

1 **Linking food availability, body growth and survival in the**
2 **black-legged Kittiwake *Rissa tridactyla***

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15 **Abstract**

16 Population dynamics of black-legged kittiwakes *Rissa tridactyla* in Bering Sea
17 colonies will be increasingly affected by climate-induced changes in the physical
18 environment. Since adult kittiwakes are central place foragers with high energy
19 requirements, increased variability of forage patch dynamics as predicted for
20 polar regions may influence both quantity and quality of food available and
21 consequently alter the population dynamics of kittiwake colonies. Here, we
22 describe, conceptualize and model the effects of environment and energy
23 resources on kittiwake growth, fledging age (from 35 to 50 days) and survival
24 from hatching up to first breeding (post-hatching productivity). For our
25 life-history model, we use a von Bertalanffy growth function for body growth in
26 mass. We model nestling mortality as a function of somatic growth, in order to
27 account for oxidative damage and trade-offs in the allocation of resources, and
28 energy available, since low food availability increases the risk of chicks'
29 starvation and predation risk. In the case of a good environment (i.e., high food
30 availability), the best strategy (i.e., highest post-hatching productivity) is to grow
31 fast (about 18.6 g d⁻¹) and to spend a moderately long time in the nest (up to 45
32 days), while in the case of a poor environment the best strategy is to grow fast
33 (about 18 g d⁻¹) and leave the nest soon (35-40 days). Different ages at first
34 breeding do not change the optimal strategies. We discuss the implications of

35 optimal growth strategy in terms of evolution of life histories in kittiwakes and
36 how our work, coupled with models of post-breeding survival and reproductive
37 dynamics, could lead to the development of a full life-history model and the
38 exploration of future evolutionary trajectories for traits like body growth and age
39 at first breeding.

40 **Keywords:** black-legged kittiwake *Rissa tridactyla*; patch dynamics; nestling
41 growth; fledging age.

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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 (black-legged kittiwake *Rissa tridactyla* and 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. The current hypothesis 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, 2009; Jenouvrier et al.,

2009; Barbraud et al. 2010; Wolf et al., 2010; Jenouvrier and Visser, 2011;
Jenouvrier et al., 2012; Satterthwaite and Mangel, in press).

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). 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 also have long-lasting consequences (Metcalf and Monaghan, 2001). In seabirds, this corresponds to the time before fledging, based on both observations and experiments (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 et al., 1995 for Black Brant *Branta bernicla*). This correlation may suggest that mass at fledging reflects the quality of the individual (Ludwigs and Becker, 2006) or conditions at recruitment (Sedinger et al., 1995), or both. If slower growth or low fledgling mass results in decreased condition later in life (Metcalf 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 the bird may be forced to trade-off 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 (individuals have been known to have lived for more than 25 years, Coulson, 2011), and annual reproductive output is low. Many species delay first breeding until several years old .

Kittiwakes occurs 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 et al. 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 coast line. Individuals show high

overall site fidelity if they breed. 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 (33g, Coulson, 2011, for colonies of North Shield, UK; 33.3 ± 2.0 g, Bech et al. 1984, for colonies of Svalbard, Norway; 30 g, Maunder and Threlfall, 1972, for colonies of Gull Island, Newfoundland; 35-40 g, Merckling 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 Maunder 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 (g d^{-1}) was virtually constant for an individual and averaged for males 16.7 g d^{-1} , with maximum growth around 18 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 g d⁻¹. Piatt et al. (2002) found growth rates at Gull and Barrens colonies (Alaska) between 16 and 18 g d⁻¹. On the contrary, chicks at the Chisik colony (Alaska) grew substantially slower (11- 14 g d⁻¹) and they were portably 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 g d⁻¹ with peak mass around 450 g (Merkling et al. 2012). Females grow slower 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, 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. Gill and Hatch (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), Maunder and Threlfall (1972), Mulard and Danchin (2008), Merklings 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., Klementz et al., 1989; Tinbergen and Boerlijst, 1990; Gaston, 1997), but there are also species where no such relationships was observed (e.g. Kersten and

182 Brenninkmeijer, 1995; Olsson, 1997).

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

190 **2.3 The model**

191 We use a simple life-history model to illustrate how, conditioned on the energy
192 available for the chick, body growth rate in weight during development and
193 length of developmental period (i.e. fledging age, in days since hatching) may
194 determine productivity of kittiwakes. We divide the life history of the kittiwake
195 in two phases: a nestling phase and a pre-breeding (i.e., immature) phase. To
196 simplify the model, we consider a single male kittiwake hatching in a nest
197 (singleton). The nestling environment is characterized by a measure of energy
198 available E , which has immediate effects on fledging weight and mortality
199 during the nestling phase. Starck and Ricklefs (1998 ch. 17) suggest that the
200 logistic, Gompertz, and von Bertalanffy growth models are appropriate to
201 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 $\left(\frac{E}{k}\right)^3$.

The weight of chick at time t , W_t , is equal to:

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

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

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 (Maunder 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

236 energy available during the nestling period. Third, we include a component
 237 $m_G(G)$ related to body growth representing: (a) the conflict between somatic
 238 growth and development of other functions, and (b) oxidative damage.
 239 Therefore:

$$240 \quad m_N = m_0 + m_E(E) + m_G(G) \quad (3)$$

241 where G is the mean realized growth rate (g d^{-1}) between day 5 and 15 of the
 242 growth period (i.e., where growth is approximately linear, Fig. 1, Coulson et al.
 243 2011; Merklings et al. 2012), dependent on both E and k . In Figure 2, we show the
 244 functional forms of $m_E(E)$ and $m_G(G)$.

245 We assume that mortality increases with a reduction of energy both for direct
 246 effects (starvation risk), and indirect effects, such as an increase in predation risk
 247 when parents are at sea more frequently due to food scarcity (Fig. 2a). We
 248 assume that mortality increases with increasing growth rate (Fig. 2b). This may
 249 be interpreted as related to oxidative damage due to oxidative stress (Halliwell
 250 and Gutteridge, 2007). In addition, the rate of development of certain body
 251 structures may constrain the growth rates of other structures or functions or
 252 induce costs related to rapid growth (Starck and Ricklefs, 1998). Similarly, rapid
 253 growth may result in compromised morphology, such as suboptimal body
 254 proportions, increased fluctuating asymmetry, and skeletal deformities (see

255 Arendt, 1997, for a general review; Starck and Ricklefs, 1998 ch. 12, specifically
 256 for birds).

257 Assuming that survival at hatching is 1 and that E and k are time-independent,
 258 survival to fledging $S(F)$:

$$259 \quad S(F) = \exp(-m_N t_F) = \exp\left\{-[m_0 + m_E(E) + m_G(G)]t_F\right\} \quad (4)$$

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

269 **2.3.3 Post-fledging mortality**

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

$$272 \quad m_{PF}(a) = m_A(a) + \frac{m_W(W_F)}{l(a)} \quad (5)$$

where W_F is mass at fledging and $m_W(W_F)$ 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 in our model. Studies provide some evidence of an higher risk of mortality immediately after independence, 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 Merklings et al. (2012) for male kittiwakes.

2.3.4 Productivity

In our model, post-hatching productivity $\phi(k, t_F | \alpha)$ (from now on simply productivity) is the survival from hatching to age at first breeding α , where age at first breeding is fixed and thus not a results of the dynamics that the model describes:

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

With $\alpha = 0$, productivity is equal to $S(F)$. Therefore, given E defining

energy/food available for kittiwakes related to food availability, and age at first breeding α , 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. Here, 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 out 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 is faster during the first days post-hatching and then approach a plateau in the time window for fledging. With increasing von Bertalanffy growth parameter k , both growth rate G and asymptotic weight $\left(\frac{E_i}{k}\right)^3$ 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 , thus basically independent of the rate of body growth, and increase with fledging age (Fig. 3b).

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, 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 paying 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,b are conserved post-fledging.

4 Discussion

The intuition emerging from our results is that in the case of good environment it pays off 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 parameter k of Von Bertalanffy's 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

348 food availability is manipulated (Gill and Hatch, 2002). According to our
349 modelling results, prolonging the nestling phase often decreases productivity of
350 kittiwakes and a different age at first breeding does not change the optimal body
351 growth strategies (Fig. 4). Cam et al. (2003) found that longer developmental time
352 increased fitness in kittiwakes living in colonies in Brittany, France. They used
353 length of the rearing period as a surrogate for parental effort, but since they did
354 not control for either fledging weight or body growth, we are unable to tease
355 apart the different contribution of somatic growth and parental effort on fitness.
356 Along the same line, Coulson (2011) found an apparent (i.e. birds can survive,
357 but fly to other colonies) important effect of nestling body growth rate on
358 post-fledging survival. When growth rate was higher, so was the proportion of
359 birds that survived to return at the colony at least a couple of years later.
360 However, since the effect of growth rate was not estimated controlling for body
361 size at fledging, we are unable to determine whether the apparent lower survival
362 was directly related to growth rate or to a lower body mass at independence.

363 The decreasing productivity with increasing fledging age we observed in our
364 results is a consequence both of the relative importance of growth-dependent
365 and -independent costs of body growth and the reduced opportunity to grow
366 larger when the chick enters the time window for fledging. In particular, while
367 some growth in the window time for fledging is possible when the von
368 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's 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. At the same time, 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 in terms of implications of food available, 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 was associated with hatching and the transition by the parents from incubating to brooding, and 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 Runneskholmen 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, 2001), body growth rates and size-at-age should 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 modelling 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 would decrease the fledging survival of slow-growing chicks (Fig. 3), but it would not substantially change the general patterns of post-fledging survival, since chicks growing relatively faster show the maximum productivity (Fig. 4).

It is worth noting that 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 seabirds individual dynamics (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. Starck and Ricklefs (1998) noted that it is important to distinguish between variations in growth and maturation (i.e., changes through which tissues and structures approach their post-development morphology and function) imposed by the environment and those that are induced (i.e., adaptive) in response to environmental cues. 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. Imposed variations may happen when a decrease in food supply during development gives rise 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

451 including seabirds, androgens enhance the frequency of begging display. In
452 manipulative experiments with physiological levels of androgen (i.e., in a range
453 found in nature), chicks from yolks with higher levels of androgens grew
454 relatively fast in terms of body mass and tarsus length (Groothuis et al., 2005).
455 From an adaptive point of view, under poor food conditions mothers may
456 benefit from producing offspring that stimulate paternal feeding by enhanced
457 begging. However, androgens-induced faster growth might be at the expense of
458 the development of immune function - while preserving the development of
459 skeleton and nervous system -, especially when resources are limited and thus
460 the problem of resource allocation is more urgent (Groothuis et al., 2005).

461 Based on model results, we predict that it is adaptive in a poor environment to
462 induce a fast body growth in chicks (Fig. 4c,d) in order to reach a fledging weight
463 that allows not to pay size-related post-fledging costs, while at the same time
464 fledging early. This picture holds when we assume that the mother has a
465 reasonably accurate knowledge of the energy available for the chick. This
466 assumption motivates some evolutionary considerations. Although body growth
467 in weight (g d^{-1}) changes through development (Fig. 1), we assumed in our
468 model that the growth strategy is fixed for the whole growth period and there
469 are no day-to-day changes in the availability of food. It is clear that the relative
470 inflexibility of the body growth strategy is adaptive when the environment is
471 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 fluctuate stochastically. The flexibility increases 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 intrinsically highly unpredictable food resources that show large temporal and spatial variations (Lack 1968, Schultner et al. in press). 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.

However, other factors may complicate of our adaptive view. 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,d), parents would 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). It has been observed that 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

512 1998).

513 However, adjustments in chick development (growth and time spent in the nest)
514 as well other post-hatching dynamics would likely be of relatively minor
515 importance for the viability of colonies as kittiwakes respond to changes in their
516 food supply. As noted by Hatch et al. (1993), only 65% of nest-building black-
517 legged kittiwakes produce eggs in an average year. When colonies fail, that is
518 when the number of chicks fledged per pair is smaller than 0.1, two-thirds of the
519 potential productivity of pairs is removed by a combination of nonbreeding and
520 reduced clutch sizes.

521 Our model of early growth and post-fledging survival, coupled with available
522 models of post-breeding survival and reproductive dynamics (e.g., Desprez et al.
523 2011; Satterthwaite and Mangel, in press), allows the development of a full life-
524 history model to explore how environmental processes and heterogeneity in food
525 availability can create different selective environments for body growth, length
526 of developmental period and age at sexual maturation (Vincenzi et al., 2012).
527 This life-history model could also be spatially-explicit to take into account the
528 colony structure, density-dependent processes and the arrival of migrants from
529 other colonies (Coulson, 2011).

530

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684 **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	
$l(0)$	1	Age-specific factor related to “experience” or “learning” of the Kittiwake
$l(1)$	2	
$l(2,3,4,5,6)$	3	
α	3-5	Age at first breeding (y)

685

686 **Table 2** – Predictions of the model that can be empirically tested. Male
 687 (singleton) chicks are predicted to have a slightly slower realized growth during
 688 the linear growth phase (between day 5 and 15) in a bad (i.e. non-optimal)
 689 environment than in a good environment and a similar peak mass before
 690 fledging. Kittiwakes are predicted to fledge (slightly) sooner when conditions are
 691 bad.

Predicted trait	Good environment	Bad environment
Growth in mass during the linear phase (g d ⁻¹)	18.62	17.99
Peak mass (g)	440-454	440-450
Fledging age (d)	35-45	35-40

692

Figure Captions

Figure 1 - Von Bertalanffy growth curves where weight (g) of kittiwake chick at

time t (d) is $W_t = \left[\left(\frac{E}{k} \right) (1 - \exp\left(-\frac{k}{3}t\right)) + W_0^{\frac{1}{3}} \exp\left(-\frac{k}{3}t\right) \right]^3$, 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.

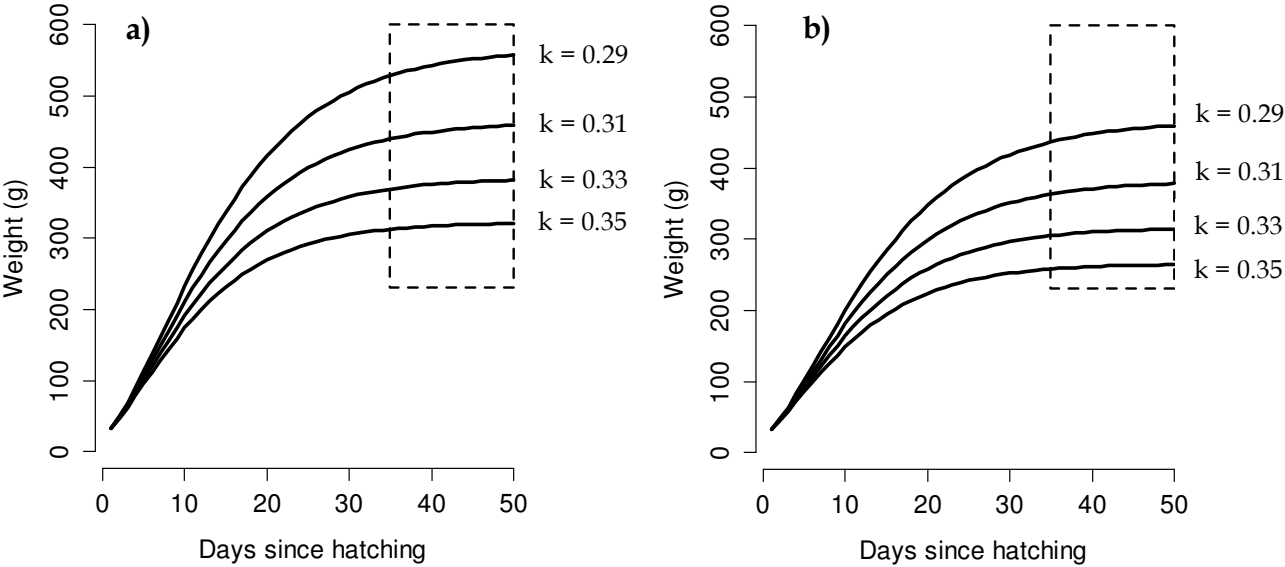
Figure 2 - Functional forms for a) daily mortality period in the nestling phase related to energy available (i.e., risk of death for starvation or increased predation risk due to low attendance of parents); b) daily mortality rate in the nestling phase related to growth (i.e., oxidative damage and/or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

Figure 3 - Survival up to fledging $S(F)$ with variable 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.

Figure 4 - Productivity $\phi(k, t_F | \alpha)$ (i.e., survival from hatching up to age at first breeding α) 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 α is 3 or 5 years old. The range of productivity is different in the two plots for easier interpretation of results.

Figure 1



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Figure 2

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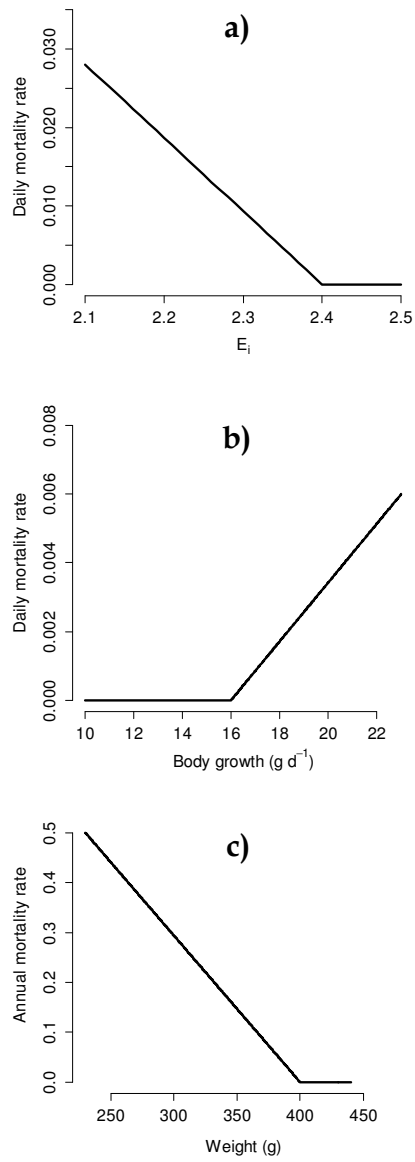
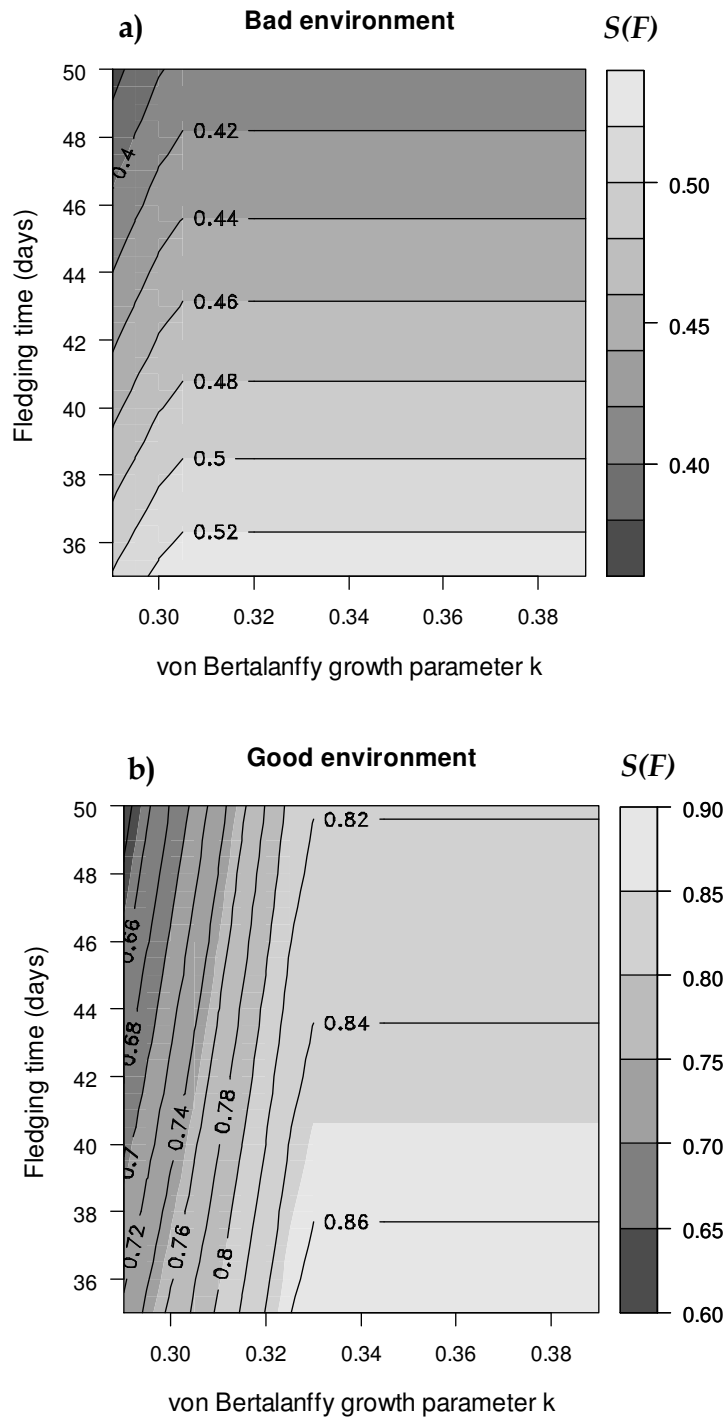


Figure 3



748 **Figure 4**

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