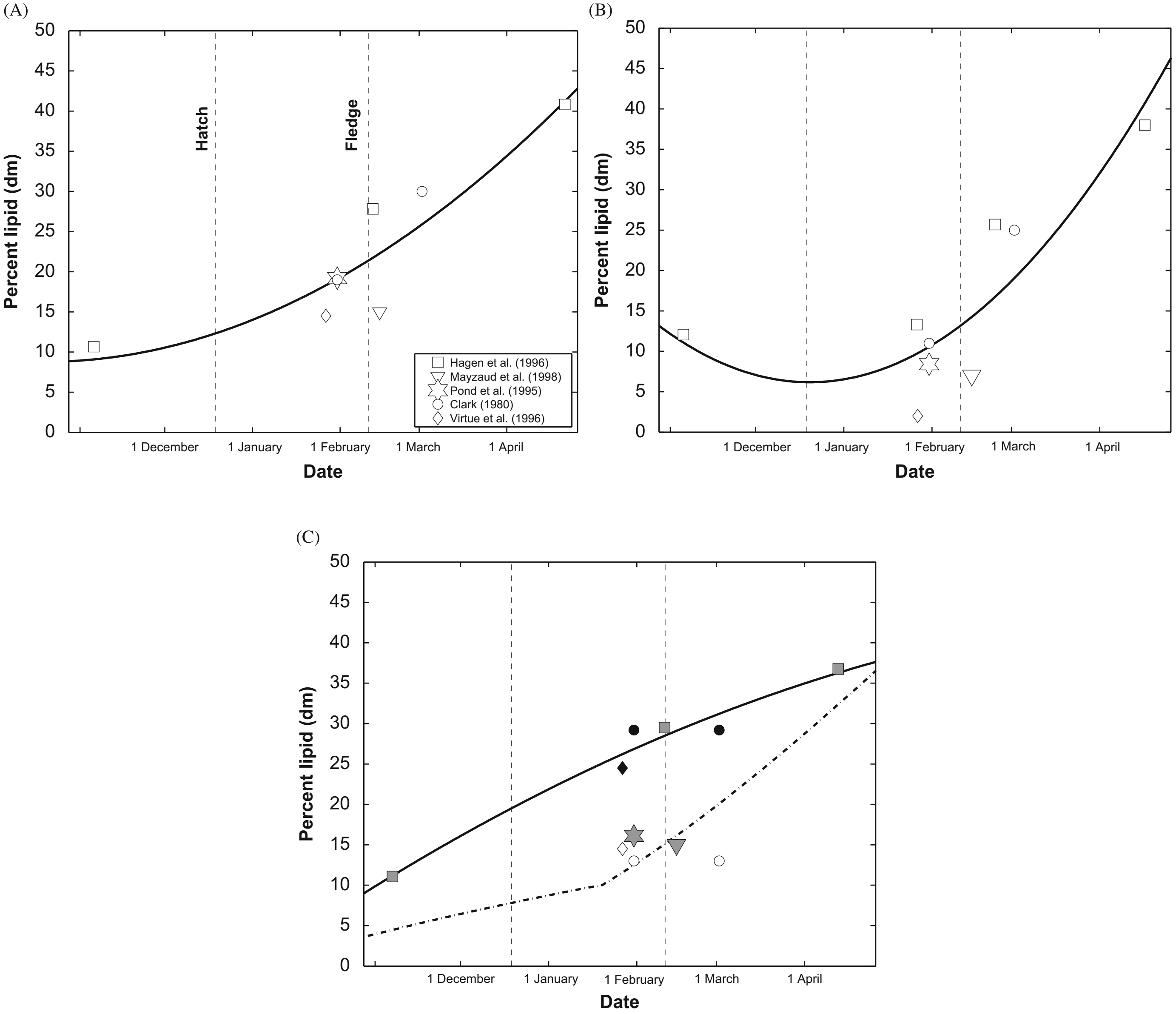

Fig. 8. Relationships used to describe the seasonal change in lipid content for (A) immature krill, (B) spawning male krill, and (C) gravid and spent (– · –) female krill. The data sets used to develop the relationships are indicated. Shading indicates the maturity stage of females in the samples (● =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 (––).

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 3C–E). Subsequent simulations investigated the influence of krill population sex-ratio and size-class frequency distribution on chick growth (Table 3F). 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 3G–I). The final set of simulations investigated the effect of variability in population-wide lipid content on penguin chick growth (Table 3K).

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. 3). This difference provides an estimate of the change in simulated fledging mass that would reduce a chick's probability of recruitment.

3. Results

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 mean value over the time-series between 1987 and 2005 (3.036 kg, Fig. 3) and the krill population ingested by chicks was not dominated by either large or small krill (Fig. 2). 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

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 noted in bold.

Parameter	Definition	Reference	Source(s)
–	Chick provisioning period	19 December–10 February	Field data
P	Provisioning rate	0.030–0.86 kg d^{-1}	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^{-1}	Calculated
$Prov_0$	Provisioining rate at time zero	0.03 kg d^{-1}	Calculated
k_{prov}	Rate of increase in provisioning rate	0.185	Calculated
MMR	Mean metabolic rate	86–2952 kJ d^{-1}	Janes (1997), Culik et al. (1990)
ED_{cdm}	Chick dry mass energy density	18.8–29.3 kJ kg^{-1}	Myrcha and Kaminski (1982)
WC_c	Proportion 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 size	Males = 0.60, females = 0.83	Siegel and Loeb (1994)
$sp_{m\|f}$	Proportion of mature males and females that spawn	1.0	Siegel and Loeb (1994), Quetin and Ross (2001)
$L_{50,m\|f}$	Length at which 50% of male or female krill has attained sexual maturity	Males = 42 mm, females = 34mm	Siegel and Loeb (1994)
S_{pk}	The date of peak krill spawning	20 January	Quetin and Ross (2001)
S_d	Duration of spawning (> 50% spawning females are gravid)	60 days	Quetin and Ross (2001)
$R_{m\|f}$	Proportion of males and females in krill population consumed by penguins	0.5	–
SC_n	Proportion of krill in each size-class (n)	0.00–0.46	Derived from 1996 field data

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^{-1})	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) [17–99d]	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}) [32–36 mm]	4.68–4.67	3.10–3.90
(I) Male and female length-at-maturity functions (L_{50m} and L_{50f}), [40/32–44/36 mm (m/f)]	4.67–4.68	3.09–3.09
(J) Population-wide lipid adjustment [− 5% to +5% lipid (dry mass)]	4.44–4.91	2.95–3.24

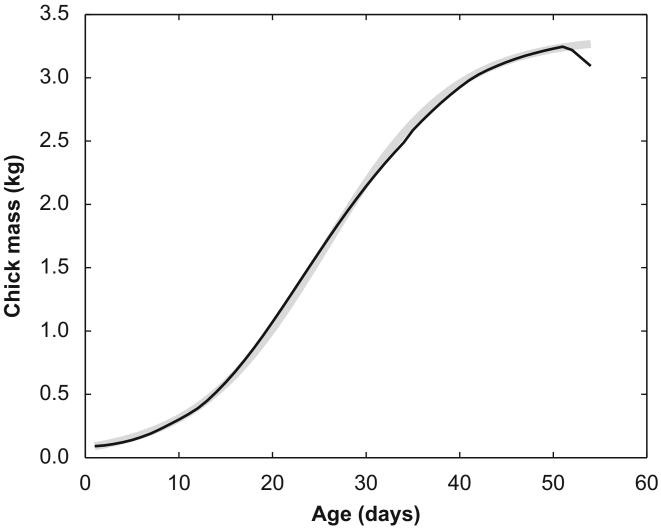

Fig. 9. Simulated time evolution of Adélie penguin chick growth (——) obtained from the reference simulation. The target growth curve used to set the provisioning rate in the reference simulation is shown (▬).

curve was set at 3.094 kg, the mean of the RFM and the NRFM (Fig. 3). 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. 9; r^2 of 0.99 prior to the starvation period). During the starvation period, an average of 54 g d^{-1} was lost by the chick (Fig. 9). The simulated chick wet-mass energy density increased from 3.1 to 8.6 kJ g^{-1}, with the fastest rate of increase between day 8 and 30 (Fig. 10A). Daily energy production increased immediately after hatching to day 40 from 112 to 3255 kJ (Fig. 10B). 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. 10B). The greatest difference between energy production and cost was the period of fastest chick growth that occurred between days 12 and 25 of the simulation. The amount of krill provisioned to the chick ranged between 0.03 and 0.85 kg d^{-1} (Fig. 10C). The total amount of krill provisioned to the chick (27.8 kg), the energy density of krill (Fig. 10D, 4.51–4.82 kJ g^{-1}), and the total energy provisioned to the chick (131 MJ) are all within the range of available estimations and measurements (Table 4).

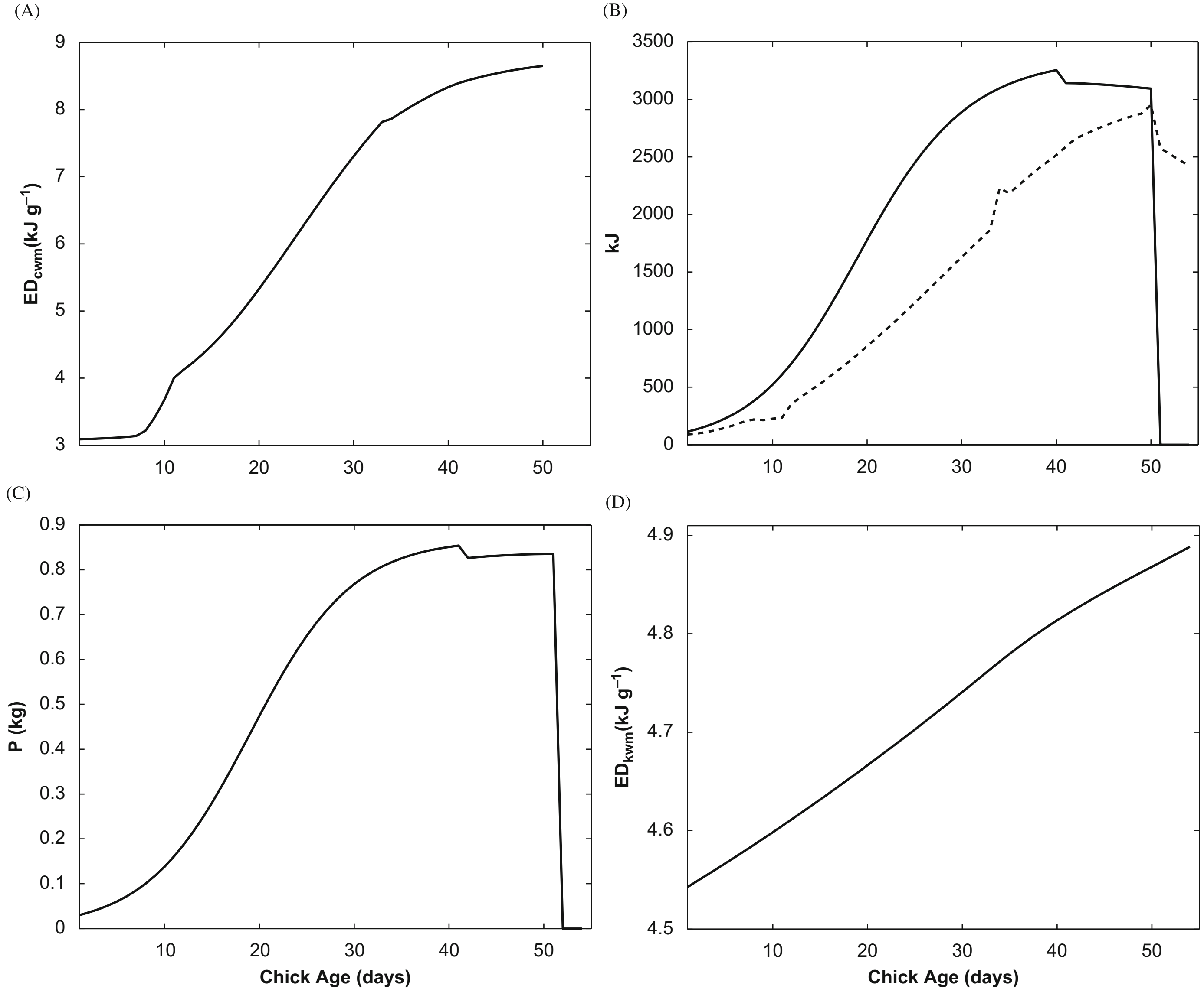

Fig. 10. Simulated evolution of (A) wet mass energy density of the chick (ED_{cwm}), (B) energy available for production (E_p, —) and energetic costs (E_c, – –), (C) provisioning rate (P) and (D) wet-mass energy density of Antarctic krill (ED_{kwm}) as a function of chick age.

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

Diagnostic variable	Value	Source	Comments
Total wet mass provisioned to chick (kg)	33.6	Janes (1997)	Estimated from observed growth
	29.8	Culik (1994)	Estimated from observed growth
	27.8	**This study**	**Model output**
	24.1	Salihoglu et al. (2001)	Estimated based on model parameters
	24.0	Chappell et al. (1993)	Measured change in adult mass before and after chick feeding
	23.0	Trivelpiece et al. (1987)	Measured from mass of adult stomach contents prior to feeding chicks
Krill wet-mass energy density (kJ g^{-1})	4.99	Nagy and Obst (1992)	Measured using bomb calorimetry
	4.51–4.82	**This study**	**Model output**
	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
	131	**This study**	**Model output**
	98	Salihoglu et al. (2001)	Estimated

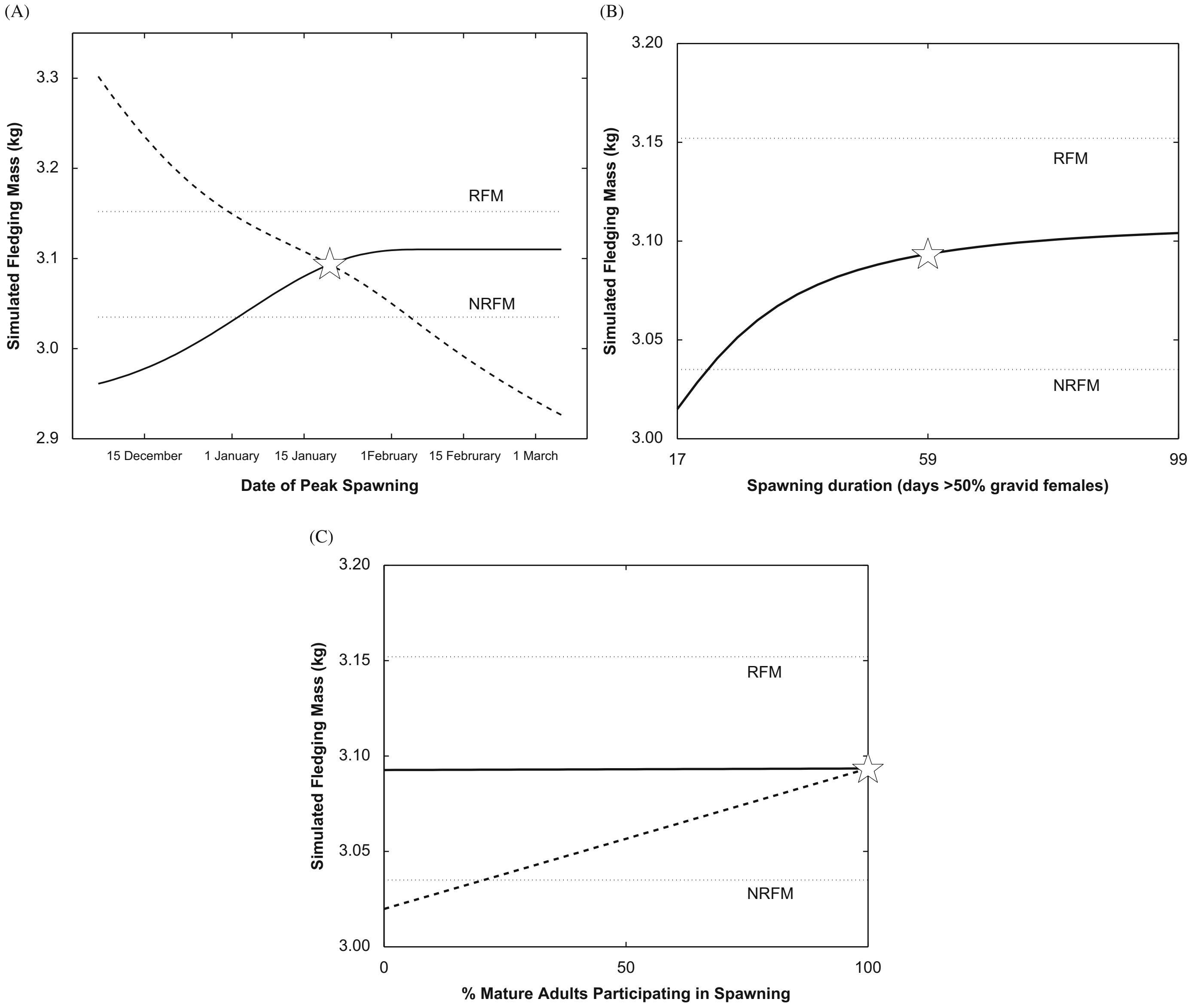

Fig. 11. .Simulated chick fledging mass produced by variability in (A) peak spawning date (—) and peak spawning date coupled with lipid accumulation (– –), (B) spawning duration, and (C) the percentage of mature adults (both male and female, —) and mature females that participate in spawning (with 100% 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 (···), as is the fledging mass obtained from the reference simulation (☆).

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. 11A). 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 proportion 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 prespawning 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. 11A). Simulated fledging mass varied by 0.37 kg, well above the difference between RFM and NRFM. Simulated fledging mass reached the 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.

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. 11B). However, decreasing the

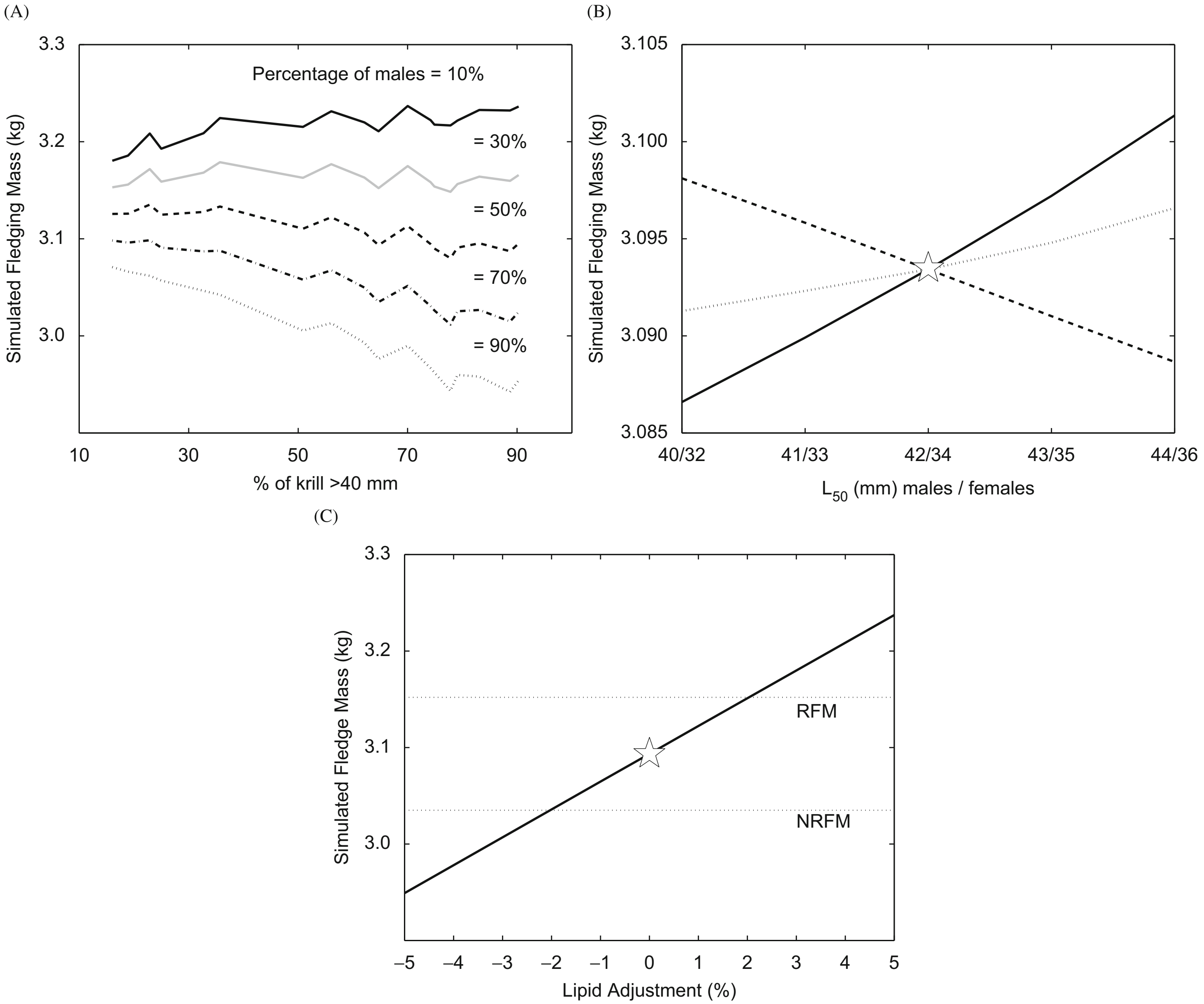

Fig. 12. Simulated chick fledging mass obtained for (A) changing percentage of krill larger than 40 mm and varying percentage of male krill in the population, (B) variability in the length-at-maturity for male (—), female (– –), and male and female (⋯) krill, and (C) variability in the population lipid content. The mean fledging mass of banded chicks that were resighted (RFM) and the mean fledging mass of chicks that were not resighted (NRFM) are indicated (⋯), as is the fledging mass obtained from the reference simulation (☆).

percentage of females that spawn from 100 to 0% decreased simulated chick fledging mass by 0.07 kg (Fig. 11B). Increasing the duration 435 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. 11C). This change reflected the greater proportion of gravid females in the chick's diet with a lengthened spawning period.

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. 12A). A population of 50% males resulted in a small increase in simulated fledging mass as the proportion of large krill increased (Fig. 12A). 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. 12A).

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. 12B). Increasing both male and female length-at-maturity at the same time (L_{50m} and L_{50f}) resulted in an 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. 12C). 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.

4. Discussion

4.1. Timing of Antarctic krill spawning initiation and duration

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 480 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–early December; late, late December–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.

4.2. The contrasting energy density of mature female and male Antarctic krill

Observations show that between 10% and 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 504 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 females dominate the population, the simulated chick fledging mass is optimal. However, if males dominate the population, 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 3–5 years 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 3–5 years 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 gravid females dominate the large size-classes, 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.

4.3. Variability in population-wide Antarctic krill 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 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 ±2% could influence Adélie penguin chick growth sufficiently to have a possible impact on recruitment.

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. 13). 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 immediately 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.

4.5. Implications

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 shown that chinstrap penguins (*Pygoscelis Antarctica*) do not alter their foraging effort with reduced prey availability (Croll et al., 2006), suggesting that in some cases penguin adults invest a

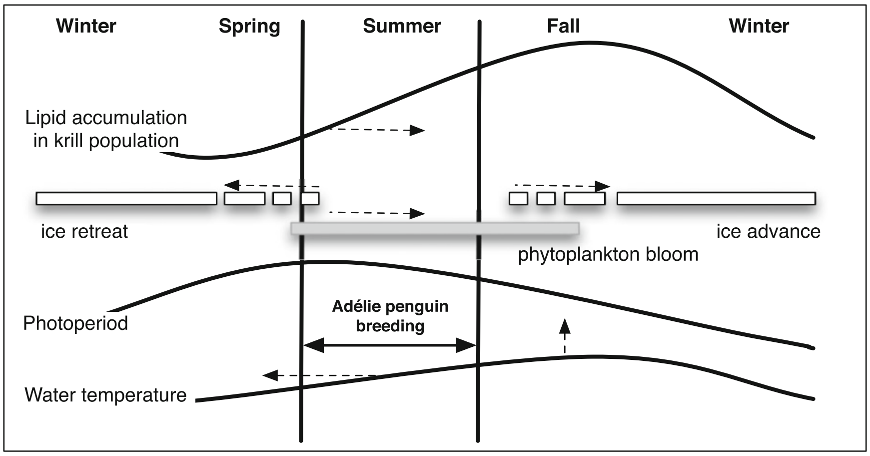

Fig. 13. A conceptual representation of the phenology of physical–biological processes that link the physical environment (sea ice, water column environment) with primary production, Antarctic krill lipid accumulation and the quality of prey ingested by breeding adult penguins and their chicks. Dashed arrows indicate the shift in phenology of processes off the WAP under climate warming based on observational studies. The diagram was adapted from Kawaguchi et al. (2006).

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 murres (*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 and 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.

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