



Seabirds as indicators of marine food supplies: Cairns revisited

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ABSTRACT: In his seminal paper about using seabirds as indicators of marine food supplies, Cairns (1987, *Biol Oceanogr* 5:261–271) predicted that (1) parameters of seabird biology and behavior would vary in curvilinear fashion with changes in food supply, (2) the threshold of prey density over which birds responded would be different for each parameter, and (3) different seabird species would respond differently to variation in food availability depending on foraging behavior and ability to adjust time budgets. We tested these predictions using data collected at colonies of common murre *Uria aalge* and black-legged kittiwake *Rissa tridactyla* in Cook Inlet, Alaska. (1) Of 22 seabird responses fitted with linear and non-linear functions, 16 responses exhibited significant curvilinear shapes, and Akaike's information criterion (AIC) analysis indicated that curvilinear functions provided the best-fitting model for 12 of those. (2) However, there were few differences among parameters in their threshold to prey density, presumably because most responses ultimately depend upon a single threshold for prey acquisition at sea. (3) There were similarities and some differences in how species responded to variability in prey density. Both murres and kittiwakes minimized variability (CV < 15%) in their own body condition and growth of chicks in the face of high annual variability (CV = 69%) in local prey density. Whereas kittiwake breeding success (CV = 63%, $r^2 = 0.89$) reflected prey variability, murre breeding success did not (CV = 29%, $r^2 < 0.00$). It appears that murres were able to buffer breeding success by reallocating discretionary 'loafing' time to foraging effort in response ($r^2 = 0.64$) to declining prey density. Kittiwakes had little or no discretionary time, so fledging success was a more direct function of local prey density. Implications of these results for using 'seabirds as indicators' are discussed.

KEY WORDS: Ecological indicators · Seabirds · Food availability · Threshold · Functional response · Predator–prey dynamics

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INTRODUCTION

Annual global fisheries landings are currently 80 million t, and seabirds worldwide consume similar quantities of fish (Brooke 2004). With such strong dependence on shared resources, it is not surprising that we look to seabirds for additional insights into the status of fish stocks and the health of marine ecosystems (Cairns 1987, Montevecchi 1993, Furness & Camphuysen 1997). For this purpose, seabirds offer many

advantages. They are highly visible at sea, and large numbers gather annually to reproduce at colonies where it is often possible to study the biology of several species in great detail every year.

However, care must be taken when interpreting seabird data as a proxy for fish abundance (Furness & Camphuysen 1997) because different components of seabird biology may respond differently to prey fluctuations, and responses also vary among species. Twenty years ago, Cairns (1987) published a seminal paper in

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which he sought to clarify relationships between seabirds and their food supplies. He predicted that many responses of seabirds to fluctuations in prey abundance would be non-linear, and further, that different parameters such as growth rates, breeding success or survival would respond over different ranges of prey density (around thresholds, Fig. 1). Finally, he predicted that different seabird species would respond differently depending on their diet and ability to adjust time budgets. Cairns had 2 main objectives in his analysis: (1) to 'develop an integrated system of parameter measurement that indicates food availability over the full spectrum of feeding conditions' and (2) 'to stimulate rigorous tests of the proposed relationships' (p. 262).

Since Cairns' paper was published, there have been a few coordinated studies of seabird biology in relation to prey abundance (e.g. Monaghan et al. 1989, 1994, Hamer et al. 1991, 1993, Uttley et al. 1994, Reid et al. 2005, Frederiksen et al. 2006), but none were designed to explicitly test Cairns' predictions. In order to flesh out functional response curves, one needs data collected over a wide range of prey densities (Piatt 1990). For most seabirds and parameters, this has simply not been done (Furness & Camphuysen 1997), owing largely to the cost and technical difficulties of measuring forage fish abundance over the times and spaces relevant to seabird colonies.

Following the 1989 'Exxon Valdez' oil spill in Alaska, understanding how seabirds had responded to concurrent large-scale fluctuations in prey abundance was paramount to understanding the effects of the spill itself (Anderson & Piatt 1999). We therefore used Cairns' hypotheses as a framework for examining relationships between seabirds and their prey in the Gulf of Alaska (Piatt & Harding 2007). Our study constituted a natural experiment to resolve predator-prey functional relationships by studying 3 closely situated colonies with markedly different prey fields over a 5 yr period. These colonies differed in other respects besides local prey density (e.g. prey distribution, colony size), but the signal from spatio-temporal variability in prey abundance overwhelmed other sources of variability, permitting us to resolve many functional predator-prey relationships (Speckman 2004, Piatt & Harding 2007, Harding et al. 2007).

In the present paper, we use results of our natural experiment to test Cairns' (1987) 3 predictions about the form and variation of seabird responses to changes in local prey density. We plot data collected on a dozen different parameters of breeding and behavior from common murre *Uria aalge* and black-legged kittiwakes *Rissa tridactyla* against prey density estimated from hydro-acoustic surveys. We analyze the fit of parameter responses to various linear and non-linear

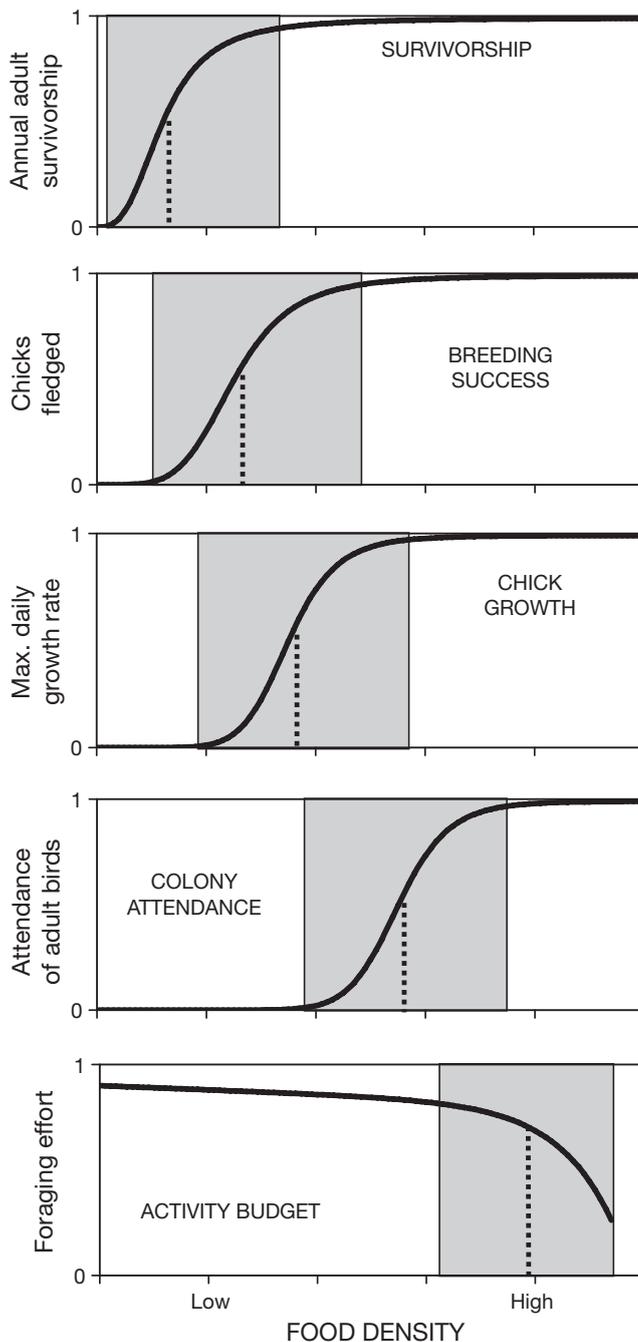


Fig. 1. Cairns' predicted relationships between population and behavioral parameters of seabirds and their food supply. Dashed vertical lines indicate approximate threshold or half-way point in parameter response to change in prey density. Modified from Cairns (1987)

models using regression and AIC analyses, compare thresholds among parameters, and then compare responses and thresholds between murre and kittiwakes. Implications of these results for using seabirds as indicators are discussed within the framework of Cairns' original hypothesis.

MATERIALS AND METHODS

Study sites and rationale. This study was conducted during 5 yr (1995 to 1999) at 3 seabird colonies in Lower Cook Inlet, Alaska (Fig. 2), providing us with 15 colony-years of data for many parameters that we investigated (less for some parameters when it was impossible to collect data, e.g. feeding or growth rates when no chicks were produced). The colonies are separated from each other by about 100 km and are in oceanographically distinct habitats (Abookire & Piatt 2005, Speckman et al. 2005). We confirmed that there were order-of-magnitude differences in forage fish densities among the 3 areas by sampling near shore with beach seines (Robards et al. 1999) and by sampling offshore with mid-water trawls and hydro-acoustic surveys (Abookire & Piatt 2005, Speckman et al. 2005). Four species comprised 99% of the catches in all areas: sand lance *Ammodytes hexapterus* (71%), herring *Clupea harengus* (17.7%), juvenile walleye pollock *Theragra chalcogramma* (8.8%), and capelin *Mallotus villosus* (1.7%), and these fish were also the

overwhelming choice of prey consumed by seabirds at all colonies (Kitaysky et al. 1999, Harding et al. 2002, Jodice et al. 2006, J. F. Piatt unpubl. data).

Local prey density. We measured local fish densities around each of 3 seabird colonies by conducting hydro-acoustic surveys on a grid of transects arranged in most years as shown in Fig. 2, within a 50 km radius of each site (Speckman et al. 2005, Harding et al. 2007). Transects around the Barren Islands were concentrated in the NE quadrant, known as foraging grounds for the majority of murre *Uria aalge* and kittiwakes *Rissa tridactyla* from the Barrens (J. F. Piatt unpubl. data). About 1100 linear km were surveyed in all areas combined each year (except 820 km in 1995) (Speckman 2004). Hydro-acoustic surveys were conducted during a 3 wk period in each year (1995, 10 to 23 August; 1996, 14 to 31 July; 1997, 19 July to 8 August; 1998, 21 July to 12 August; 1999, 25 July to 16 August), usually encompassing periods of late incubation and early chick rearing for common murre (overall colony/year mean date of hatch was 10 August; J. F. Piatt & A. B. Kettle unpubl. data).

Hydro-acoustic data were collected with a single beam 120 kHz BioSonics DT4000 system with a 6° beam angle. Before each cruise the acoustic system was calibrated using a tungsten carbide sphere. To identify acoustic signals and measure the size of individual fish, we conducted 163 mid-water trawls (Abookire & Piatt 2005). Acoustic data were analyzed using SonarData Echoview software (Ver. 2.1) and integrated with a minimum threshold of -70 dB to obtain relative measures of acoustic biomass (S_A). These were converted to absolute estimates of fish density (fish m^{-3}) by dividing S_A by σ (backscattering cross-sectional area of single prey) for species with the following known target strengths (TS): walleye pollock $TS = 21.1 \log(L) - 70.5$, herring $TS = 202.0 \log(L) - 67.6$, capelin $TS = 28.4 \log(L) - 81.8$, sand lance $TS = 20.0 \log(L) - 80$, and cod $TS = 20.0 \log(L) - 65$; which accounted for 99.2% of all fish caught (see Speckman et al. 2005 for TS sources). The proportion of catch, expressed as catch per unit effort, standardized to the number captured per km trawled, was used to convert acoustic backscatter to species-specific fish density ($g m^{-3}$). Geometric mean acoustic densities were calculated from transformed data as the mean ($\log x + 1$) values, and then transformed back to original density units.

Seabird parameters. Density of seabirds at sea was determined from strip transects conducted simultaneously with hydro-acoustic surveys (above). All species of seabirds observed within 150 m on either side of the vessel were counted using protocols described by Gould & Forsell (1989). Average densities on transects were calculated for each species in each area (Fig. 2) and year (except 1995, Speckman 2004).

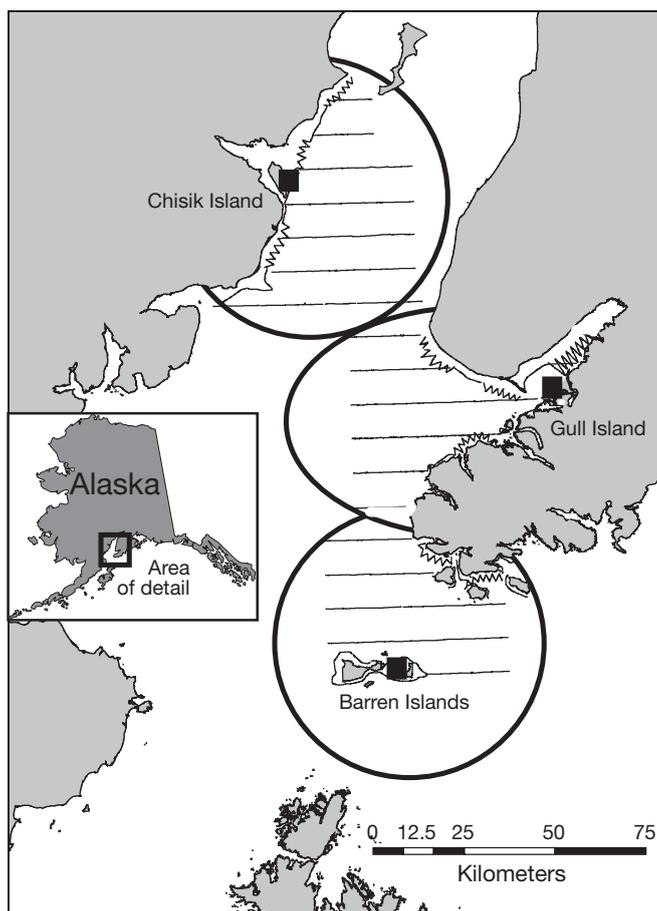


Fig. 2. Study areas in lower Cook Inlet, Alaska. Illustrated are tracks of hydro-acoustic and bird surveys conducted within about a 50 km radius (circles) of each colony

Behavioral activity budgets were determined from all-day observations of 8 to 12 nest-sites of adult murres and kittiwakes at each colony during the incubation and chick-rearing period in each of the 15 colony-years (see Harding et al. 2007 for more details). During observations, the time was recorded for each adult arrival, delivery of prey to chicks (chick-rearing period), exchange of incubation or brooding duty, and adult departure. On Gull (1996 to 1997) and Barren (1997 to 1999) islands, murre observations were recorded by video from first to last light and analyzed later (Zador & Piatt 1999). In most instances, we observed murres and kittiwakes on 3 or more observation-days during incubation and chick-rearing of each year.

From these observations, we calculated average annual rates of nest-site attendance by 1 and 2 adults, chick-feeding rates, and foraging-trip durations. Nest attendance was measured in bird-minutes per nest per h (e.g. a nest with 1 bird attending for a full hour and its mate attending for half of the hour has 90 bird-minutes that hour). Adult provisioning frequency was measured in feedings per nest per h. The mass and species composition of kittiwake chick meals was measured and used to estimate total energy delivered to chicks daily (see Jodice et al. 2006). Analysis of variance indicated that neither nest-site nor observation-day contributed significantly to variability in behavioral parameters in a given year, and we therefore used nest-site as the sample unit. Sample sizes ranged from 20 to 35 nest-site-days watched per island-year (except at Chisik, where kittiwakes failed in all years but 2).

Measures of murre and kittiwake breeding biology were derived from data recorded during regular (3 d average) observations of 20 to 30 nest-sites on 7 to 10 plots scattered around the colony (e.g. Uttley et al. 1994, Suryan & Irons 2001). For kittiwakes, we estimated laying success, clutch size, hatching success, fledging success, brood size at fledging, chick age, and reproductive success. Chicks were considered fledged at 32 d of age. For murres, we estimated hatching success, fledging success, chick age, and reproductive success. Chicks were considered to have fledged if they disappeared from the nest-site >15 d after hatching (minimum fledging age, Gaston & Jones 1998).

We captured or collected both adult and chick murres and kittiwakes at their colonies to measure body size and body mass and to calculate growth rates and fledging condition of chicks. Adult body mass of both murres and kittiwakes was obtained from 2 sources: (1) adults captured at the colony throughout breeding to assess body condition (1997 to 1999) and (2) adults shot near colonies for diet studies (1995 and 1996). Only birds measured during late incubation through early chick-rearing were used to calculate an annual index of body condition, and a minimum of 10 to 35

birds was included in each colony-year estimate. For murres, there was no difference in mean size of birds among colonies (ANOVA, $F_{2,12} = 0.522$, $p = 0.61$), so here we simply present data on body mass. Because kittiwakes are sexually dimorphic and samples were unevenly composed of both sexes, we used the ratio of body mass to wing length as an index of body condition (Benson et al. 2003).

Kittiwake chick growth rates were calculated from a plot of mass versus age during the linear phase of growth, defined as falling between 6 and 22 d of age or between 60 and 300 g of mass (Benson et al. 2003). We tried to measure a total of 30 to 45 kittiwake chicks for growth in each colony and year, but in 6 of 15 possible colony-years fewer chicks were available for measuring and sample sizes ranged from 2 to 16 birds. It was not possible to repeatedly capture and weigh murre chicks without major disturbance, so murre chicks were captured only once immediately after fledging from nests at dusk. Samples were obtained throughout the fledging period (average of 65 chicks per colony during 10 colony-years). An index of fledgling body mass was calculated by dividing mass by wing length, and this serves as a proxy for chick growth rate.

Analysis. Parameters of murre and kittiwake biology were plotted against forage fish biomass to examine the form of each response. Because we were testing Cairns' hypothesis that responses should be non-linear and thresholds should differ among parameters and species, we used least-squares estimation to fit linear and several non-linear models (Reid et al. 2005). Thresholds were estimated from the inflection mid-points of sigmoidal and step functions and as the 50% mid-point of exponential curves (Fig. 1). The potential strength of relationships between forage fish abundance and response parameters was assessed from the r^2 of each regression, and statistical significance was determined from the corresponding F -statistic (Reid et al. 2005). We assumed statistical significance at the $p < 0.05$ level.

Data were fit to 1 linear and 4 different non-linear models, including hyperbolic, sigmoidal (logistic), step, and exponential decay functions. These were the forms predicted by Cairns (1987) and might be reasonably expected from foraging seabirds (Piatt 1990). They also correspond to the Type I (linear), Type II (hyperbolic), and Type III (sigmoid/step) predator-prey functional relationships described by Holling (1959) and commonly observed in vertebrate predators (Murdoch & Oaten 1975).

The following 2-parameter function was used to fit hyperbolic curves:

$$f = (a \times x)/(b + x)$$

where a is the maximum value, b is the dissociation constant, and f starts at zero and rises to a .

The following 4-parameter logistic function was used to fit sigmoidal curves:

$$f = (a - d) / [1 + (x/c)^b] + d$$

where a is the asymptotic maximum, b is the slope parameter ($b < 0$ gives slope > 0), c is the value at inflexion point and d is the asymptotic minimum.

The step function represents a simplification of the sigmoidal curve. A simple box model (Piatt & Methven 1992) of a step function was used to locate thresholds in response plots and estimate goodness of fit (r^2). The model used was:

$$f = k_1 D \text{ if } D > D_T$$

$$f = k_2 D \text{ if } D < D_T$$

where f is the bird parameter value, D is the forage fish density, D_T is the test threshold for forage fish density, and k_1 and k_2 are mean parameter values above and below the test threshold D_T . The best fit (highest r^2) to the step function occurs at the inflection point (Piatt 1990).

A non-linear exponential decay function was used to model negative, declining responses to prey density using the following:

$$f = a \times \exp(-b \times x)$$

where a is amplitude and b is the rate constant.

Whereas regression is useful for determining the strength of possible functional relationships and for identifying thresholds, it was more appropriate to use AIC, adjusted for finite sample size (AIC_c ; Burnham & Anderson 2002) to identify the best-fitting model among several possible alternatives. For positive relationships between seabirds and prey, we compared 5 possible functional models: (1) null—no relationship whatsoever between seabird parameters and food density (slope equals zero), (2) linear (positive slope), (3) hyperbolic, (4) sigmoidal, and (5) a step function. For negative relationships, we compared 3 likely or possible models: (1) null (as above), (2) linear (negative slope), and (3) a negative exponential function.

Each model was statistically represented with a least-squares regression model in which the error sums of squares, sample size, and number of estimated parameters all influenced the AIC_c calculation (Burnham & Anderson 2002). The model with the lowest AIC_c was assumed to best represent the data. Models in which the difference in AIC_c from the minimum value (ΔAIC_c) is < 2 are considered plausible alternative models. For each model, we also calculated an AIC_c weight (w) that reflects the relative likelihood of that model being the best-fitting model among those considered, and in which all AIC_c weights within an analysis sum to 1 (Burnham & Anderson 2002).

RESULTS

Form of responses

For common murre *Uria aalge*, no linear relationships were observed among the 10 parameters investigated (Fig. 3, Table 1). Most (8/10) responses to prey density could be fit significantly with sigmoidal or step functions, 1 response was fit significantly with an exponential decay function, and 2 responses exhibited no significant relationship with prey density. AIC_c analysis confirmed that non-linear models were best among the choices we examined (Table 2) and suggested that 6 of 10 responses were best fit by step, hyperbolic, or exponential functions. AIC_c analysis penalizes models with more equation parameters and small sample sizes, and so ΔAIC_c values and likelihood weights (Table 2) should be considered for alternate models (Burnham & Anderson 2002). The weight of evidence strongly supports null models for body condition, fledging success, and breeding success, and non-linear models for fledgling body condition and attendance during incubation and chick-rearing. Other responses were more ambiguous and could be fit reasonably well by 2 or 3 competing models (Table 2).

These results indicate that for murre, relations between reproductive parameters (hatching, fledging, and breeding success) and food supply were marginal at best. Adult body condition was most independent of food supply, while chick condition at fledging exhibited a strong non-linear relation to food and growth was restricted at low levels of prey density. Foraging trip duration increased in an exponential fashion with decreasing prey density. While the chick-feeding rate was weakly related to prey density, other measures of foraging activity such as density at sea (aggregative response) and discretionary attendance at the nest site during incubation and chick-rearing (time that can be allocated instead to foraging) were strong non-linear functions of prey density.

As for murre, no linear relationships were observed among 12 parameters investigated for black-legged kittiwakes *Rissa tridactyla* (Fig. 4, Table 1). Most (8/12) responses to prey density could be fit significantly with sigmoidal or step functions, 1 response was fit significantly with an exponential decay function, and 4 responses exhibited no significant relationship with prey density. AIC_c analysis confirmed that non-linear models were best among the choices we examined (Table 2), and suggested that 6 of 12 responses were best fit by step, hyperbolic, or exponential functions. The weight of evidence (1) strongly supports null models for attendance, body condition, and clutch size and (2) strongly supports non-linear models for chick growth rate, fledging success, and breeding success.

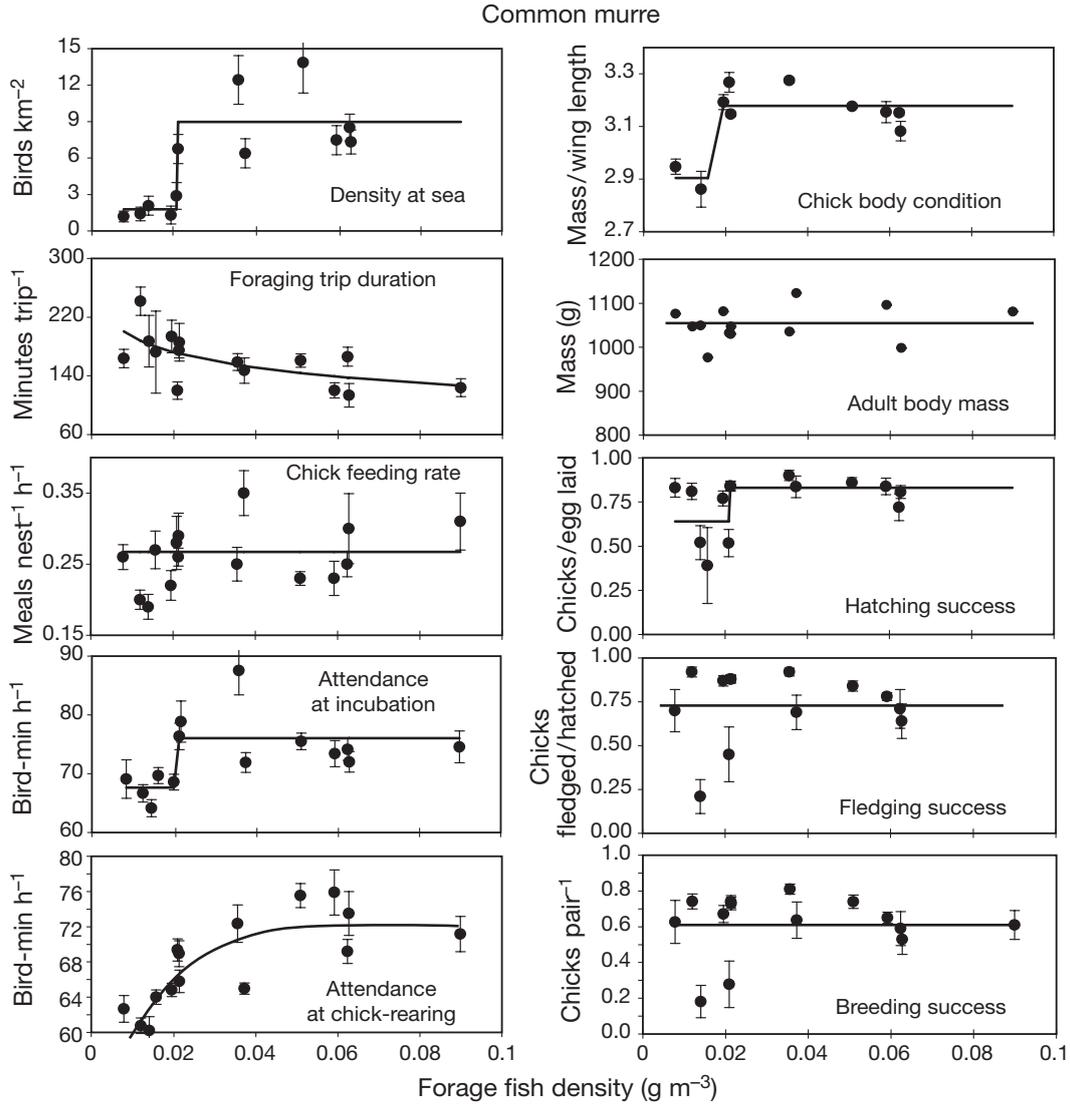


Fig. 3. *Uria aalge*. Response of different parameters of murre biology or behavior to variation in prey density. Graphs include predicted form (solid line) of relationship from the best-fitting model function (null, linear, hyperbolic, sigmoidal, step, or exponential decay) as determined by using Akaike's information criterion adjusted for sample size (AIC_c) analysis

Other parameter responses were more ambiguous, and could be fit reasonably well by 2 or 3 competing models (Table 2), but tended towards either null or linear fits (laying and hatching success, chick feeding rate), or non-linear fits (density at sea, foraging trip duration, brood size).

These results indicate that, in contrast with murres, reproductive parameters for kittiwakes such as fledging and breeding success were strongly related to fluctuations in prey density. Other reproductive parameters such as clutch size, laying success, and hatching success were essentially independent of food supply. Also, in contrast to murres, the discretionary attendance of paired adults at the nest site during chick-rearing did not vary with food supply. As for murres, kittiwake chick condition was markedly reduced at

low prey densities and adult body condition remained remarkably constant over a wide range of prey densities.

The average prey density threshold for all parameters in murres that exhibited significant relationships with prey density ($n = 8$; Table 1) was $0.022 \pm 0.00033 \text{ g m}^{-3}$ and in kittiwakes ($n = 8$) was $0.021 \pm 0.00028 \text{ g m}^{-3}$. A 2-way ANOVA indicated no significant difference in thresholds among species ($F = 3.06$, $p = 0.11$, $df = 1,15$), but a significant difference in thresholds among different types of parameters (see Table 1; $F = 44.6$, $p < 0.001$, $df = 4,15$). This was entirely due to the higher threshold values estimated for foraging trip durations, which differed significantly from all other types of parameters (Tukey test; Act > Gro, Att, Br, and For, $p < 0.05$; see Table 1).

Table 1. *Rissa tridactyla*, *Uria aalge*. Functional relationships between different measures of seabird biology or behavior and prey density, and variability in those measures among colony-years. n = number of colony-years of data. Types of parameters: Att = colony attendance; Gro = body condition or growth; Br = breeding success; Act = activity budget; For = foraging behavior. Relationships were modeled as null, linear, hyperbolic (hyper), sigmoidal (sigm), step, or exponential (exp) functions. w: Akaike weight; ns: not significant. Variability ranked as low (CV < 20%), medium (20% < CV < 40%), and high (CV > 40%), where CV is the coefficient of variation

Parameter	n	Type	Relationship with fish density							Variability	
			Model with highest explained variance				AIC _c best-fit model			CV	Rank
			Form	R ²	p	Threshold	Form	r ²	w		
Black-legged kittiwake <i>R. tridactyla</i>											
Attendance at chick-rearing	11	Att	–	0.03	ns	–	Null	0.00	0.77	7.1	Low
Adult body condition	15	Gro	–	0.00	ns	–	Null	0.00	0.65	7.5	Low
Clutch size	15	Br	–	0.07	ns	–	Null	0.00	0.59	12.3	Low
Chick growth rate (alpha/single)	12	Gro	sigm	0.73	0.012	0.018	Step	0.62	0.57	12.6	Low
Brood size at fledging	11	Br	step	0.59	0.005	0.020	Step	0.59	0.35	13.5	Low
Foraging trip duration	11	Act	exp	0.36	0.048	0.028	Exp	0.36	0.37	22.8	Medium
Laying success	15	Br	–	0.16	ns	–	Null	0.00	0.53	28.7	Medium
Hatching success	14	Br	step	0.30	0.043	0.018	Null	0.00	0.52	37.2	Medium
Chick feeding rate	10	For	step	0.31	0.075	–	Null	0.00	0.65	42.0	High
Forage fish biomass	15	–	–	–	–	–	–	–	–	68.7	High
Density at sea	12	For	sigm	0.86	<0.001	0.021	Hyper	0.68	0.36	72.3	High
Fledging success	13	Br	sigm	0.89	<0.001	0.020	Step	0.89	0.94	81.2	High
Breeding success	15	Br	step	0.63	<0.001	0.020	Step	0.63	0.88	87.0	High
Common murre <i>U. aalge</i>											
Adult body condition	13	Gro	–	0.04	ns	–	Null	0.00	0.72	3.8	Low
Fledgling body condition	10	Gro	step	0.79	0.006	0.018	Step	0.79	0.85	4.2	Low
Chick feeding rate	15	For	step	0.29	0.040	0.020	Null	0.00	0.38	15.5	Low
Hatching success	14	Br	step	0.39	0.016	0.021	Step	0.39	0.36	20.9	Medium
Foraging trip duration	15	Act	exp	0.41	<0.001	–	Exp	0.41	0.51	21.1	Medium
Fledging success	13	Br	–	0.07	ns	–	Null	0.00	0.71	28.3	Medium
Breeding success	14	Br	step	0.23	0.004	0.021	Null	0.00	0.63	29.2	Medium
Attendance at incubation	14	Att	step	0.53	0.003	0.021	Step	0.53	0.59	44.3	High
Attendance at chick-rearing	15	Att	sigm	0.71	0.003	0.020	Hyper	0.64	0.70	65.8	High
Forage fish biomass	15	–	–	–	–	–	–	–	–	68.7	High
Density at sea	12	For	sigm	0.77	0.006	0.021	Step	0.74	0.52	72.4	High

Difference in responses among species

In addition to assessing the form of functional relationships (above), we examined the range in variability of seabird responses (Table 1), as measured by the coefficient of variation (CV).

Forage fish biomass varied about 12-fold among colony-years, with a CV of 79% (Table 1, Fig. 5). In some respects, murre and kittiwakes responded in the same way to this variation in prey density. Both species exhibited similar levels of variability in density of foraging aggregations at sea (up to 20-fold, CV = 72% for both species), which also reflected the variability in forage fish biomass. Despite this large variability in prey biomass, both species exhibited minimal variability in adult body condition or chick growth (<2-fold, CV < 15%) and only moderate variability in foraging-trip duration (ca. 2-fold, CV = 20 to 25%).

Murre and kittiwakes differed dramatically in other respects. Whereas murre maintained low variability in chick-feeding rates (<2-fold, CV = 15%) and moderate levels of variability in hatching, fledging, and breeding success (up to 5-fold, CV = 21 to 29%), kitti-

wakes exhibited much higher levels of variation in chick-feeding rate (up to 5-fold, CV = 42%) and in hatching, fledging, and breeding success (up to 36-fold, CV = 37 to 87%). Also in contrast, kittiwakes exhibited little variation in discretionary attendance of adults at nest-sites (<2-fold, CV < 10%), whereas this was the most variable parameter in murre (up to 30-fold, CV = 65 to 69%).

DISCUSSION

Non-linearity of response

Cairns' (1987) first prediction was upheld: where there was a significant functional relationship with prey density, it was non-linear for parameters such as aggregation at sea, colony attendance, foraging trip duration, chick growth brood size, fledging success, and breeding success. A few studies have demonstrated similar results, albeit with fewer parameters. For example, breeding success in several seabird species has been shown to be a curvilinear function of food

Table 2. *Rissa tridactyla*, *Uria aalge*. Identification of best-fit models using Akaike's information criterion, adjusted for finite sample size. Possible models included linear, hyperbolic (hyper), sigmoidal (sigm), step and negative exponential (exp) functions. The best-fitting model is indicated by $\Delta AIC_c = 0$, but all models with $\Delta AIC_c < 2$ (in bold) and high AIC_c weights relative to other models have substantial support and offer plausible alternative models of functional relationships

Measurement	n	AIC _c weights (w)						ΔAIC _c					
		Null	Linear	Hyper	Sigm	Step	Exp	Null	Linear	Hyper	Sigm	Step	Exp
Black-legged kittiwake <i>R. tridactyla</i>													
Attendance at chick-rearing	11	0.77	0.11	0.11	0.00	0.01	–	0.00	3.86	3.87	16.03	8.71	–
Adult body condition	15	0.65	0.18	0.14	0.00	0.02	–	0.00	2.57	3.06	11.67	6.88	–
Clutch size	15	0.59	0.21	0.14	0.01	0.06	–	0.00	2.05	2.92	9.13	4.65	–
Chick growth rate (alpha/single)	12	0.12	0.02	0.09	0.20	0.57	–	3.05	6.44	3.69	2.11	0.00	–
Brood size at fledging	11	0.24	0.16	0.24	0.01	0.35	–	0.72	1.51	0.75	7.33	0.00	–
Foraging trip duration	11	0.27	0.36	–	–	–	0.37	0.66	0.07	–	–	–	0.00
Laying success	15	0.53	0.26	0.14	0.01	0.07	–	0.00	1.46	2.71	8.93	4.09	–
Hatching success	14	0.52	0.10	0.20	0.01	0.16	–	0.00	3.26	1.87	7.28	2.40	–
Chick feeding rate	10	0.46	0.23	0.26	0.00	0.05	–	0.00	1.40	1.16	13.31	4.61	–
Density at sea	12	0.00	0.25	0.36	0.10	0.28	–	11.72	0.72	0.00	2.49	0.50	–
Fledging success	13	0.00	0.00	0.00	0.06	0.94	–	13.63	15.52	14.55	5.57	0.00	–
Breeding success	15	0.02	0.01	0.01	0.09	0.88	–	7.72	10.04	8.48	4.67	0.00	–
Common murre <i>U. aalge</i>													
Adult body condition	13	0.72	0.13	0.13	0.00	0.02	–	0.00	3.38	3.39	12.95	7.32	–
Fledgling body condition	10	0.06	0.01	0.07	0.01	0.85	–	5.31	8.50	5.09	9.03	0.00	–
Chick feeding rate	15	0.38	0.22	0.23	0.02	0.15	–	0.00	1.07	1.00	6.46	1.79	–
Hatching success	14	0.30	0.19	0.13	0.03	0.36	–	0.36	1.29	2.06	5.27	0.00	–
Foraging trip duration	15	0.05	0.45	–	–	–	0.51	4.82	0.25	–	–	–	0.00
Fledging success	13	0.71	0.13	0.13	0.00	0.03	–	0.00	3.34	3.47	11.95	6.32	–
Breeding success	14	0.63	0.13	0.14	0.00	0.10	–	0.00	3.14	3.00	12.07	3.74	–
Attendance at incubation	14	0.13	0.05	0.18	0.05	0.59	–	3.01	4.86	2.36	4.99	0.00	–
Attendance at chick-rearing	15	0.00	0.14	0.70	0.08	0.08	–	11.48	3.24	0.00	4.35	4.25	–
Density at sea	12	0.01	0.14	0.27	0.06	0.52	–	7.41	2.70	1.33	4.40	0.00	–

density (i.e. Arctic skua *Stercorarius parasiticus*, Furness & Camphuysen 1997; Arctic tern *Sterna paradisaea*, Suddaby & Ratcliffe 1997; and black-browed albatross *Thalassarche melanophris*, Reid et al. 2005), and the aggregative response of common murres *Uria aalge* and Atlantic puffins *Fratercula arctica* to prey schools at sea is sigmoidal (Piatt 1990).

We did not exhaust the list of possible seabird parameters that could be examined (e.g. survival), and we might not have been able to resolve relationships in some parameters, owing in part to small sample sizes and inter-colony sources of variability that were not accounted for in our study (Harding et al. 2007). It is also noteworthy that some parameters were independent of prey density over a wide range of poor to excellent feeding conditions, and this is discussed in more detail below (see 'Poor indicators').

The fact that many of these functional relationships were non-linear demonstrates that, like other vertebrate predators (Murdoch & Oaten 1975), seabirds are constrained by basic physical (e.g. prey dispersion) and biological (e.g. prey quality, assimilation) factors in how efficiently they can exploit local prey resources (Piatt 1990). Constraints may operate at each end of the prey-density spectrum, leading to suppression of a response at low prey densities or a plateau in response

at high prey densities (Holling 1959). Whatever the ecological explanation, non-linearity has practical implications for using seabirds as indicators of prey stocks. Indicators are most useful if they have sensitive and predictable relationships with the environmental feature we wish to monitor over the full, continuous range of environmental variation likely to be encountered (Dale & Beyeler 2001). Unfortunately, our study suggests that few seabird parameters are correlated in a continuous fashion to changes in prey or, at best, they are linearly related over a small range of prey densities.

Different parameter thresholds

Therefore, we are often left with interpreting non-linear seabird responses, which tend to fluctuate rapidly between low and high values over relatively small ranges of prey density. This is still useful, but obviously more limiting. It is also why Cairns proposed using a suite of concurrently measured parameters to assess changes in prey stocks. In order for this to work, however, Cairns' second prediction would need to be true: that different seabird parameters would have differing thresholds to prey density (Fig. 1).

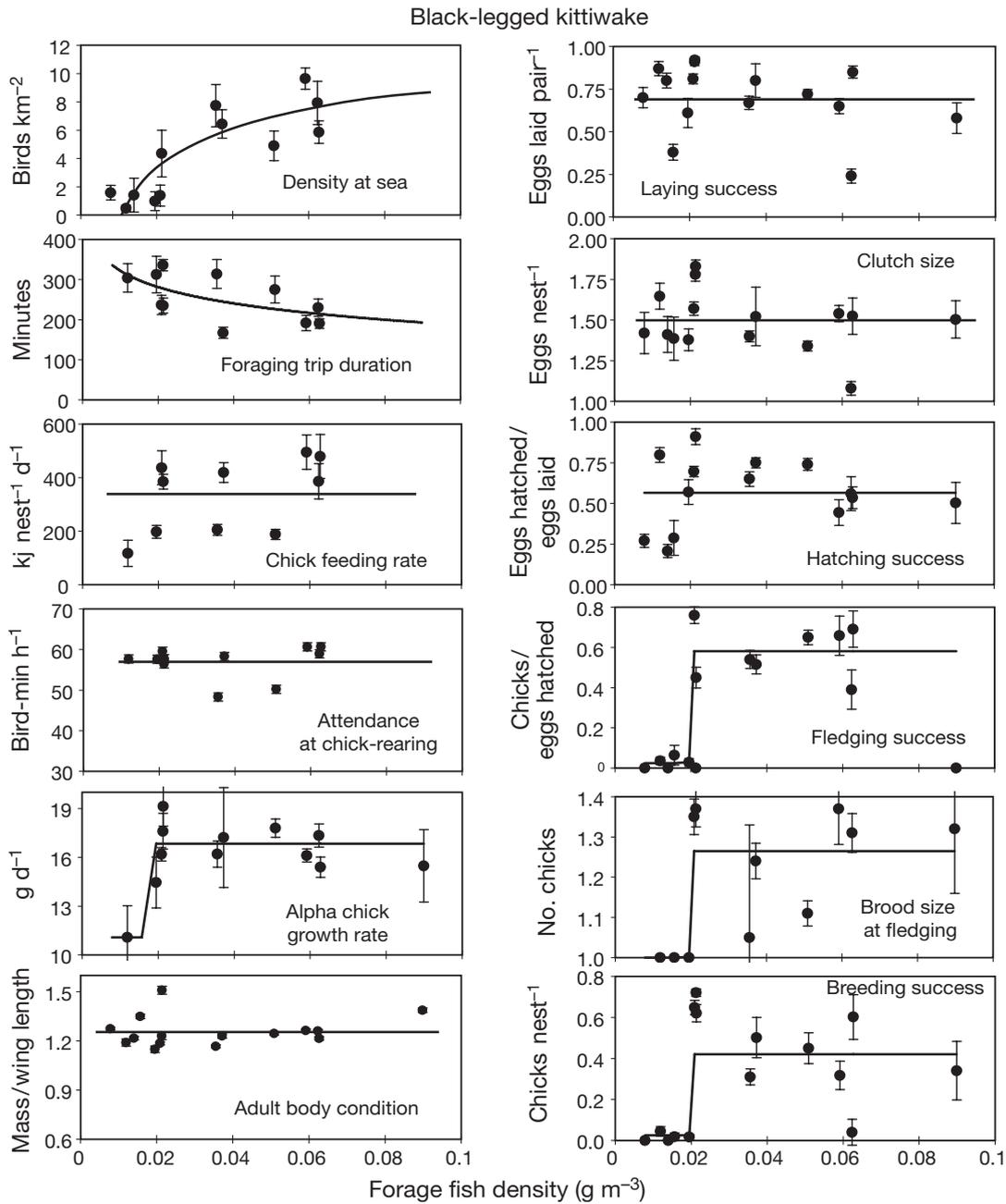


Fig. 4. *Rissa tridactyla*. Response of different parameters of kittiwake biology or behavior to variation in prey density. Graphs include predicted form (solid line) of relationship from the best-fitting model function (null, linear, hyperbolic, sigmoidal, step, or exponential decay) as determined by using Akaike's information criterion adjusted for sample size (AIC_c) analysis

Our results did not provide strong support for this prediction. Mid-point thresholds (inflection points) in our sigmoidal and step response curves (Table 1) were very similar, occupying a narrow range of prey densities (0.018 to 0.021 $g\ m^{-3}$) within the range (0.008 to 0.090 $g\ m^{-3}$) observed during 15 colony-years of acoustic surveys. However, we did observe higher mid-points (e.g. 0.028 $g\ m^{-3}$) in foraging-trip durations of murres *Uria aalge* and kittiwakes *Rissa tridactyla*.

This is consistent with Cairns' prediction that activity budgets would change at higher prey densities in order to buffer foraging success. This was the only parameter type with significantly higher thresholds, but also the only parameter with a threshold measured as the 50% mid-point (in contrast to inflection point).

Aside from this possible exception, why should prey density thresholds for other foraging activities, attendance, chick growth, and breeding success all be the

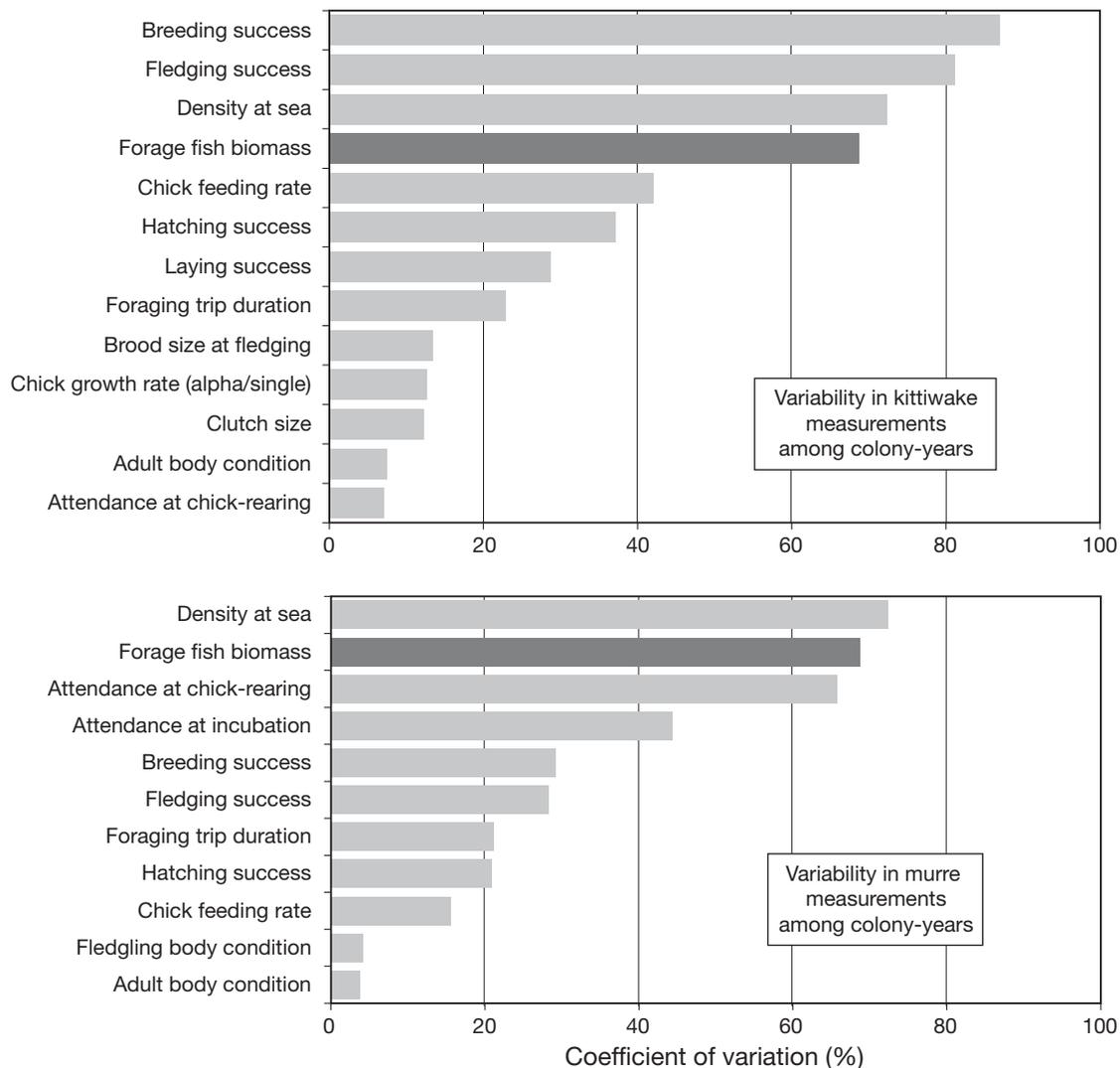


Fig. 5. *Rissa tridactyla*, *Uria aalge*. A comparison of variability among colony-years in different parameters of kittiwake and murre biology and behavior, with respect to variability in the food supply (darker bar)

same? Perhaps because there is only one true physical threshold, and that is the fish school density above which seabirds can successfully acquire food energy at a rate that is sufficient to support daily metabolic demands (Piatt 1990). Tracking of prey at sea (aggregative response) sets the *baseline variability* for all other parameters, because success in prey acquisition (which dictates foraging-trip duration and time-activity budget) depends on success in tracking the prey, and, in turn, all other parameters (chick-feeding rate, chick growth, reproductive success) vary with the rate of prey acquisition and subsequent rate of energy delivery (e.g. Jodice et al. 2006). In contrast to Cairns' prediction, then, we conclude that most response parameters should have the same threshold, rather than a wide range of thresholds, to prey density.

On the other hand, murres can buffer breeding success against declining prey densities by re-directing discretionary colony attendance time towards foraging (Burger & Piatt 1990, Zador & Piatt 1999). Consequently, we observed little or no response in murre breeding success, while attendance time-budgets varied with prey density in non-linear fashion (Harding et al. 2007). In this case, Cairns' prediction was probably correct: a failure in murre breeding success would indicate much lower food supplies than a failure or decline in any other parameter we measured, or at least point to some unusual changes in the environment. For example, recent unusual breeding failures of murres in the North Sea were attributed not to scarcity of prey, but to unusually low (and unexplained) energy value of prey (Wanless et al. 2005).

Differential species responses

We found strong support for Cairns' prediction that different species would respond differently to fluctuations in food supply. In the most extreme example, kittiwake breeding success was strongly influenced by food supply (Table 1) and slightly more variable (Fig. 5), whereas murre breeding success was independent of food supply in our study and less than half as variable. One explanation for this difference is that murre have little difficulty meeting their nutritional needs over a wide range of prey availabilities, and when they do, they simply reallocate some discretionary time to foraging effort in order to buffer their reproductive success (Harding et al. 2007). In contrast, kittiwakes are near their maximum performance limits most of the time and have little or no discretionary time to buffer against a reduction in prey availability.

Consider the differences in morphology, life history, and foraging behavior that account for this differential response. Murres must acquire more food than kittiwakes to sustain themselves each day because of differences in body size (1040 vs. 405 g, respectively, in Cook Inlet), costs of flight (wing loading: 1.86 vs. 0.39 g cm⁻²; Gabrielsen 1994), and foraging (diving vs. surface-feeding). We calculate from measures of field metabolic rates (FMR; Gabrielsen 1994) and assimilation efficiency (87%; Romano et al. 2006) that murres (2.14 kJ d⁻¹ g⁻¹ FMR) and kittiwakes (2.03 kJ d⁻¹ g⁻¹ FMR) feeding on sand lance (5.0 kJ g⁻¹ wet; Van Pelt et al. 1997) would need to capture and eat 512 and 189 g, respectively, of fish per day. This is actually a similar burden for each species because it represents about half their respective body masses.

From this point forward, however, additional daily needs may diverge markedly between species, owing to costs of rearing and feeding chicks (Gabrielsen 1994). The cost of rearing 1 chick increases demand from 49 to 53% of body mass in adult murres (an 8% increase), but from 46 to 67% of body mass in adult kittiwakes (a 46% increase). Adult kittiwakes raising 2 chicks need to acquire 381 g of sand lance daily, or 94% of their body mass (a 104% increase in demand). Since murres lay only 1 egg, and raise chicks to only one-quarter adult mass before fledging, they never incur the same obligation as kittiwakes that often try (and more often fail) to raise 2 chicks in Alaska (Hatch et al. 1993).

Furthermore, even though murres need to acquire 1.5 to 2.7 times more prey biomass daily than kittiwakes, they typically acquire what they need in about half the time. On average, kittiwake foraging trips were about 1.4 h longer than those of murres (typically 2 h) in Cook Inlet, a difference also observed elsewhere (Hamer et al. 1993, Monaghan et al. 1994).

Because murre and kittiwake chicks need about 4 meals per day, the cumulative result is an enormous difference in foraging time-budgets between species. It explains why murres have several hours of extra discretionary time to reallocate to foraging when prey are scarce, while kittiwakes have almost none. The difference may arise from the fact that kittiwakes are restricted to feeding only on organisms found at the sea surface (<0.5 m), whereas murres can dive deep enough to exploit the entire water column of lower Cook Inlet. If most of the exploitable fish biomass is above 50 m (Speckman 2004), murres would have access to 100 times more prey biomass than kittiwakes at any given distance from a colony.

In summary, every species of seabird has a different set of biological and behavioral adaptations for responding to changes in food supply, so we do not expect all species to react the same way. A further point made by Cairns (1987) and corroborated in our study is that if we wish to use multiple seabird species as indicators of marine food supplies, we had better first characterize the similarities and differences in their response to variability in food supply. Additionally, it may be useful to combine response data from different species using a multivariate index that captures the essence of the response and allows us to use a selection of species as multivariate indicators of food supplies (Reid et al. 2005, Fredericksen et al. 2006, Piatt & Harding 2007).

Poor indicators

It is equally important and biologically interesting to consider which parameters are *not* useful indicators of marine food supplies. The list of parameters that we studied is by no means exhaustive, but did include some that are often listed among useful indicators (Cairns 1987, Weimerskirch et al. 2001, Reid et al. 2005). In particular, this includes body condition and clutch size.

We found no relationship between adult body condition and food density for either murres or kittiwakes. These results were not expected. It was reasonable to assume that body condition would be sensitive to variations in food supply (Monaghan et al. 1989, Hamer et al. 1991). Experimental studies have shown that adult body condition can be affected negatively by increasing workload (Golet & Irons 1999). In field studies where seasonal variability in body mass was accounted for in the analysis, however, variability in adult body condition among years was exceedingly low (CV = 0.6 to 6.6%) for skua, terns, albatross, murres, and kittiwakes (Harris & Wanless 1988, Hamer et al. 1991, Suddaby & Ratcliffe 1997, Weimerskirch et al.

2001). Reid et al. (2005) examined annual variability in 32 parameters of seabird and mammal biology in the Antarctic, and found that the 7 least variable parameters involved measures of body mass (e.g. birth mass, fledging mass, adult arrival mass, etc.) and all had CVs < 10%.

This suggests that both murres and kittiwakes minimize variability in their own body condition. This is consistent with the idea of a trade-off between investment in the current year's reproductive effort and subsequent adult survival (Stearns 1992). The importance of maintaining adult body condition is implied from the strong linkage between body condition and survival in seabirds (Erikstad et al. 1998, Golet et al. 1998, Weimerskirch et al. 2001). After taking care of themselves, it follows that adults would try to minimize variation in chick growth and condition, which is linked with survival to breeding age (Sagar & Horning 1998, Weimerskirch et al. 2000).

Black-legged kittiwakes lay up to 3 eggs per clutch, but clutch size and laying success in kittiwakes were independent of food supply in Cook Inlet. On average, 69% of pairs that attempted to breed eventually laid eggs. For those that laid, the average clutch size was 1.49 ± 0.18 SD eggs per nest. Laying success (CV = 29%) was more variable than clutch size (CV = 12%). These observations may be explained in at least 2 ways. First, there was a gap in time between measurements: clutch size and laying success were measured in June, while food supply was measured in late July to early August. Alternatively, kittiwakes may have a programmed approach to egg-laying that is largely independent of food supply except under extreme conditions, i.e. when food supplies and nutrient reserves are so low as to preclude egg formation. Evidence from a variety of seabirds suggests that clutch size is usually maximized and regulation of breeding effort occurs later, by brood reduction or nest desertion (e.g. Monaghan et al. 1989, Sydeman et al. 1991, Hamer et al. 1993, Suddaby & Ratcliffe 1997).

Conclusions and future considerations

We join the ranks of those who promote the cautious use of seabirds as indicators of marine food supplies and call for more studies to elucidate the form of functional relationships and sources of variability (Cairns 1987, Montevecchi 1993, Furness & Camphuysen 1997, Reid et al. 2005). However, it is now clear that we ought not to expect many linear relationships between parameters of seabird biology and food supply (Reid et al. 2005). Seabirds are in most circumstances unlikely to gauge subtle or continuous changes, but they may perform well as binary indicators (Montevecchi 2007,

this Theme Section) that signal changes from good to bad, and vice versa. On the other hand, foraging-trip duration was one parameter that varied continuously (if not linearly) with prey density, and is perhaps deserving of more attention.

While other factors such as weather and predation can influence kittiwake breeding success (Hamer et al. 1993, Hatch et al. 1993), the species appears to be very sensitive to fluctuations in food supply. This parameter should, therefore, prove to be a reliable long-term indicator of variability in the marine environment (e.g. Aebischer et al. 1990, Piatt & Harding 2007). In contrast, murre breeding success may tell us little about food supplies, except under extreme circumstances, whereas murre time-budgets are sensitive to prey fluctuations. Given that murre species are widely being monitored in the Northern Hemisphere (Gaston & Jones 1998), it is perhaps time to add attendance time-budgets to the repertoire of parameters we routinely measure at murre colonies.

It is useful to know the form of a seabird's response to changing prey density, but the variability of its response is equally important in assessing its ability to deal with change. We find it intriguing that independent studies of seabirds in Alaska (Fig. 5) and the Antarctic (penguin and albatross; Reid et al. 2005), with similar sampling effort, found that (1) the highest CV of any parameter was <90% in both studies and (2) that some parameters in both studies fell into similar groupings of those with low CVs (e.g. body condition), moderate CVs (e.g. foraging), and high CVs (e.g. breeding success). This leads us to wonder: are there limits in variability, and do these differ much among species and ecosystems? To what extremes of variation can seabirds be pushed by climate change and regime shifts (e.g. Sydeman et al. 1991, Anderson & Piatt 1999) before they collapse? If there are differences among species, can we predict which species will be the best indicators of unusual variability in their environments?

Finally, we note that despite many advances in knowledge since Cairns' predictions were made, much uncertainty remains about using seabirds as indicators of marine food supplies (Fredericksen et al. 2006). More research is needed on a wider variety of seabird species and their functional relationships with prey. Also, we think that for some parameters, responses may not be evident except under the most extreme conditions of prey scarcity. It may be that experimental situations (e.g. with captive birds in aquaria, manipulative experiments in the wild) are needed to address this gap. In general, some of the best indicators in our study (and Reid et al. 2005) were those which had both high annual variability *and* a strong functional relationship with prey density. Paradoxically, highly variable parameters are not recommended for use as eco-

logical indicators (Dale & Beyeler 2001). Less variable parameters might be just as sensitive, but less practical if they have a weaker signal-to-noise ratio. Owing to these many uncertainties, and until we better understand the responses of individual species, it may be most prudent to combine data from multiple parameters and species to generate robust multivariate indicators of prey stocks (Fredericksen et al. 2006, Piatt & Harding 2007). In any case, we find it encouraging that increasing evidence points to bottom-up control of seabird populations (Aebischer et al. 1990, Speckman et al. 2005, Fredericksen et al. 2006), which further suggests that seabirds are likely to track spatial and temporal variation in prey abundance.

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