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Baris Salihoglu · William R. Fraser · Eileen E. Hofmann

Factors affecting fledging weight of Adélie penguin (*Pygoscelis adeliae*) chicks: a modeling study

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Abstract An individual-based model is developed to examine mechanisms that potentially underlie the observed constancy in fledging weight (2.8–3.2 kg) of Adélie (*Pygoscelis adeliae*) penguin chicks, in spite of large variability in the abundance of Antarctic krill (*Euphausia superba*), the primary food source. The model describes the energetic requirements of the chick, with growth resulting from the difference between assimilated energy and respiration. Parameterizations of these metabolic processes are based upon experimental and field observations. Ingestion of Antarctic krill by the chick is dependent on the frequency of food delivery to the chick by the adults, which is based on measured foraging times. The mass, size, and size frequency distribution of Antarctic krill fed to the chick are specified using empirical data. The energy content of the Antarctic krill provided to the chick is taken to be constant or allowed to vary with size. The simulations show that food availability is most critical in the latter portion of chick development, when growth rates and food demands are high. Low food availability during this time must be compensated by either feeding chicks with larger krill of higher caloric value or by increased assimilation efficiency. Periods when small krill with lower caloric value dominate require more frequent feeding of the chicks in order to attain their observed fledging weight. Thus, although the total food energy given to the chick is the main factor determining chick growth, the distribution of food availability relative to chick size (i.e., different net growth rates) and food quality are also factors influencing the fledging weight of penguin chicks. The simulations provide insight into the compensating effects of food delivery, food quality, and metabolic processes that allow Adélie penguin chicks to reach their observed fledging weight in spite of considerable environmental variability in food supply.

Introduction

One of the observations arising from almost 25 years (Parmelee et al. 1977; Parmelee and Parmelee 1987) of monitoring Adélie penguin (*Pygoscelis adeliae*) colonies around Anvers Island (64°46′S, 64°04′W) is that the fledging weight of Adélie penguin chicks is relatively constant at 2.8–3.2 kg. This constancy in chick fledging weight occurs in spite of large variations in the marine habitat which influence the food that is available to foraging parents.

Antarctic krill (*Euphausia superba*) constitutes about 99% (by wet weight) of the diet of Adélie penguins (Volkman et al. 1980; Lishman 1985; Trivelpiece et al. 1987), which makes the species primarily dependent on a single food source during the breeding season. This dependency provides a potential link between penguin chick survival and changes in the marine habitat that modify the availability of krill. Recent studies (Siegel and Loeb 1995; Loeb et al. 1997) have shown correlations between krill recruitment and sea-ice extent and concentration, with recruitment increasing following a winter of extensive sea ice. Sea-ice concentration and extent in the Antarctic Peninsula region are cyclic, with highs and lows separated by about 4–5 years (Murphy et al. 1995; White and Peterson 1996); therefore, the size and availability of krill to predators undergo annual variations (Fraser and Hofmann, unpublished work). Because Antarctic krill live for 4–5 years (Siegel 1987), the cyclic variation in sea ice has consequences for krill availability to Adélie penguins that extend beyond a single season.

B. Salihoglu (✉) · E. E. Hofmann
Center for Coastal Physical Oceanography,
Department of Oceanography,
Old Dominion University,
Norfolk, Virginia 23529, USA
E-mail: baris@ccpo.odu.edu
Tel.: +1-757-6833234

W. R. Fraser
Polar Oceans Research Group,
Montana State University, Bozeman, MT 59717, USA

The observed constancy in chick fledging weight, in spite of large variations in the availability of food supply (Siegel and Loeb 1995; Lascara et al. 1999), suggests that the chicks may modify their energetic and/or metabolic demands to attain an optimal mass that potentially enhances their survival after fledging. Alternatively, the parent can modify the timing and frequency of food delivery to the chick to compensate for variations in food supply. To investigate these potential explanations for the observed constancy in chick fledging weight, a time-dependent physiologically based model of Adélie penguin chick growth is constructed. The model is formulated using physiological data available in the literature, in addition to empirical data obtained from Adélie penguin colonies near Anvers Island. The model allows investigation of the effects of the type and amount of krill consumed (food quality and quantity) on chick growth. The model-based investigations highlight aspects of the relationship between Adélie chick growth and food supply that are deserving of more field and laboratory measurements.

Materials and methods

Observations

Adélie penguin chick growth

Concurrent measurements of culmen length and body mass were obtained from Adélie penguin chicks captured in colonies on Torgersen and Humble Islands, which are just offshore of Anvers Island. These measurements began in early January of 1989 and 1990, and were made at about 5-day intervals until the end of the month; 50–150 chicks were typically measured per 5-day sampling interval. January brackets the period of highest chick growth rates in the colonies near Anvers Island. Chick culmen length (CL) is converted to chick age, given in days, using the linear relationship given in Eq. 1 in Table 1.

Adélie penguin chick fledging weight

Fledging weights for Adélie penguin chicks are routinely measured at beaches on Humble Island. For this study, the fledging weights from the 1988/1989 and 1989/1990 seasons are used. Sample sizes during these 2 seasons were 267 and 135 chicks, respectively, which gives a statistically significant estimate of the mean fledging weight. For the 1988/1989 and 1989/1990 seasons, the average fledging weights were 2.97 ± 0.32 kg and 2.99 ± 0.31 kg, respectively. Five-day means of the fledging weight measurements show that this value ranges between 2.75 and 3.16 kg.

Adélie penguin parent stomach content

The contents of the parent stomachs were obtained using the lavage method (Wilson 1984). Stomachs were flushed until clear water was obtained, which typically requires two to three flushings. Adults were captured near colonies and before feeding their chicks. Stomach contents were weighed and sorted, and the sizes of individual krill were measured to 5-mm intervals to obtain the size frequency distribution. Stomach content measurements have been made for the Torgersen Island penguins since 1987. For this study, the measurements from the 1988/1989 and 1989/1990 seasons are used.

The krill length frequency distributions obtained from season averages of the stomach contents (72 samples) for the 2 seasons differ (Fig. 1). The 1988/1989 stomach samples showed that large krill, 40–55 mm, dominated the size frequency distribution (Fig. 1a), with the modal class being 46–50 mm. In the following season, the dominant krill sizes were smaller and the modal class was shifted to 30- to 40-mm krill (Fig. 1b).

Table 1 Equations used in the penguin chick growth model

Equation	No.	Comments and parameter definitions
Age = $a \times CL – b$ (1)	1	$a = 2.1299$ days mm^{-1}, $b = 24.619$ days. The regression is based on 149 measurements from 43 chicks, 0–48 days in age, and has $r^2 = 0.7984$. The regression is based on data from 1996–1997, which was a season of high chick survival to the crèche stage
$\frac{\mathrm{dCM}}{\mathrm{d}t} = A - R_\mathrm{a} - R_\mathrm{p}$ (2)	2	The first term represents the growth rate which is determined by the difference between assimilation of ingested food (A) and respiratory losses, which include those incurred while chicks are active (R_a) or resting (R_p)
$K(t) = \alpha + \beta t + \gamma t^2$ (3)	3	$K(t)$ is the amount of krill (g) given to the chick and t is time in days. The coefficient α is the initial amount of krill fed to the chick and has the value of 50 g. The coefficients β and γ describe the time-dependency of the food given to the chick and have the values 2.3 g day^{-1} and 0.046 g day^{-1}, respectively
$A = C_\mathrm{ktp}(t)K(t)\mathrm{AE}$ (4)	4	$K(t)$ is the amount of krill fed to chicks, C_ktp is the krill-to-penguin tissue conversion and AE is the assimilation efficiency
$\dot{V}_{\mathrm{O}_{2\mathrm{p}}} = cM^d$ (5) $\dot{V}_{\mathrm{O}_{2\mathrm{a}}} = eM^f$ (6)	5 6	$\dot{V}_{\mathrm{O}_{2\mathrm{p}}}$ and $\dot{V}_{\mathrm{O}_{2\mathrm{a}}}$ are the oxygen consumptions, in terms of liters O_2 consumed per hour, for resting and active chicks, respectively and M is the chick mass in kilograms. The coefficients c and e represent passive and active basal respiration rate and have the values of 1.50 l O_2 consumed h^{-1} g^{-1} and 2.25 l O_2 consumed h^{-1} g^{-1}, respectively. The dependency of respiration rate on chick mass is given by d and f, which have the values of 0.921 and 1.024, respectively
$R_\mathrm{p} = C_\mathrm{otp}\dot{V}_{\mathrm{O}_2}\delta$ (7) $R_\mathrm{a} = C_\mathrm{otp}\dot{V}_{\mathrm{O}_2}\theta$ (8)	7 8	C_otp provides the conversion to chick tissue equivalents (20.1 kJ (4.83 kcal) (l O_2)$^{-1}$ and 21.3 kJ (g dry mass chick issue)$^{-1}$) as described in Culik (1994). The chick metabolic demand, $\dot{V}_{\mathrm{O}_2}$, is obtained from Eqs. 5 and 6. The coefficients δ and θ determine the fractions of time that the chicks are active and resting which are 0.80 and 0.20, respectively, as reported by Culik et al. (1990)

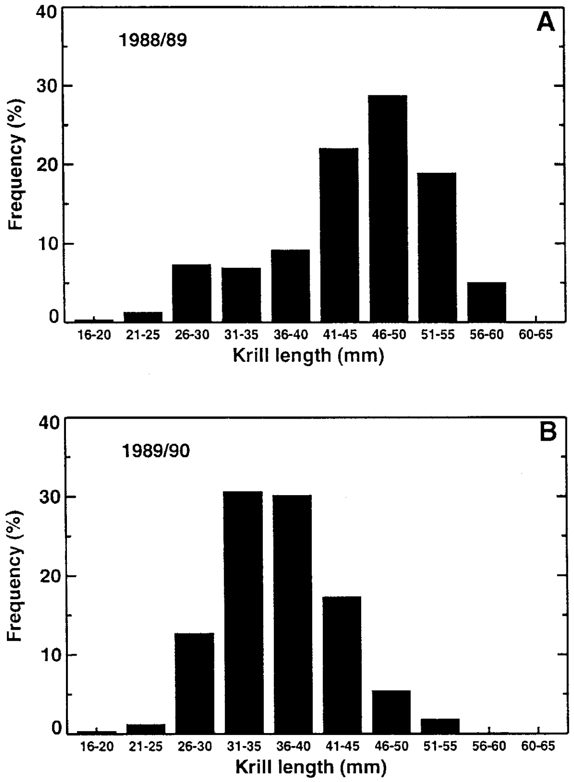


Fig. 1 Length-frequency distributions of krill consumed by Adélie penguins in **A** 1988/1989 and **B** 1989/1990 around Anvers Island

Adélie penguins are visual opportunistic feeders and do not selectively take krill of certain sizes (Fraser and Hofmann, unpublished work. Recent studies show good correspondence between krill length frequency distributions in penguin diet samples and those obtained from krill caught in nets (Lishman 1985; Croxall et al. 1997, 1999; Reid et al. 1999), thereby demonstrating that penguin stomach contents are reflective of the food available in the environment. Therefore, changes in krill size frequency distribution observed in Adélie penguin stomach contents reflect changes in the food that is available to the adults during foraging trips.

Adélie penguin foraging trip duration

Foraging trip durations were determined each field season by instrumenting 30–40 adult penguins with 12-g radio transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA). Trip durations are calculated from data obtained using automatic data loggers set to record (date-hour-minute) the presence of instrumented birds near their breeding colonies every 20 min. Because the receivers can detect instrumented birds on land up to 1.5 km away, undetected birds are assumed to be at sea foraging (cf. CCAMLR 1992). Foraging trip duration is thus inferred with a resolution of ±20 min from the presence-absence patterns evident in the data.

For this study, an average foraging time was calculated based on 245 penguins and an 8-year time series collected between 1987/1988 and 1995/1996 (no data were available in 1988/1989; Fraser and Hofmann, unpublished work). To avoid any possible effects on foraging behavior due to annual variability in penguin breeding chronology, data selection for each season used in calculating this average was standardized on the date when approximately 70% of the chicks had crèched and 30% were being brooded, and the data considered in the analyses limited to 5 days on either side of this date. This index also ensures adequate sampling of the peak chick growth phase, or the period when adults are likely to be under the greatest constraints to effectively provision their young (Fraser and Ainley 1990). The mean foraging trip duration calculated by these biological markers was 13.89 h, with a standard deviation of 8.86 h.

Governing equation

The Adélie penguin chick growth model assumes that the time-dependent change in chick mass is determined by the difference in assimilation of ingested food and respiratory losses (Eq. 2, Table 1). The ingestion and assimilation formulation is such that unassimilated ingestion (1-*A*) includes excretion as well as loss of unassimilated food. Equation (2) does not explicitly include the effect of thermoregulation on chick growth, which can be about 10–11% of assimilated energy, depending on environmental conditions (Chappell et al. 1990). The implications of this process are discussed later within the context of specific simulations.

Model parameterization

Food supply and feeding frequency

Penguin chick development can be partitioned between the brood and crèche periods (Spurr 1975), the latter period being when groups of chicks band together, allowing the parents to leave and spend more time foraging at sea. Throughout both periods, the chicks are fed by the parents with regurgitated food until just prior to fledging at about 48–54 days. The food demands of the chicks increase markedly during the crèche period. Thus, a basic component of the penguin chick growth model is determining the time-dependence of the food supplied to the chick. The stomach content of the parent, the proportion of this provided to the chick, the rate of delivery (feeding frequency), and the size frequency distribution of the available krill all contribute to krill supplied to chicks.

The mean weight of adult Adélie penguin stomach contents, measured for 420 birds from the Anvers Island colonies for the period 1987/1988–1997/1998, is 377.25 g with a standard deviation of 125.10 g (W.R. Fraser, unpublished data). It is assumed that the range in stomach mass represents an increase in adult stomach content in response to the increased food demands of the chick as it grows (Trivelpiece et al. 1987; Culik 1994). Therefore, the lower limit of stomach mass of 250 g was assumed to represent the food at the time when chicks just begin feeding. The upper stomach mass of 500 g was taken to be the food load available for older chicks. These values were then used to derive a relationship that describes the change in adult stomach content over time (Eq. 3, Table 1).

The amount of krill given to the chick obtained from Eq. 3 increases with time and thus with chick age. In some simulations (discussed below), the coefficients β and γ were given the values 2.8 g day^{-1} and 0.046 g day^{-2}, respectively, which in effect provides the same mass of total krill over the time of chick growth, but allows this to occur in a shorter amount of time. In another simulation (discussed below) β and γ were given the values 1.67 g day^{-1} and 0.046 g day^{-2}, respectively, to examine chick growth response to reduced food availability.

At any feeding, the entire content of the parent's stomach is not fed to the chick. Initially the chick, which is small, receives 16.56% of the adult stomach food content. As the chick grows, it receives a larger portion of the adult stomach content, reaching 54.44% before fledging.

Direct measurements of the frequency at which Adélie penguin chicks at the Anvers Island colonies are fed are not available. However, the adult foraging trip durations provide a means for estimating the interval at which food is potentially available to the penguin chicks. The mean foraging trip duration was taken as the initial value for feeding frequency for the chicks, which represents 1.7 feedings per day per parent. Observations show that Adélie penguin chicks enter the crèche period at the age of 21 days (Trivelpiece et al. 1987) and this is the time when their energy requirements are higher (Culik et al. 1990). During this period of the simulations, the food given to the chicks by the parents is

Table 2 Summary of simulation characteristics, the total amount of krill consumed by the chicks, the maximum (asymptotic) weight reached by chicks, the time of maximum weight, and the fledge weight of the chicks (* designates simulations shown as figures)

Simulation	Total amount of krill (g)	Max. chick weight (kg)	Time of max. weight (days)	Fledge weight (kg)
Reference*	24,124	3.440	51	3.075
Food fed to chick is from Culik (1994)*	30,212	3.685	36	2.501
Feeding frequency is not increased during crèche	14,196	1.855	54	1.855
Starvation period doubled	22,822	3.246	48	2.520
Colony time shortened (52 days); krill given kept same	24,161	3.561	49	3.207
Colony time shortened; krill delivered is reduced	22,102	3.246	49	2.876
Krill caloric content varies (1988/1989), mode: 41–55*	24,124	4.081	51	3.652
Krill mode moved to 26–45 mm (1989/1990)*	24,124	3.567	51	3.189
Krill given reduced by 2.8 kg in total (–50 g/day)	21,305	3.184	51	2.809

doubled, as suggested by Lishman (1985), resulting in 3.4 feedings per day (1.7 feedings per day per parent).

An additional modification made to the food supplied by the parents is to reduce the food given to chicks by ~150 g day^{-1} during the last 3 days of the crèche period. Observations show that the parents usually discontinue feeding the fledglings 1–3 days before fledging (Janes 1997).

Energy conversions

The increase in chick mass due to assimilation of the ingested krill is done by converting krill mass to energy content and then converting this to equivalent tissue growth. Measurements of energy density of fresh krill tissue range from 3.699 kJ (0.884 kcal) g^{-1} to 4.9874 kJ (1.192 kcal) g^{-1} (Davis et al. 1989; Nagy and Obst 1992) and these values (Fig. 2) were tested with the model. Additionally, measurements of krill energy density made for different sized krill (Clarke and Morris 1983; Torres et al. 1994; Nicol et al. 1995; Virtue et al. 1996) were used to construct an empirical relationship that allows caloric content to vary with krill size (Fig. 2). This relationship was used in simulations that examined the effect of different size krill on penguin chick growth. For the reference simulation (discussed below), the energy content of regurgitated krill is taken to be a constant value of 20.4 kJ (4.8756 kcal) $(\text{g dry mass})^{-1}$, with a water content of 80% (Janes and Chappell 1995), which gives an energy content for fresh weight krill of 4.08 kJ g^{-1} (Fig. 2).

The energy density of the chick tissue is assumed to be constant at 21.3 kJ $(\text{g dry mass})^{-1}$ [5.0907 kcal $(\text{g dry mass})^{-1}$] as there is no change in overall energy density as Adélie chicks grow (Janes and Chappell 1995). It is assumed that the chick has a water content of 75%, which gives an energy density value of 5.325 kJ (1.2727 kcal) $(\text{g tissue})^{-1}$, resulting in a ratio of 1 kJ g^{-1} for the krill tissue to 1.3 kJ g^{-1} for the penguin chick.

Assimilation

The assimilation of ingested food is determined from Eq. 4 in Table 1. The krill-to-penguin tissue conversion is specified as either a constant value or with a dependency on krill length, $C_{\text{ktp}}(l)$, where l is krill length. The assimilation efficiency for Adélie penguin chicks is assumed to be constant at a value of 0.80 (Kooyman et al. 1982).

Respiration

Metabolic losses due to respiration were parameterized using oxygen consumption measurements determined by O_2/CO_2 respirometry in a field laboratory (Culik et al. 1990). These data provide relationships describing oxygen consumption rate as a function of chick mass (Eqs. 5, 6, Table 1). Energy consumption by the chicks is calculated from oxygen utilization for resting (R_p) and active (R_a) chicks (Eqs. 7, 8, Table 1). The respiration rates for passive and active chicks increase with chick mass, with the rate for active chicks being higher.

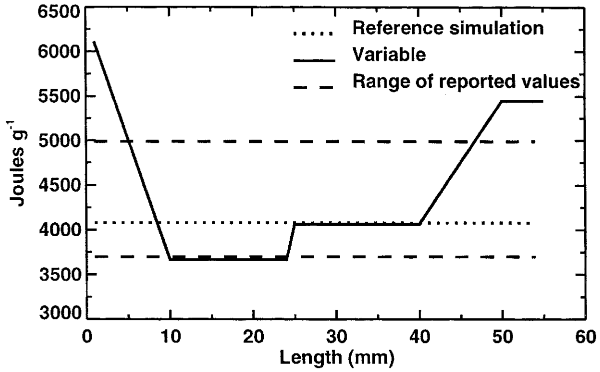


Fig. 2 Caloric content of Antarctic krill as a function of krill size (*solid line*) constructed using caloric content measurements for krill ovarian tissue (Clarke and Morris 1983) and measurements for different size krill (Torres et al. 1994; Nicol et al. 1995; Virtue et al. 1996). The constant energy content of regurgitated krill of 4.08 kJ g^{-1} (0.975 kcal g^{-1}, measured by Janes and Chappell (1995), was used for the reference simulation (*dotted line*). Measurements of caloric content of fresh krill tissue range from 3.698 kJ g^{-1} (0.884 kcal g^{-1}) (Culik 1994) to 4.987 kJ g^{-1} (1.192 kcal g^{-1}) (Nagy and Obst 1992) and these are shown for reference (*dashed lines*)

Model implementation

The initial chick mass is taken to be 90 g (Croxall 1984; Williams 1995) and simulations of chick growth extended for 54 days, which is the average time required to reach fledging weight (Culik 1994). The time integration of the chick growth model equations was done using a 4th order Runge-Kutta routine with a time step of 1 day, which is sufficient to avoid numerical dispersion and to capture the fastest time scales in the model.

The first simulation with the chick model used the basic parameter set obtained from the Anvers Island penguin colony measurements and the basic metabolic relationships derived as described previously. The simulation obtained with these provides a basis for comparing (a reference simulation) other simulations in which food quality, feeding frequency, and metabolic relationships were varied. Additional simulations considered the effects of variations in the amount (mass), composition (size of krill), and delivery frequency of the food supply (Table 2). Other simulations were designed to evaluate the effects of changes in metabolic processes/rates in determining chick mass at fledgling. Comparisons among simulations were made using differences in the simulated chick mass at fledging and the total amount of food delivered to the chick by the parent (Table 2).

Results

The reference simulation

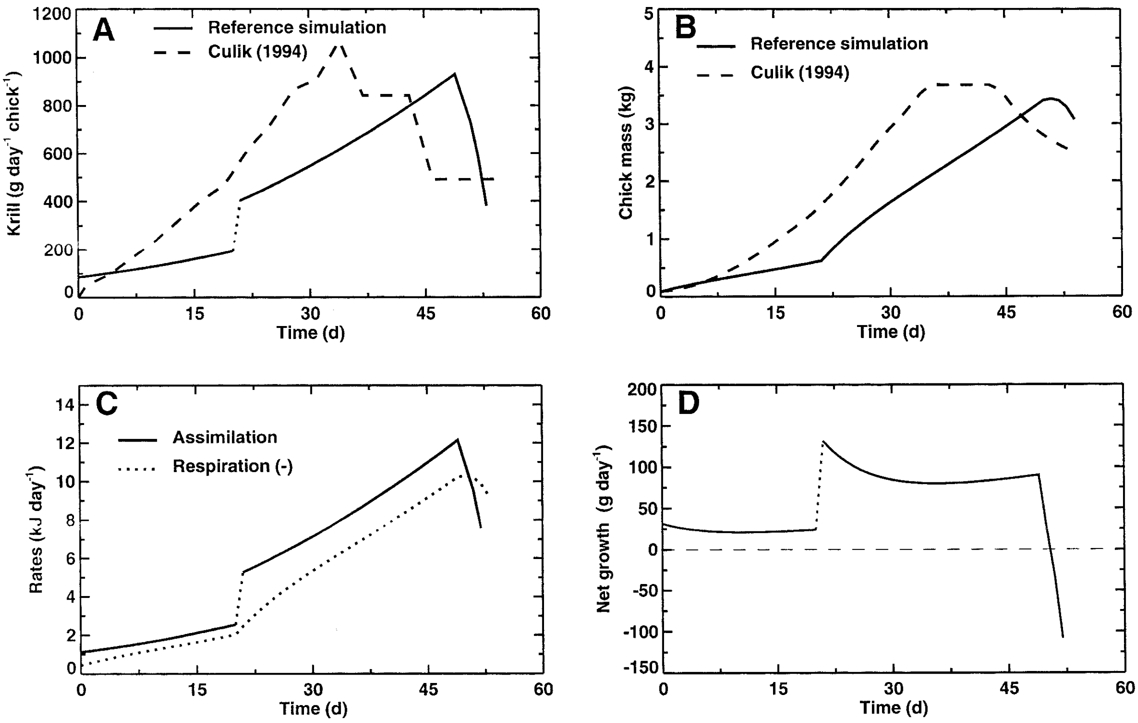
The food supply given to the chick was determined from Eq. 3, and provided a total of 24.12 kg of fresh krill over the 54-day growth period. This value is within the range of measured values for total mass of krill delivered to penguin chicks, which are reported as 33.6 kg (Janes 1997), 23 kg (Trivelpiece et al. 1987), and of the same order as the value of 29.8 kg suggested by Culik (1994). The time distribution of the food supply (Fig. 3a, solid line) included doubling of the feeding frequency of the chick during the crèche period (days 21–51) and decreased food supply during the last 3 days (days 52–54).

Chick mass increases from its initial (hatching) mass of 90 g to almost 800 g in the first 21 days of the simulation (Fig. 3b, solid line). During this period, assimilated energy exceeds respiration losses (Fig. 3c), which gives a positive net growth rate (Fig. 3d). During the first 21 days, the difference between assimilation and respiration decreases (Fig. 3c) as the chick becomes larger, which produces a reduction in net growth rate (Fig. 3d).

After day 21, the chick enters the crèche period and the food supplied by the parents doubles (Fig. 3a, solid line). Mass gain by the chick is rapid (Fig. 3b, solid line), with the chick increasing in mass by a factor of 3 in 30 days. Net growth rate during the crèche period is higher than that during the brood period (Fig. 3d). The assimilation rate exceeds the respiration rate by about 50% at day 25 and this difference narrows to about 10% by day 50 (Fig. 3c). Chick mass loss occurs during the last 3 days of the simulation as the food supply is decreased (Fig. 3b, solid line). During this period, respiration losses exceed assimilation and the net growth rate becomes negative (Fig. 3d).

The maximum mass attained by the chick in this simulation was 3.44 kg at day 51 (Table 2). However, by the time the chick fledged at day 54, its mass had reduced to 3.075 kg, which is within the range of limits, 2.75–3.16 kg, measured for fledgling chicks.

Fig. 3 **A** The time distribution of food supply used for the reference simulation (*solid line*). The feeding frequency of the chicks doubled during the crèche period (days 21–51) and food supply was decreased during the last 3 days of the rookery time (days 52–54). *Overlaid* is the time distribution of the food supply suggested by Culik (1994). **B** The simulated chick growth curves obtained for the reference simulation (*solid line*) and the simulation using the time distribution of food supply suggested by Culik (1994) (*dashed line*). **C** Simulated time change in assimilation (*solid line*) and respiration (*dotted line*) rates of the Adélie penguin chick obtained from the reference simulation. **D** Time change in chick net growth for the reference simulation obtained from the difference in assimilated ingestion and respiration shown in **C**. *Dotted lines* represent the point at which the feeding rate of the chick changes



Over the 54 days of this simulation, the total energy derived from krill by the chick was 98 MJ. Of this value, 16.3 MJ are stored as tissue. The remaining 81.7 MJ are lost as either respiration or unassimilated food or excretion. Janes (1997) calculated a total excreta loss for Adélie penguin chicks of 50.2 MJ. Direct comparison of the total loss value from the model and that calculated by Janes (1997) is not possible since the two numbers do not represent identical loss processes. However, the value reported by Janes (1997) provides an order of magnitude comparison.

Effects of food quantity

Observations given in Culik (1994) suggest that Adélie penguin chicks may receive more food in the early crèche period (days 21–44), with a reduction in food amount in the remainder of the crèche period. This feeding pattern (Fig. 3a, dashed line) produces chicks that are heavier (maximum mass of 3.685 kg) than those in the reference simulation (Fig. 3b). However, the mass loss by these chicks is drastic during the last half of the crèche period and the fledge weight of the chick is less, 2.501 kg versus 3.075 kg, at the end of the 54-day simulation (Fig. 3b, dashed line).

The assumption is made in the model that the chicks receive double the amount of food during the crèche period. This assumption is tested by reducing the feeding frequency during this period by half which reduces the total amount of krill delivered to the chick from 24.124 kg to 14.2 kg (Table 2). This food delivery results in chicks that grow slowly and have fledging weights that are considerably less, a 40% reduction, than those obtained in the reference simulation (Table 2). The simulated chick growth is not sensitive to increases in feeding frequency if there is no corresponding increase in the daily food supply.

A second assumption in the model is that the chicks are starved for only their final 3 days in the colony. The effect of this assumption is examined by increasing the starvation period to 6 days. The food supply to the chicks until the starvation time is the same as that used in the reference simulation. However, the increased period of reduced food results in less total krill being delivered to the chick (Table 2). The extended starvation period results in a chick mass loss of 555 g relative to the reference simulation, which results in chicks with maximum weights of 3.246 kg and fledging weights of 2.52 kg (Table 2). Interestingly, if the growth period is shortened (52 vs 54 days) by beginning the starvation period early and the total krill delivered is kept at the value used for the reference simulation, fledging weight actually increases (Table 2). This arises because the period during which the respiratory and assimilation rates approach one another is reduced (Fig. 3c). By comparison, reducing the colony time with a corresponding decrease in total krill produces a smaller chick (Table 2).

Effects of food quality

The measured krill size frequency distribution from the 1988/1989 season (Fig. 1a) potentially has a higher effective energy density (Fig. 2) than that from the 1989/1990 season because of the dominance of the larger, and higher energy density, krill in this season. Thus, the effect of these factors, which alter food quality, on Adélie penguin chick growth was next tested.

Using a food supply modeled on the 1988/1989 krill size frequency distribution results in a simulated chick growth that is higher than that obtained in the reference simulation (Fig. 4). The difference in the simulated chick mass becomes pronounced during the latter portion of the simulation. The food supply based on the 1988/1989 krill size frequency distribution gives a higher maximum chick mass and a heavier chick at fledging. In contrast, the krill size frequency distribution measured in the 1989/1990 season gives simulated chick masses that are only slightly higher than those obtained with the reference simulation (Fig. 4), which used a constant energy density for the krill.

Comparison with observations

The final set of simulations with the chick growth model are attempts to simulate actual field measurements of chick growth made in 1988/1989 and 1989/1990. The simulations for the 1988/1989 season used a food supply that was based on the krill size frequency distribution in the corresponding diet samples and a variable krill energy density. From about day 20 onward, these simulations accurately reproduced the trend in chick growth observed in the 1988/1989 measurements made at Humble Island (Fig. 5a) and Torgersen Island (Fig. 5b). However, the simulated mass for the oldest chicks is at the upper range of values measured at both sites.

Simulations for the 1989/1990 season, however, underestimate chick mass over the entire growth period at both locations (Fig. 5c, d). The degree of mis-match in

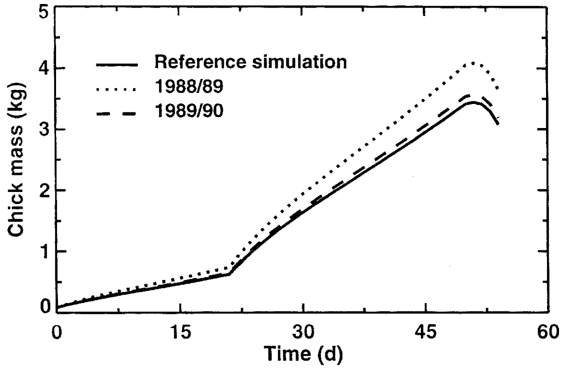


Fig. 4 Comparison of the simulated chick growth obtained using the 1988/1989 (*dotted line*) and 1989/1990 (*dashed line*) krill size frequency distributions shown in Fig. 1A and B, respectively, with that from the reference simulation (*solid line*)

observed and simulated chick mass is largest during the first 20 days of chick life. If food supply is not the cause for the discrepancy between simulated and observed chick masses, then other factors, such as changes in metabolic processes or in behavior, must be compensating to result in the observed chick masses.

Increasing chick assimilation efficiency from 0.80 to 0.85 results in an overall increase in simulated chick mass at both colonies (Fig. 5c, d, dotted line). A decrease from 20% to 10% in the time that the chick is active gives the same result (Fig. 5c, d, dotted line). In both cases, the correspondence between the simulated and measured chick masses is improved for chicks older than 20 days, but the simulated masses are still at the lower end of the measured values. Increasing chick assimilation efficiency at the same time that activity level is decreased results in increased chick masses and an increase in fledging weight of 436 g (Fig. 5c, d, dashed line). This simulation better matches the range of observed chick masses during the 1989/1990 season. However, none of the modifications to metabolic processes increased chick mass during the first 20 days to the level of observed values.

Discussion

Chick fledging weight

The simulations described in the previous section show that the quantity, quality, and timing of food delivery to the Adélie penguin chick by the parents have large effects on mass gain by the chick. Reaching a fledging weight of 2.8–3.2 kg requires that a chick receives about 25 kg of krill food during the growth period. Providing this amount of food to the chick is done with two feedings by the parents within a 24-h period during the crèche period. Decreasing the feeding frequency to one meal per day, and hence the total amount of krill delivered to the chick, resulted in chicks that were low in mass (Table 2). Chicks of this size would not be expected to survive to fledge.

Other simulations in which the total food amount is reduced by as little as 2.8 kg over the growth period (21.30 kg vs 24.12 kg) result in chicks with fledging weights that are lower than the observed range (Table 2). These simulations suggest that there is a lower threshold to the total amount of krill that a chick needs during the growth period in order to attain an optimal fledging

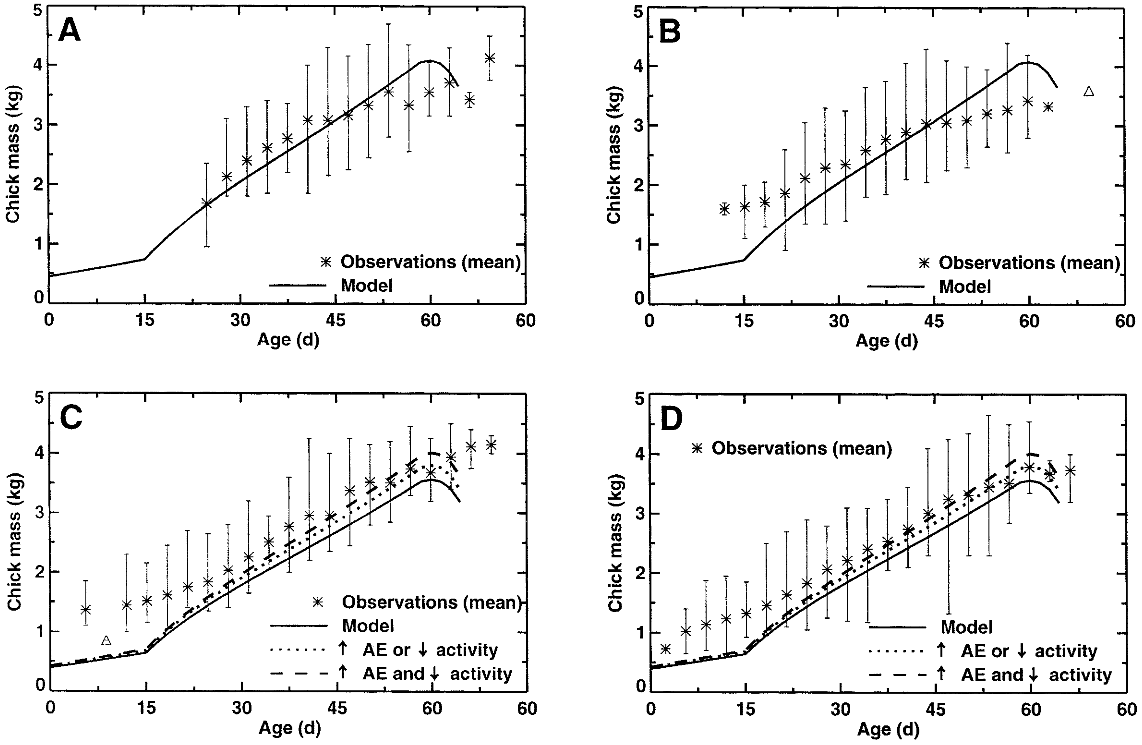


Fig. 5 Simulated growth of Adélie penguin chicks for **A** Humble Island, and **B** Torgersen Island produced using the food supply based on the krill size frequency distribution measured in the 1988/1989 diet samples. Simulated growth of Adélie penguin chicks for **C** Humble Island and **D** Torgersen Island produced (*solid line*) using the food supply based on the krill size frequency distribution measured in the 1989/1990 diet samples. Increasing the assimilation efficiency (*AE*) from 80% to 85% or decreasing activity time from 20% to 10% result in similar simulated patterns of chick growth (*dotted line*). As a comparison, the simulated chick growth resulting from increasing *AE* and also decreasing chick activity time is shown (*dashed line*). The mean of the observed chick weights (*) and the maximum and minimum limits of the measured chick weights (*vertical bars*) at specific ages are shown for each location and each year. Chick age was estimated from culmen length using Eq. 1 in Table 1. Single measurements of chick weight are represented by Δ and data points with no chick mass range indicated represent multiple values of the same weight. Note that the period over which chick age was measured is different in 1988/1989 (**A**, **B**) and 1989/1990 (**C**, **D**)

weight. It is estimated that a chick needs 21.3 kg of fresh krill, if energy density of regurgitated krill is taken to be a constant value of 20.4 kJ (g dry mass)$^{-1}$, with a water content of 80%, in order to reach the mass of 2.8 kg, which is the observed minimum fledging weight value. Small deviations from this total amount result in reduced chick growth, and probably survival, since these chicks that do fledge are at masses not likely to be conducive to survival at sea.

Increasing the total amount of food delivered to the chick is not necessarily good. A 16% increase in integrated food mass resulted in a heavier chick during the brood and crèche periods relative to the reference simulation (Fig. 3b, dashed line), but the fledge weight was less. In this case, the potential benefits of increased mass are offset by the increased metabolic demands of a heavier chick during the latter part of the crèche period when the food delivery by adults is reduced (Fig. 3a, dashed line). In this simulation, the fledge weight is less than the lower values observed.

The increased food simulation also shows that the timing of food delivery to the chick is critical. The maximum food supply to the chick occurs around day 35 (Fig. 3a, dashed line), at a time when chick growth rate is high, but also at a time when the difference between assimilation and respiration rates is decreasing (Fig. 3c) due to the increased respiratory costs of the larger chicks. The constancy in chick mass (days 33–43) following the increase in food supply suggests that, during this time, assimilation and respiration rates are essentially equal. Thus, the added benefit of increased food is offset by increased respiration demands. Alternatively, providing additional food earlier in chick development may allow the chick to reach its optimal mass earlier during mid-crèche, thereby offsetting the effects of reduced food supply during the starvation period.

The 54-day growth period seems to be an optimal time for chicks to reach a fledging weight that potentially enhances the likelihood of their survival upon leaving the colonies. Shortening the growth period by beginning the starvation phase earlier resulted in chicks with a fledging weight that is less than observed (Table 2). These chicks are beyond their metabolic point of no-return and are likely to die even if food becomes available. Extending the growth period by beginning the starvation period later (not shown), simply allows heavier chicks to develop. In these simulations, the chicks exceed the observed upper masses for fledgling chicks. Shortening or extending this period may be deleterious to chick survival.

The quality of the krill fed to the chicks is also important. The size frequency distribution of krill and the corresponding energy value are important factors determining the energetic gain by the chick. Diets composed of small krill with low caloric value produce chicks that are lighter at fledge (Fig. 4, dashed line) than those grown on diets of larger and higher-caloric-content krill (Fig. 4, dotted line). This simulation suggests that there is a threshold total energy value that is needed by the Adélie penguin chick. This threshold value is also dependent on the krill size other than total krill mass. Thus, years in which small krill dominate within the feeding range of adults may require more frequent feeding of the chicks by the adults in order for the chicks to attain an optimal fledging size. Years characterized by larger krill may require less frequent feedings. Limited observations of krill distributions in the region around Anvers Island suggest that there is a spatial gradient in krill size, with larger krill located further offshore (Siegel 1988; Lascara et al. 1999). Such a krill distribution will potentially affect foraging trip duration, as well as the food quality supplied to the chicks.

Humble and Torgersen Island simulations

The simulations of chick mass for the Humble and Torgersen Island Adélie penguin colonies that used the 1989/1990 krill length frequency distribution to define the food supply, suggest that factors other than food quantity and/or quality were contributing to produce the observed chick masses (Fig. 5c, d). In the simulation, the frequency at which the adults feed the chicks is time-invariant throughout the brood and crèche periods. Thus one possibility is to allow feeding frequency to increase with time, which will give an overall increase in total food supplied. If foraging trip durations were shorter at the start of the crèche period (higher provisioning rates) than later in this period, the chicks would receive more food earlier and the result would be overall larger chicks. Foraging trip durations for 1989/1990 provide some evidence that this may have occurred (Fraser and Ainley 1990). However, other variations in metabolic processes, such as increased assimilation efficiency, decreased activity, or a combination of both, are equally likely explanations for maintaining relatively constant fledge weights for the Humble and Torgersen Island penguin chicks, as suggested by the simulations. Ricklefs et al. (1987) suggested that chicks can regulate their consumption of energy and change their metabolic rate depending on the quality and quantity of the food supplemented. The smaller krill with low energy density, available in 1989/1990, may have produced such a response in the penguin chicks. The 5% increase in assimilation efficiency needed for the simulated chick masses to match observed masses at these locations is within observed variations for Adélie penguins (Kooyman et al. 1982; Davis and Darby 1990).

Reducing metabolic demands by decreasing overall activity is a common strategy for animals coping with stress. Observations to confirm that the Adélie penguin chicks adopted this strategy in 1989/1990 are not available, but this is strongly suggested by the simulations. For conditions in which sufficient food is supplied, e.g., 1988/1989 season (Fig. 5a, b), the effect of chick activity is to lower overall chick mass and fledging weight, but this effect is not strong enough to prevent the chicks from reaching a mass that is optimal for fledging.

However, under adverse conditions of insufficient food or food of lower quality, the period that the chick is active is a strong determinant of final fledging weight.

Thermoregulation is another factor that potentially affects the comparisons between the simulated and observed chick growth at the Torgersen and Humble Island penguin colonies. The 1988/1989 and 1989/1990 observations were made during a time when the Antarctic Peninsula region was moving into the next major ice cycle and temperatures were getting progressively colder (W.R. Fraser, unpublished data). The energy loss by the chicks to thermoregulation processes, which are not included in the model, could explain the higher simulated chick masses for the older chicks at Humble and Torgersen Islands in 1988/1989, relative to observations. In the 1989/1990 season, the effect of thermoregulation on chick weight may have been masked by the effects of reduced food quality and quantity. Therefore, thermoregulation effects are likely only important in some years, as suggested by Chappell et al. (1990). However, it is an important component of understanding interannual variability in Adélie penguin chick growth in relation to climate variability.

The mis-match in observed and simulated chick masses in the first 20 days of the Humble and Torgersen Island simulations may result from too little food being provided to the chick or metabolic losses that are too high, both of which result in reduced growth. The frequency at which the adults feed the chick is specified to be 1.7 times per day. The model-data comparison allows the possibility that feeding during this time is more frequent and/or more food is given per feeding. Conversely, metabolic losses during this time may be reduced through lowered activity or reduced thermoregulation losses because of the parent brooding the chick. The exact cause of the difference in simulated and observed weights of chicks remains to be determined, and the simulations suggest that measurements of metabolic processes for chicks of age 20 days and younger are needed. Culmen length to chick age conversion becomes less accurate as culmen growth slows in older chicks, possibly causing some discrepancy between simulated and observed mass for the larger chicks.

Future directions

The development of the chick model and the simulations with this model identified gaps in our knowledge of the physiology, biology, and ecology of Adélie penguins. Primary among these is the need to collect field observations of chick feeding frequency, adult foraging trip duration, and adult stomach content as a function of chick age. Additionally, experimental measurements are needed to define Adélie penguin chick assimilation efficiency in terms of food quantity, food quality, and chick age. Also, field studies that provide estimates of chick activity level within the context of environmental conditions are needed. Studies of Adélie penguin chick growth energetics need to be concurrent with measurements of the energy content of Antarctic krill as a function of size and possibly gender, because gravid females potentially contain higher energy value per gram tissue (Nicol et al. 1995). Addressing these needs will permit further development of quantitative models for this species.

The simulations described above show clearly the importance of food quantity and quality in determining chick growth and the ability of the chick to reach an optimal fledging weight. This provides a direct linkage between Adélie penguin chick survival and environmental conditions that alter the availability and size distribution of Antarctic krill. Thus, future studies of the biology and ecology of Adélie penguin chicks need to include aspects of the marine, as well as terrestrial, environments.

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