



## Linking food availability, body growth and survival in the black-legged kittiwake *Rissa tridactyla*

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### ABSTRACT

Population dynamics of black-legged kittiwakes *Rissa tridactyla* in Bering Sea colonies are likely to increasingly experience climate-induced changes in the physical environment. Since adult kittiwakes are central place foragers with high energy requirements, increased variability of forage patch dynamics, as predicted for polar regions, may influence both quantity and quality of food available and consequently alter the population dynamics of kittiwake colonies. Here, we describe, conceptualize, and model the effects of environment and energy resources on kittiwake growth, fledging age (from 35 to 50 days) and survival from hatching up to first breeding (post-hatching productivity). For our life-history model, we use a von Bertalanffy growth function for body growth in mass. We model nestling mortality as a function of somatic growth, in order to account for oxidative damage and trade-offs in the allocation of resources, and energy available, since low food availability increases the risk of chicks' starvation and predation risk. In the case of a good environment (i.e., high food availability), the best strategy (i.e., highest post-hatching productivity) is to grow fast (about 18.6 g d<sup>-1</sup>) and to spend a moderately long time in the nest (up to 45 days), while in the case of a poor environment the best strategy is to grow fast (about 18 g d<sup>-1</sup>) and leave the nest soon (35–40 days). Different ages at first breeding do not change the optimal strategies. We discuss the implications of optimal growth strategy in terms of evolution of life histories in kittiwakes and how our work, coupled with models of post-breeding survival and reproductive dynamics, could lead to the development of a full life-history model and the exploration of future evolutionary trajectories for traits like body growth and age at first breeding.

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### 1. Introduction

Understanding and predicting the temporal and spatial dynamics of populations is a fundamental issue in ecology. In the Bering Sea, populations of seabirds (the black-legged kittiwake *Rissa tridactyla* and the thick-billed murre *Uria lomvia*) are either declining (St. Paul) or are stable (St. George) on the Pribilof Islands and are increasing at Bogoslof Island (Byrd et al., 2008). The three islands have peculiar environmental conditions: St. Paul is a shelf colony that is closest to the maximum edge of the winter ice; St. George is located near the shelf edge, and Bogoslof is an oceanic colony. One of the hypotheses concerning these differences is that the population dynamics of seabirds in these colonies are affected by climate-induced changes in the physical environment, which controls forage patch dynamics (i.e., spatial or temporal heterogeneity of food availability) and thus may alter both quantity and

quality of food for seabirds (Ciannelli et al., 2005; Byrd et al., 2008; Coyle et al., 2011). However, how individual and population dynamics of seabirds will change in response to climate change is still unclear.

Models building from the effects of the behavior of individuals on their survival, growth and reproductive success, to the outcomes emerging at the population level, have already shown particular promise in explain observed temporal patterns of population dynamics and predicting consequences of alteration of climate, and habitat and food availability (Hollowed et al., 2009; Jenouvrier et al., 2009; Barbraud et al., 2011; Wolf et al., 2010; Jenouvrier and Visser, 2011; Jenouvrier et al., 2012; Satterthwaite et al., 2012).

Recently, different studies have investigated the post-fledging survival and reproductive behavior of seabirds using long-term datasets and novel statistical methods (e.g., Steiner et al., 2010; Aubry et al., 2011; Desprez et al., 2011). However, less attention has been given to the nestling phase and its carry-over effects to the subsequent life stages. It is well known that early environmental influences are more likely to lead to irreversible or at least less reversible modification of phenotypes (e.g., West-Eberhard, 2003).

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Harsh environmental conditions can have important consequences for survival and life-history traits of seabirds, and this may depend on the life-stages at which the individuals are exposed to them (Starck and Ricklefs, 1998 ch. 14). In particular, when sub-optimal or harsh conditions are experienced during the developmental stage, they may not only have immediate effects on the organism, but can have long-lasting consequences (Metcalfe and Monaghan, 2001). In seabirds, based on both observations and experiments, this corresponds to the time before fledging (e.g., Cam and Aubry, 2011; Coulson, 2011). Cam and Aubry (2011) provided a critical analysis on whether there is evidence of long-term fitness consequences of early conditions in long-lived birds and they concluded that whether early conditions have long-term fitness consequences is still ambiguous.

In seabirds, although heavier fledglings may be more likely to survive, growth in mass (we will use mass and weight interchangeably in this work) is only one component of nestling development that might affect juvenile survival. For example, in addition to being more likely to survive to recruitment, larger and better-developed seabird fledglings might be younger at recruitment (Sedinger and Flint, 1995 for Black Brant *Branta bernicla*). This correlation suggests that mass at fledging reflects the quality of the individual (Ludwigs and Becker, 2006) or conditions at recruitment (Sedinger and Flint, 1995), or both. If slower growth or low fledgling mass results in decreased condition later in life (Metcalfe and Monaghan, 2001), then light and/or small fledglings may be constrained or restrain themselves from breeding at an early age (Curio, 1983). However, there are trade-offs in the allocation of resources. For instance, the development of the immune system is probably energetically costly (e.g., Moreno, 2003), and an individual may be forced to trade the costs of immune suppression against allocation of energy to growth.

However, understanding the response to climate change, and the effects of temporal variability in food availability, requires conceptualizing and modeling the effects of environment on chicks' growth and survival and the carry-over effects of the early life history decision on organism's fitness. That is the focus of this paper.

## 2. Material and methods

We focus on the black-legged kittiwake *Rissa tridactyla* and from now on we will refer to it simply as the kittiwake. We limit our analysis to the prebreeding (i.e., immature) phase.

### 2.1. Species description

Seabirds are extremely K-selected species: adult (i.e., post-breeding) survival is generally high, and annual reproductive output is low. Many species delay first breeding until several years old.

Kittiwakes occur in both the North Atlantic Ocean and North Pacific Ocean and present differences in life histories and demographic traits according to a latitudinal gradient (Coulson, 2011). Most of the information both at the population and individual level comes from colonies living in the North Atlantic (Coulson, 2011), while less information is available for colonies of the North Pacific (but see Kitaysky et al. 2000; Piatt, 2002). However, most of the life histories can be considered equivalent for the scope of the present work and thus in general we do not explicitly differentiate between them.

The kittiwake is a pelagic seabird wintering at sea whose adults usually come back annually to breed on vertical cliffs on the coastline. Individuals show high overall site fidelity. Breeders tend to lay one- or two-egg clutches in Alaska, while in North Atlantic

colonies three-egg clutches can be observed (Coulson, 2011), and chicks remain in the nest until nearly adult size.

The food of breeding kittiwakes has been shown to vary markedly from year to year both in quality and quantity (Jodice et al., 2008).

## 2.2. Overview of kittiwake life cycle

### 2.2.1. Nestling phase

The weight of kittiwake chicks at the time of hatching is around 33 g (Coulson, 2011), for colonies of North Shield, UK; 33.3±2.0 g, (Bech et al., 1984), for colonies of Svalbard, Norway; 30 g, (Maurder and Threlfall, 1972), for colonies of Gull Island, Newfoundland; 35–40 g, (Merkling et al., 2012), for colonies of Middleton Island, Alaska). The maximum (peak) weight of the chick coincides with the approach of fledging and is similar to the weight of adults (peak weight is about 96% of adult weight according to Maurder and Threlfall (1972)). Kittiwakes reach peak weight some days before fledging, and they have lost around 10% of it at fledging (Coulson, 2011). For kittiwakes in the North Shields (UK), Coulson (2011) found that between 75 and 300 g the growth rate ( $\text{g d}^{-1}$ ) was virtually constant for an individual and averaged for males  $16.7 \text{ g d}^{-1}$ , with maximum growth around  $18 \text{ g d}^{-1}$ . Kitaysky et al. (2000) found that mean growth rates (6–22 days post-hatch) of kittiwakes breeding on the Pribilofs (Alaska) varied between 13 and  $16.7 \text{ g d}^{-1}$ . Piatt (2002) found growth rates at Gull and Barrens colonies (Alaska) between 16 and  $18 \text{ g d}^{-1}$ . On the contrary, chicks at the Chisik colony (Alaska) grew substantially slower ( $11\text{--}14 \text{ g d}^{-1}$ ) and they were probably strongly food-limited. For kittiwakes living in Middleton Island (Alaska, US), maximum body growth of male chicks (i.e., maximum slope of the growth curve) in 2006–2009 was between 20 and  $22 \text{ g d}^{-1}$  with peak mass around 450 g (Merkling et al., 2012). Females grow more slowly than males and reach a lower peak mass before fledging (Coulson, 2011; Merkling et al., 2012).

Seabirds experiencing harsh conditions during development, such as high parasite load, severe weather or low food availability, may exhibit smaller mass at fledging or independence, lower survival probability in the first year after fledging, and lower reproductive success (Braasch et al., 2009 for common terns *Sterna hirundo*; Cam and Aubry, 2011 provide a review for seabirds).

Fledging success (fraction of hatched chick successfully fledging) is generally high for kittiwakes, and is in part a consequence of the greater safety from predators arising from cliff-nesting. Over a 30-year period, Coulson and Thomas (1985) found fledging success consistently greater than 80% for colonies in the North Shields, UK. Hamer et al. (1993) found for kittiwake colony of Sumburgh Head (Shetland, England) in 1990 and 1991 a fledging success of 0% and 85%, respectively. Gill et al. (2002) found fledging success of about 50% for kittiwakes laying eggs in Middleton Island (Alaska). However, Barrett and Runde (1980) found fledging successes as low as 20% in some Norwegian colonies. Kitaysky et al. (2010) found that fledging success was consistently low on Duck Island (Cook Inlet, Alaska) from 1996 to 2000, ranging from 0 to 3.6%, and likely to be caused by low food availability.

Time at fledging is variable in kittiwakes and it has been linked to post-fledging survival (Cam et al., 2003), although it is not clear whether it is a direct effect of it or a longer developmental period allows for a greater body size or mass at fledging. According to data reported in Coulson (2011) for North Shields colonies, the number of days from fledging to hatching was from 35 to 50 days, with an average of 41.5 days. Similar results were reported by Coulson and White (1958), Maurder and Threlfall (1972), Mular and Danchin (2008) and Merkling et al. (2012).

### 2.2.2. Post-fledging

Very little is known about the behavior and risk of mortality of kittiwakes during their pelagic pre-reproductive period. However, the main causes of death for kittiwakes during the pelagic phase are likely to be starvation and disease (Coulson, 2011).

A positive relationship between condition or weight at the time of fledging and post-fledging survival has been reported for a variety of bird species (e.g., Krementz et al., 1989; Tinbergen and Boerlijst, 1990; Gaston, 1997), but there are also species where no such relationships was observed (e.g. Kersten and Brenninkmeijer, 1995; Olsson, 1997).

Here, we provide a simple quantitative framework to analyze how food availability, body growth during the nestling phase, length of the developmental period (fledging time or age) may interact to define post-hatching productivity of kittiwakes. Since the effort required to monitor seabirds' population is enormous due to their peculiar life cycle, we also want to provide additional information to biologists on the traits and parameters most critical for seabirds' individual dynamics along with predictions to be empirically tested.

### 2.3. The model

We use a simple life-history model to illustrate how, conditioned on the energy available for the chick, body growth rate in weight during development and length of developmental period (i.e. fledging age, in days since hatching) may determine productivity of kittiwakes. We divide the life history of the kittiwake in two phases: a nestling phase and pre-breeding (i.e., immature) phase. To simplify the model, we consider a single male kittiwake hatching in a nest (singleton). The nestling environment is characterized by a measure of energy available  $E$ , which has immediate effects on fledging weight and mortality during the nestling phase. Starck and Ricklefs (1998 ch. 17) suggest that the logistic, Gompertz, and von Bertalanffy growth models are appropriate to describe body growth in mass during the nestling phase. The body growth rate of chicks during the linear phase of growth is a parameter commonly used to examine spatial and temporal effects of changes in food availability on the reproductive performance of seabirds. Clearly, body growth is not a single trait, but it is the outcome of a complex suite of behavioral, morphological and physiological processes.

### 2.3.1. Body growth

We use the von Bertalanffy growth model to describe the nestling growth in body mass of chicks, since its parameters can be more readily interpreted in term of bio-energetic determinants than those of the other growth models (Mangel, 2006). In the von Bertalanffy model, the growth in weight  $W$  ( $\frac{dW}{dt}$  in weight time $^{-1}$ ) results from the difference between anabolism, which is proportional to  $EW^{\frac{2}{3}}$ , and catabolism, which is proportional to  $kW$ , where  $E$  is the coefficient of anabolism and  $k$  the coefficient of catabolism (i.e. cost of growing):

$$\frac{dW}{dt} = EW^{\frac{2}{3}} - kW \quad (1)$$

According to Eq. (1), the individual will reach an asymptotic weight ( $\frac{E}{k}$ )<sup>3</sup>.

If  $W_0$  is the weight of chick at age 0,  $k$  is the von Bertalanffy growth parameter (it is a rate, but not a growth rate since the unit of measure is  $t^{-1}$ ), and  $E$  can be interpreted as a measure of the energy to be available to the chick during the nestling period (Mangel, 2006) (Fig. 1), the weight of chick at time  $t$ ,  $W_t$ , is equal to:

$$W_t = \left[ \left( \frac{E}{k} \right) \left( 1 - \exp \left( -\frac{k}{3} t \right) \right) + W_0^{\frac{1}{3}} \exp \left( -\frac{k}{3} t \right) \right]^3 \quad (2)$$

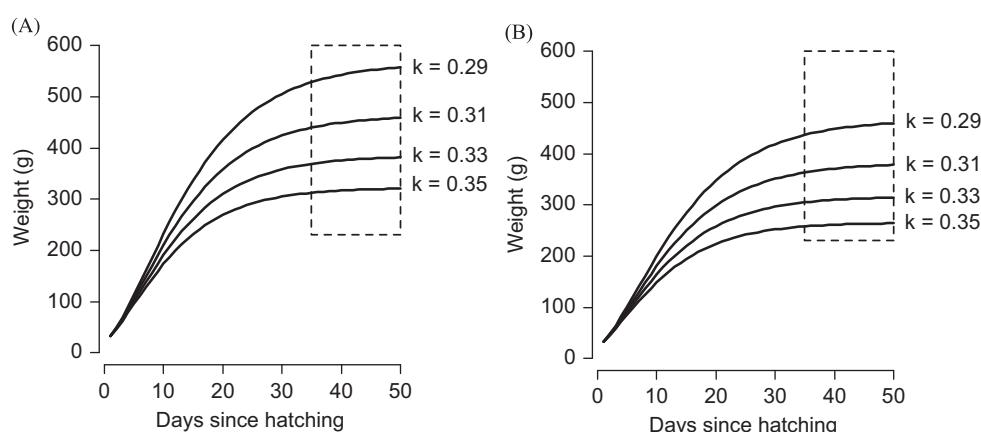
For simplicity, we did not model the residual body growth after fledging and we assumed that weight at fledging remained constant through the lifetime of the bird (Maurder and Threlfall, 1972; Helfenstein et al., 2004). In addition, to simplify the model we did not include the loss of weight after it peaks before fledging.

### 2.3.2. Nestling mortality

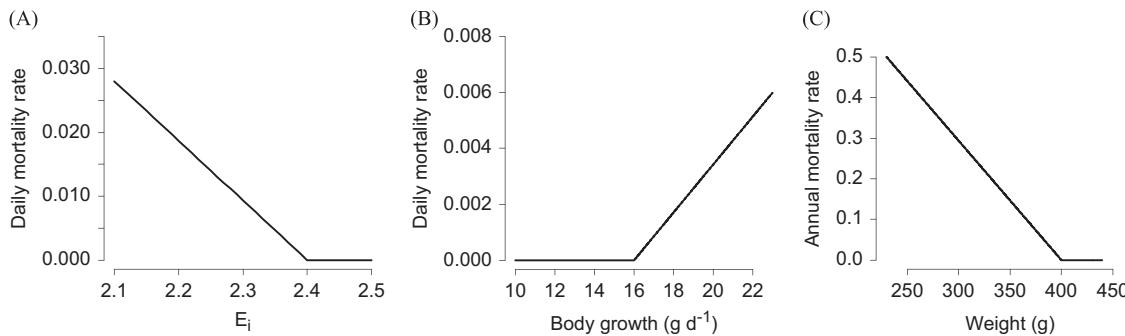
Juvenile mortality risk is typically modeled as an increasing function of body growth rate to reflect the conflict between reaching a large body size and using calories and nutrients for maintenance and development of other functions (e.g., immune system, repair).

We model the daily rate of mortality  $m_N$  during the nestling period  $N$  having contribution from different components. First, there is a baseline of mortality characterized by rate  $m_0$ . Second, we include a component  $m_E(E)$  related to the energy available during the nestling period. Third, we include a component  $m_G(G)$  related to body growth representing: (a) the conflict between somatic growth and development of other functions, and (b) oxidative damage. Therefore:

$$m_N = m_0 + m_E(E) + m_G(G) \quad (3)$$



**Fig. 1.** von Bertalanffy growth curves where weight (g) of kittiwake chick at time  $t$  (d) is  $W_t = \left[ \left( \frac{E}{k} \right) \left( 1 - \exp \left( -\frac{k}{3} t \right) \right) + W_0^{\frac{1}{3}} \exp \left( -\frac{k}{3} t \right) \right]^3$ , with (A)  $E=2.4$ , (B)  $E=2.25$ , with  $k$  varying from 0.29 to 0.35  $t^{-1}$ . The rectangle identifies a window of opportunity for fledging. The chick must trade-off the time in the nest, where body growth is possible, but potentially the mortality rate is higher, and fledging (equivalent to independence in our model), after which the risk mortality is usually lower, but there is virtually no body growth. In our model, post-fledging mortality decreases with increasing weight at fledging.



**Fig. 2.** Functional forms for (A) daily mortality period in the nestling phase related to energy available (i.e., risk of death for starvation or increased predation risk due to low attendance of parents), (B) daily mortality rate in the nestling phase related to growth (i.e., oxidative damage and/or incomplete development) and (C) annual mortality rate related to weight of kittiwake for the pre-breeding phase.

where  $G$  is the mean realized growth rate ( $\text{g d}^{-1}$ ) between day 5 and 15 of the growth period (i.e., where growth is approximately linear, Fig. 1, Coulson, 2011; Merkling et al., 2012), depending on both  $E$  and  $k$ . In Fig. 2, we show the functional forms of  $m_E(E)$  and  $m_G(G)$ .

We assume that mortality increases with a reduction of energy both for direct effects (starvation risk), and indirect effects, such as an increase in predation risk when parents are at sea more frequently due to food scarcity (Fig. 2a). We assume that mortality increases with increasing growth rate (Fig. 2b). This may be interpreted as physiological damage due to oxidative stress (Halliwell and Gutteridge, 1999). In addition, the rate of development of certain body structures may constrain the growth rates of other structures or functions or induce costs related to rapid growth (Starck and Ricklefs, 1998). Similarly, rapid growth may result in compromised morphology, such as suboptimal body proportions, increased fluctuating asymmetry, and skeletal deformities (see Arendt, 1997, for a general review; Starck and Ricklefs, 1998 ch. 12, specifically for birds).

Assuming that survival at hatching is 1,  $t_F$  is the number of days from hatching to fledging (i.e., fledging age), and that  $E$  and  $k$  are time-independent, survival to fledging  $S(F)$  is:

$$S(F) = \exp(-m_N t_F) = \exp\{-[m_0 + m_E(E) + m_G(G)]t_F\} \quad (4)$$

Days from hatching to fledging can vary from 35 to 50 days (Coulson, 2011). Although kittiwakes reach independence some days after fledging (approximately 11 days, Mulard and Danchin, 2008), to simplify the model we consider the fledging age equal to the time of independence. Thus, in our model there is a window of opportunity for fledging (Fig. 1). It is clear that the chick must trade-off the time in the nest, where body growth is possible, but potentially the mortality rate is higher, and fledging, after which the risk mortality is usually lower, but body growth basically stops.

### 2.3.3. Post-fledging mortality

We model post-fledging and pre-breeding mortality  $m_{PF}(a)$ , where age  $a$  ranges from 0 to 6, as:

$$m_{PF}(a) = m_A(a) + \frac{m_W(W_F)}{l(a)} \quad (5)$$

where  $W_F$  is mass at fledging,  $m_W(W_F)$  is a decreasing function of  $W_F$  (Fig. 2c),  $m_A(a)$  is the age-dependent mortality rate and  $l(a)$  is an increasing function of age representing “learning” or “experience”. In our model, learning or experience allow the mortality due to low body weight to decrease with age. Studies provide some evidence of a higher risk of mortality in the first year after independence (Callum and Coulson, 1990), and it is likely that during that first days and months after leaving the nest higher body mass, and a consequent higher resistance to starvation, may be particularly favorable.

We parameterized the models using a pattern-oriented procedure (Grimm et al., 2005) and data from Coulson (2011), Desprez et al. (2011) and Merkling et al. (2012) for male kittiwakes.

### 2.3.4. Productivity

Post-hatching productivity  $\phi(k, t_F | \alpha)$  (from now on simply productivity) is the survival from hatching to age at first breeding  $\alpha$ , where age at first breeding is fixed and thus not a results of the dynamics that the model describes. With  $\alpha=0$ , productivity is equal to  $S(F)$ . If  $\alpha \geq 1$ :

$$\phi(k, t_F | \alpha) = S(F) \prod_{a=0}^{\alpha-1} \exp[-m_{PF}(a)] \quad (6)$$

Therefore, given  $E$  defining energy/food available for kittiwakes related to food availability, and age at first breeding  $\alpha$ , we explore the productivity of kittiwakes with different von Bertalanffy growth parameter  $k$  and days spent in the nest  $t_F$  (i.e. fledging age).

## 3. Results

The parameter space for this model is rich (Table 1) and a full exploration of the model is clearly beyond the scope of this work. Hence, we present the results of a number of particular cases to illustrate the main insights that the model provides for the link between food availability, body growth and productivity.

We fix body weight at hatching at 33 g. We use numerical simulations to find the combinations of von Bertalanffy coefficients  $E$  and  $k$  (Eq. (2)) that allow body growth rates and mass at fledging to be comparable to what is observed in nature (Fig. 1). Body growth in mass rapidly increases a few days after hatching and then approaches a plateau in the time window for fledging. With increasing von Bertalanffy growth parameter  $k$ , both growth rate  $G$  and asymptotic weight  $(\frac{E}{k})^3$  decrease, and the growth plateau is approached earlier (Fig. 1).

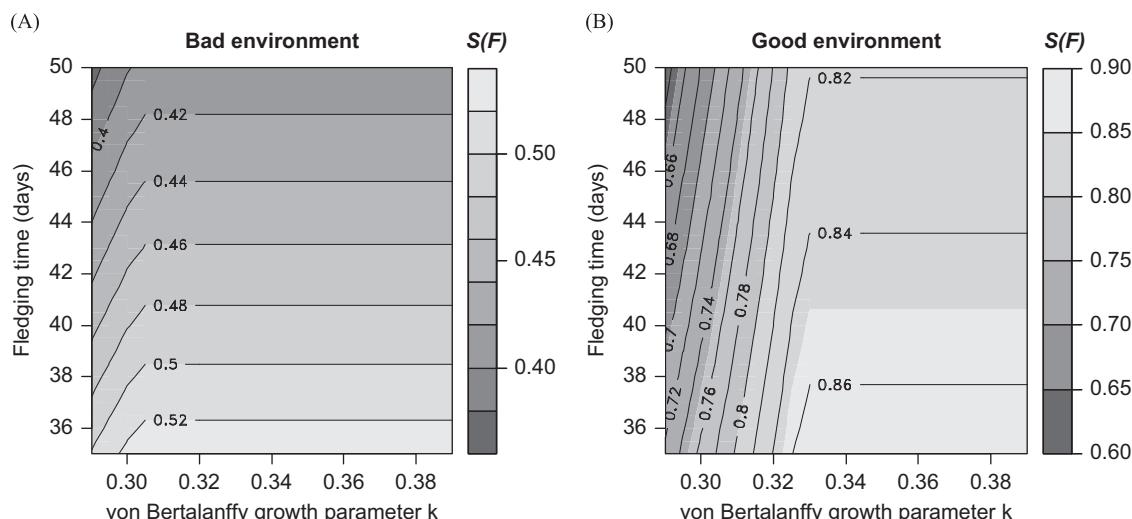
When feeding conditions are good (“good environment”,  $E_i=2.4$ ), there is no mortality due to starvation and/or low attendance of parents increasing predation. Growing fast comes at a cost (Fig. 2b) and the survival probability of fast growers (low  $k$  values) is lower than for slow growers (high  $k$  values) and decreases with fledging age (Fig. 3).

Apart from the extreme case of very fast growth and prolonged nestling phase (i.e., top left of Fig. 3a), survival probabilities are consistently greater than 0.65. On the contrary, when feeding conditions are not optimal (“bad environment”,  $E=2.25$ ), survival probabilities to fledging are flat over different values of  $k$ , that is, basically independent of the rate of body growth, and increase with fledging age (Fig. 3b).

**Table 1**

Values and description of the parameters used in the model.

Parameter	Value	Description
$E_i$	2.1–2.4	Energy/food available in the environment
$k$	0.29–0.39	von Bertalanffy growth parameter ( $t^{-1}$ )
$t_F$	35–50	Fledging date or age (d)
$m_o$	0.004	Base daily mortality rate in the nestling phase( $t^{-1}$ )
$m_E$	0.028	Daily Mortality due to starvation and/or low attendance of parents when energy is minimum ( $t^{-1}$ ) (see Fig. 2)
$m_G$	0.006	Daily Mortality rate due to fast growth (oxidative damage and/or incomplete development) in the nestling phase when growth is maximum ( $t^{-1}$ ) (see Fig. 2)
$m_W$	0.5	Annual mortality rate related to weight in the post-fledging phase when weight is minimum ( $t^{-1}$ ) (see Fig. 2)
$m_A(0)$	0.3	Age-specific post-fledging mortality
$m_A(1)$	0.2	
$m_A(2)$	0.2	
$m_A(3)$	0.2	
$m_A(4)$	0.3	
$m_A(5)$	0.3	
$I(0)$	1	Age-specific factor related to "experience" or "learning" of the Kittiwake
$I(1)$	2	
$I(2,3,4,5,6)$	3	
$\alpha$	3–5	Age at first breeding (y)



**Fig. 3.** Survival up to fledging  $S(F)$  with different von Bertalanffy growth parameter  $k$  (from 0.29 to 0.39) and time at fledging (from 35 to 50 days since hatching), with (A) bad environment ( $E_i=2.25$ ) and (B) good environment ( $E_i=2.4$ ). Body growth  $G$  in  $g d^{-1}$  (mean body growth between days 5 and 15 since hatching) increases with decreasing values of  $k$ . The range of survival is different in the two plots for easier interpretation of results.

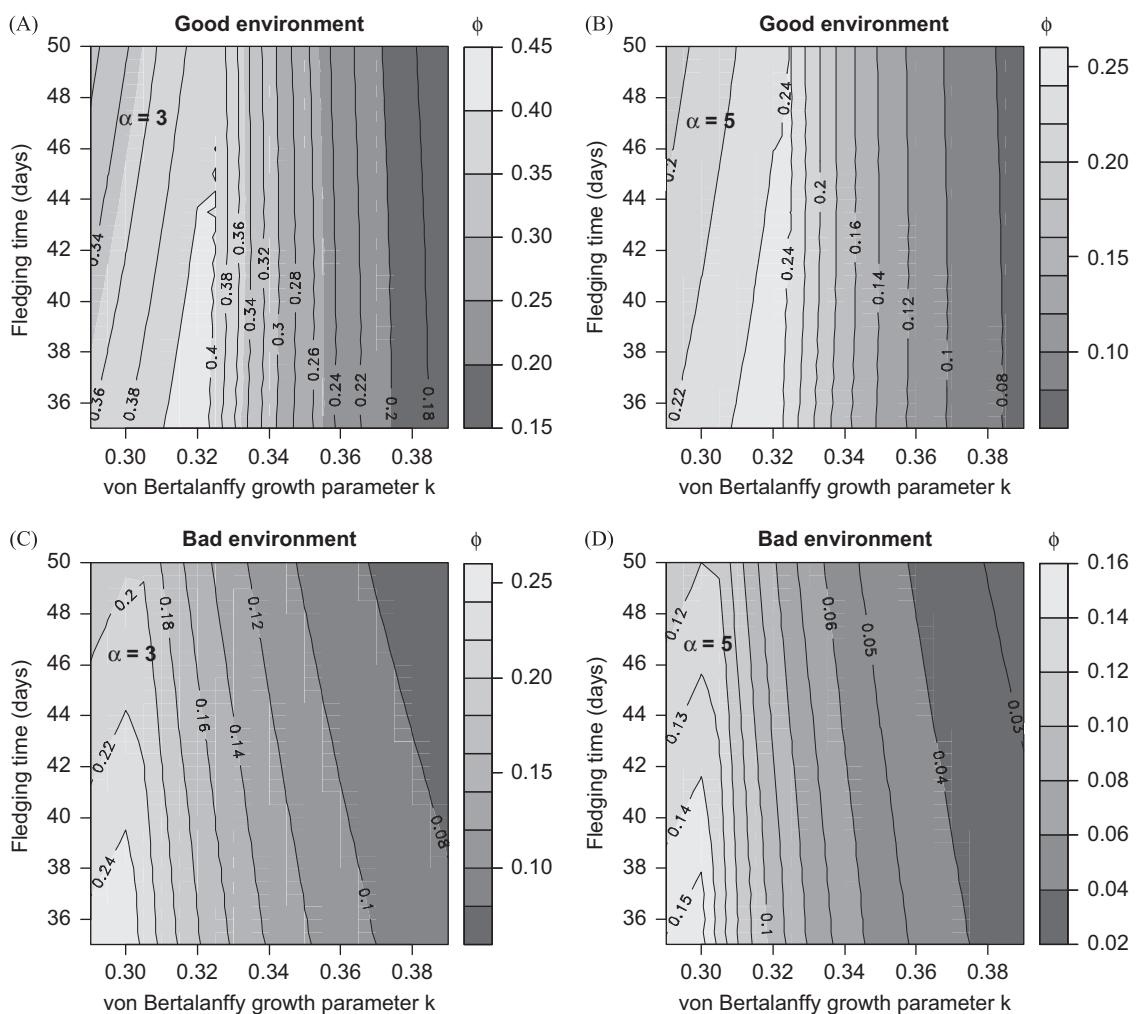
However, the picture changes when we consider productivity, that is survival from hatching to age at first breeding (Fig. 4). In the case of good environment, maximum productivity is reached by kittiwakes that grew moderately fast during the nestling phase for between 35 and 45 days, thus reaching a weight at fledging of about 450 g (Fig. 2c and Table 2). This allows the individual to pay lower mortality costs than faster growers and to be able to reach an optimal weight (i.e., for which no post-fledging mortality costs are paid) at fledging. The same picture is basically conserved when the age at first breeding is either 3 (Fig. 4a) or 5 years old (Fig. 4b), with individuals growing slowly during the nestling phase displaying the minimum productivity.

When feeding conditions during the nestling phase induce energy-dependent mortality (Fig. 2a), individuals with the faster growth during the nestling phase, but with the shortest length of time spent in the nest, have the highest productivity when first breeding is either at age 3 or 5 (Fig. 4c,d, Table 2). Those individuals can thus reach the optimal weight at fledging and at the same time pay lower costs due to the poor environment during nestling. Clearly, this depends on the relative costs of growing too fast, that is of increasing oxidative damage and/or allocating a

suboptimal amount of resources to the development or use of other function, and of spending time in a poor environment with consequent risks of starvation or predation. When survival post-fledging does not depend on body weight at fledging ( $m_W = 0$ ), the patterns of survival at fledging of Fig. 3a and b are conserved post-fledging.

#### 4. Discussion

The intuition emerging from our results is that in the case of good environment it pays to grow fast and to spend a moderately long time in the nest, while in case of poor environment the best strategy is to grow fast and leave the nest soon. In this case, growth refers to the value of the parameter  $k$  of the von Bertalanffy model, since the realized growth in  $g d^{-1}$  depends on both  $k$  and  $E$ . Our model provides predictions that can be empirically tested (Table 2). As chicks' growth rates are often used as a proxy of food availability, in order to avoid circular reasoning predictions may be more rigorously tested using experimental set-ups in which food availability is manipulated (Gill et al., 2002).



**Fig. 4.** Productivity  $\phi(k, t_F|\alpha)$  (i.e., survival from hatching up to age at first breeding  $\alpha$ ) with (A) and (B) good environment ( $E_i=2.4$ ), and (C) and (D) bad environment ( $E_i=2.25$ ), where age at first breeding  $\alpha$  is 3 or 5 years old. The range of productivity is different in the two plots for easier interpretation of results.

**Table 2**

Predictions of the model that can be empirically tested. Male (singleton) chicks are predicted to have a slightly slower realized growth during the linear growth phase (between day 5 and 15) in a bad (i.e. non-optimal) environment than in a good environment and a similar peak mass before fledging. Kittiwakes are predicted to fledge (slightly) sooner when conditions are bad.

Predicted trait	Good environment	Bad environment
Growth in mass during the linear phase ( $\text{g d}^{-1}$ )	18.62	17.99
Peak mass (g)	440–454	440–450
Fledging age (d)	35–45	35–40

According to our modeling results, prolonging the nestling phase often decreases productivity of kittiwakes and a different age at first breeding does not change the optimal body growth strategies (Fig. 4). Cam et al. (2003) found that longer developmental time increased fitness in kittiwakes living in colonies in Brittany, France. They used length of the rearing period as a surrogate for parental effort, but since they did not control for either fledging weight or body growth, we are unable to tease apart the different contribution of somatic growth and parental effort on fitness. Similarly, Coulson (2011) found an apparent (i.e. birds can survive, but fly to other colonies or not be observed) important effect of nestling body growth rate on post-fledging survival. When growth rate was higher, so was the proportion of birds that survived to return at the

colony at least a couple of years later. However, since the effect of growth rate was not estimated controlling for body size at fledging, we are unable to determine whether the apparent lower survival was directly related to growth rate or to a lower body mass at independence.

The decreasing productivity with increasing fledging age we predict is a consequence both of the relative importance of growth-dependent and -independent costs of body growth and the reduced opportunity to grow larger when the chick enters the time window for fledging. In particular, while some growth in the window time for fledging is possible when the von Bertalanffy  $k$  is low (and thus both realized body growth and asymptotic weight are larger, Fig. 1), in the other cases (i.e., increasing values of von Bertalanffy  $k$ ) the plateau in body growth is basically reached when the chick enters the time window for fledging. This is especially true when the environment is poor (Fig. 1b); with scarce feeding opportunities and with low body growth the chick can never reach the minimum body fledging weight that allows it not to pay post-fledging survival costs. However, since there are no costs for slow growth, we observe a fledging success of slow-growing chicks equal (Fig. 3a) or greater (Fig. 3b) than that of fast-growing chicks. Equal survival of slow- and fast-growing chicks has been observed in kittiwakes (e.g., Coulson and Porter, 1985), but in other birds a decreasing survival with depressed body growth in the nest has been reported (Starck and Ricklefs, 1998 ch. 14), mostly due to starvation. However, other studies found

that faster growth can make chicks more susceptible to starvation (Lack, 1968; Starck and Ricklefs, 1998), and that a trade-off between growth rate and energy supply may guide the evolution of nestling growth.

The literature contains conflicting evidence concerning implications of food availability, body growth and body size for survival during the nestling phase. According to Coulson and Porter (1985), for kittiwakes in the North Shields (UK) the risk of dying during the nestling phase progressively declined with the age of the chicks and three-quarters of the deaths occurred during the first two weeks of life. Coulson and Porter (1985) did not find any evident correlation between growth rate in mass and fledging success. The most frequent cause of death for chicks in the North Shields (UK) was associated with hatching and the transition by the parents from incubating to brooding; no predation was observed. The mortality rates of chicks declined as their food requirements increased, suggesting that food shortage experienced by the parents was not a major cause of the chicks' deaths. For Kittiwake populations living in Norwegian islands, Barrett and Runde (1980) found that on one island (Runde) the majority of chicks that died were lighter at the time of death than those which survived 30 days or more. On the contrary, in the islands Hekkingen and Runnesholmen chicks that died weighed nearly the same as, and some were even heavier than the average surviving chick.

However, food shortage is considered to have been the cause of mortality, acting both directly and indirectly. The direct effect was through starvation, and the indirect effect was through an unusually low adult attendance at nests with chicks. Nest attendance is normally 100% during nestling period, but chicks may be left unattended when food availability is low and more feeding flights are required (Coulson, 2011).

According to life-history theory (e.g., Roff, 2002), in general body growth rates and size-at-age are expected to be subject to strong directional selection, since both survival and reproductive success are usually positively correlated with body size at different life-stages in a variety of taxa. However, body growth commonly occurs at rates lower than the physiological maximum (Arendt, 1997), thus implying that (a) growth rates are optimized rather than maximized and (b) slower growth could be favored under certain conditions. Realized growth rate thus results from a compromise between the costs and advantages of growing rapidly, and the optimal rate of growth is not equivalent to the maximum rate.

From a modeling perspective, in the case of an increasing risk of starvation for both fast- and slow-growing chicks, we can substitute the linearly increasing function (after a threshold) of body growth during the nestling phase (Fig. 2b) with a quadratic function increasing mortality costs for both slow- and fast-growing chicks. This will decrease the fledging survival of slow-growing chicks (Fig. 3), but it will not substantially change the general patterns of post-fledging survival, since chicks growing relatively faster show the maximum productivity (Fig. 4).

Longitudinal studies of kittiwake populations have revealed a great diversity in individual life histories within populations and large amounts of phenotypic variation among individuals for traits such as survival, sexual maturity and reproductive output, and reproductive behavior (e.g., skipped breeding) (e.g., Aubry et al., 2011; Coulson et al., 2011). The concept of "quality" (of parents, eggs or offspring) has been used to explain these large differences in individual life-histories and lifetime reproductive success and the concept is now pervasive in studies of the individual dynamics of seabirds (Steiner et al., 2010; Vergara et al., 2010; Coulson et al., 2011; Cam and Aubry, 2011). Since the concept of quality is still ill-defined (e.g., Moreno 2003) and often leads to circular and/or *a posteriori* arguments (e.g., high quality birds defined as birds with

high reproductive success and viceversa), we do not model possible differences in "quality". The relationship between body growth, length of the nestling period and time-dependent mortality in kittiwakes has not yet been resolved. Determining whether the responses of a growing organism are adaptive is central for an understanding of evolutionary processes and for the prediction of future demographic and life-history responses. Starck and Ricklefs (1998) noted that it is important to distinguish between variation in growth and maturation imposed by the environment and those that are induced (i.e., adaptive) in response to environmental cues. Imposed variation may happen when a decrease in food supply during development leads to a stunted, poorly performing individual (Monaghan, 2008; Starck and Ricklefs, 1998). On the contrary, maternal androgen deposition in eggs provides a flexible mechanism the developmental and/or body growth trajectories to prevailing environmental conditions, thus producing different phenotypes (reviewed in Groothuis et al., 2005). In a variety of bird species including seabirds, androgens enhance the frequency of begging display. In manipulative experiments with physiological levels of androgen (i.e., in a range found in nature), chicks from yolks with higher levels of androgens grew relatively fast in terms of body mass and tarsus length (Groothuis et al., 2005). From an adaptive point of view, under poor food conditions mothers may benefit from producing offspring that stimulate paternal feeding by enhanced begging. However, androgen-induced faster growth might be at the expense of the development of immune function – while preserving the development of skeleton and nervous system – especially when resources are limited and thus the problem of resource allocation is more urgent (Groothuis et al., 2005).

Thus, we predict that it is adaptive in a poor environment to induce a fast body growth in chicks (Fig. 4c and d) in order to reach a fledging weight that allows not to pay size-related post-fledging costs, while at the same time fledging early. This picture holds when we assume that the mother has a reasonably accurate knowledge of the energy available for the chick. This assumption motivates some evolutionary considerations. Although body growth in weight ( $\text{g d}^{-1}$ ) changes through development (Fig. 1), we assumed that the growth strategy ( $k$ ) is fixed for the whole growth period and there are no day-to-day changes in the availability of food. It is clear that the relative inflexibility of the body growth strategy is adaptive when the environment is stable and/or when the expected environment and the realized environment coincide, since maintaining growth plasticity is costly for the organism (Auld et al., 2010). However, the variability of both within- and between-years food availability in polar regions like the Bering Sea is predicted to increase with climate change, and this will increase the probability of a mismatch between prediction of environment/resources made by the parents or the chick and actual environment/resources, thus theoretically favoring the evolution of more flexible growth strategy.

Flexible growth rates can be adaptive when food availability fluctuates stochastically. Such flexibility increases the chances of survival chances during food shortages, and the appropriate – in terms of timing and magnitude – induced response when a chick is confronted by a food shortage depends on the severity, duration and predictability of the deprivation. Most seabirds depend on food resources that are intrinsically highly unpredictable with large temporal and spatial variation (Lack, 1968; Schultner et al., 2013). However, it is difficult to determine the immediate and delayed costs of a flexible growth strategy (i.e., costs of adaptive phenotypic plasticity, Auld et al., 2010), the existence of reaction norms (that is, genotype X environment interactions, Davidowitz and Nijhout, 2004), and for how long during development the flexibility can be maintained without compromising other functions.

Other factors may complicate our adaptive view of this situation. First, singletons are rare in kittiwakes (Coulson, 2011) and this may reduce the correlation between the fitness of any single chick and parents' fitness. For example under food restriction, while a single chick may be better served by growing rapidly (Fig. 4c and d), parents are predicted to increase their fitness by reducing the whole growth of the brood in order to reduce the total food requirement (Starck and Ricklefs, 1998). Siblicide, as mediated by food supply, is an important aspect of kittiwake behavior and survival during chick-rearing (Braun and Hunt, 1983). For example, when two or more chicks are produced, androgen concentrations in the yolk increase over the laying order (Groothuis et al., 2005). The later hatched chick competes with older and bigger siblings for food and care (i.e., warmth) provided by the parents. An increase of yolk androgen levels over the laying sequence may function as a maternal tool to diminish the disadvantage of being a late chick, since it may increase begging behavior and thus solicit paternal feeding. In addition, higher androgen levels are predicted to induce a preferential allocation of energy from immune function to growth, adaptively increasing the probability of survival when the chick is the younger sibling.

An opposite pattern of androgen concentration in the yolk (i.e., decreasing with hatching order) can also be adaptive, since it leads to an increased variance in size and growth within the brood that allows parents, in case of food shortage, to sacrifice the smallest chicks before overinvesting in them (Starck and Ricklefs, 1998).

However, adjustments in chick development (growth and time spent in the nest) as well other post-hatching dynamics would likely be of relatively minor importance for the viability of colonies as kittiwakes respond to changes in their food supply.

Hatch et al. (1993) found for Pacific colonies that only 65% of nest-building black-legged kittiwakes produce eggs in an average year, although in the most productive years the mean increases to 80%, and the highest single rate observed was 97%. When colonies fail, that is when the number of chicks fledged per pair is smaller than 0.1, two-thirds of the potential productivity of pairs is removed by a combination of non-breeding and reduced clutch sizes.

Our model of early growth and post-fledging survival, coupled with available models of post-breeding survival and reproductive dynamics (e.g., Desprez et al., 2011; Satterthwaite et al., 2012), allows the development of a full life-history model to explore how environmental processes and heterogeneity in food availability can create different selective environments for body growth, length of developmental period and age at sexual maturation (Vincenzi et al., 2012). This life-history model could also be spatially-explicit to take into account the colony structure, density-dependent processes and the arrival of migrants from other colonies (Coulson, 2011).

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