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Seabirds maintain offspring provisioning rate despite fluctuations in prey abundance: a multi-species functional response for guillemots in the North Sea

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Summary

1. Seabirds that consume more than one prey type may adjust their foraging to maintain provisioning rates for their chicks. How energetically effective are these strategies, and what are the implications for the management of seabirds and their marine habitat?

2. A multi-species functional response links consumption rates to the availability of multiple prey types, but fitting multi-species functional responses to field data can be difficult, requiring consumption measurements over a range of different prey abundances. Such detailed data may be especially difficult to obtain in marine ecosystems.

3. We used annual time-series data on chick provisioning for the common guillemot *Uria aalge* together with abundance indices for its two main prey (lesser sandeel *Ammodytes marinus* and sprat *Sprattus sprattus*) to parameterize a multi-species functional response for parents provisioning chicks at a major North Sea colony from 1992 to 2005.

4. The fitted model reproduced changes in diet and consumption rate which were consistent with changes in local prey abundance including a long-term decline in sandeels.

5. The model predicted that energy intake by chicks would be more sensitive to changes in sprat abundance than sandeel abundance. Guillemots appeared able to adjust their foraging tactics over a wide range of prey abundances to maintain a consistent energetic intake rate for chicks.

6. *Synthesis and applications*. Our results suggest guillemot chicks obtain adequate calorific intake from their parents despite fluctuating prey abundances, conferring some resilience in the face of environmental variation. The parameterized multi-species functional response model can be used to estimate levels of severe prey shortage that compromise provisioning. It also enables us to interpret predator consumption rates so that these can be used as a metric of prey availability. Further, quantifying trophic links between marine prey and apex predators is needed to support the development of multi-species models in which the predators can be included. Such models are needed as tools to effectively manage the marine ecosystem, taking into account the objectives of fishing, conservation and the need to maintain Good Environmental Status.

Key-words: *Ammodytes marinus*, chick provisioning, generalist, Good Environmental Status, indicator species, MCMC, predator–prey interactions, seabird diet, *Sprattus sprattus*, *Uria aalge*

Introduction

Management of marine ecosystems should allow for sustainable fishing and the conservation of dependent species such as seabirds. Seabird populations may act as indicators of the health of the ecosystem of which they are a part, informing the management of fisheries that impact their key prey (Boyd & Murray 2001; Frederiksen *et al.* 2008; Hjernquist & Hjernquist 2010). If a seabird demographic rate such as breeding success is to be used as an indicator, then we need to quantify the relationship between that rate and the abundance of suitable prey

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(Cury *et al.* 2011). However, if the birds exploit several sizes and/or species of fish, and if their response to changing prey fields is nonlinear, then it may be difficult to attribute changes in their vital rates to the abundance of any one prey (Durant *et al.* 2009). To make inferences about the state of the prey community, we need to understand the relationship between food intake by the predator, and the abundance of multiple prey (Asseburg *et al.* 2006). This can be represented by the predator's multi-species functional response (MSFR).

The simplest form of MSFR has the predator consuming prey in proportion to prey abundance. However, predators may show preferences for some prey. Functional responses may also 'saturate', reaching a maximum when prey is plentiful and consumption is limited either by handling or digestion time (Jeschke, Kopp & Tollrian 2002) or because 'sufficient' prey has been acquired so that further foraging effort is not justified. Depending on what it is that limits consumption, this asymptotic intake rate may be more appropriately represented in terms of energy, biomass or a count of individual prey items.

As a result of preference alone, predator diets are expected to change composition as the relative abundances of different prey types in the system change. However, it is also possible that preferences themselves change as a function of prey abundance, for example, if aggregated prey are preferentially targeted by the predator (Murdoch & Oaten 1975; Chesson 1983; Yodzis 1994). Preference, switching and saturation can all be represented by parameters in a mathematical model. By fitting data to estimate these parameters, we can improve our understanding of the corresponding biological effects.

Multi-species functional responses are often difficult to determine for marine species. Sufficient data are needed to represent a range of prey abundance for all prey types, and consumption may be difficult to measure directly, leaving us to rely on diet composition estimates, for example, from faecal and stomach samples (Rindorf & Gislason 2005; Matthiopoulos *et al.* 2008). Even where intake rates can be quantified, these may exhibit skewed statistical distributions and be subject to uncertainty in the identification of prey. Further, there are often problems in estimating the abundance of prey at relevant scales in time and space, especially in marine systems where the distribution of prey may be highly variable (Harbitz & Lindstrom 2001). This problem is particularly acute for central-place foragers with restricted foraging ranges, such as the small-to-medium-sized seabirds which dominate the avian predator community in Atlantic shelf seas. It is therefore important that an analysis is carried out within a framework that takes account of uncertainties in the raw data and in derived quantities (such as prey abundance) that contribute to the final estimation of functional response parameters.

We model chick provisioning for the common guillemot *Uria aalge* during the period 1992 to 2005 using data from a large North Sea breeding colony (the Isle of May, southeast Scotland) and the associated foraging area for the birds at sea. This system provides an unusually rich data set including time-series estimates of local prey abundance from trawl surveys (ICES 2010; Jensen *et al.* 2011) and detailed annual observations of the rate at which chicks are provisioned (Wanless *et al.* 2005).

The guillemot is the most abundant seabird in the north-western North Sea (Mitchell *et al.* 2004) breeding in colonies on cliffs or among boulders from late April to mid-July. Unless conditions are severe, one parent remains at the site to incubate the egg or brood the chick while the mate is feeding at sea (Wanless *et al.* 2005). Parents bring back one prey item, held lengthways in the bill for the chick, making prey consumption relatively straightforward to study because an observer can identify feeding events and identify prey items without causing disturbance. Prey consist mainly of small pelagic fish, which at the Isle of May are principally lesser sandeels *Ammodytes marinus* and sprats *Sprattus sprattus* (Thaxter *et al.* 2009).

Sprats are small schooling clupeids associated with shallow waters such as the Firth of Forth. The distribution of sprat is variable, as are fishery catches, making stock assessments uncertain, though acoustic and trawl survey data suggest an increasing trend in abundance (ICES 2012). Sandeels are an important forage species for predatory fish and mammals (Frederiksen *et al.* 2004; Hammond & Grellier 2005; Kempf *et al.* 2010). They bury in sediment during the winter but forage in the water column during spring and summer, becoming accessible to foraging guillemots (Jensen, Wright & Munk 2003; Thaxter *et al.* 2009; Embling *et al.* 2012). Due to shifts in environmental conditions (Arnott & Ruxton 2002; Poloczanska *et al.* 2004) and changes in the level of industrial fishing for sandeels including fishery closure (Wanless *et al.* 2007), sandeel abundance varied substantially over the study period with some very low years during the later part of the time series (ICES 2008a,b).

The objective of our study is to connect local forage fish abundance with changes in seabird consumption. To this end, we use guillemot chick provisioning data together with abundance estimates for sprat and sandeel to parameterize an MSFR and predict energetic provision for the chicks by the parent birds. We explore how parents can maintain provisioning of chicks as the abundance of prey species changes and show how it is possible to suggest conditions in which they are likely to fail in these efforts. From a conservation perspective, these results indicate how sensitive guillemots are to likely changes in prey abundance and thus whether they could provide a useful indicator of Good Environmental Status (Durant *et al.* 2009). From the standpoint of marine management, our findings highlight that to avoid adverse effects on predators, periods when abundances of multiple prey species are low require a more precautionary approach than periods when abundance is only reduced in one prey species.

Materials and methods

To parameterize a functional response, two sets of contemporary data are needed: consumption rates for each important prey and estimates of the abundance of each prey type at appropriate temporal and spatial scales (Smout & Lindstrom 2007; Matthiopoulos *et al.* 2008). We used a series of analytical steps which are outlined in Fig. 1. We used direct observations of prey items provided for guillemot chicks to estimate consumption rates and identify important prey items in the chick diets. Prey abundance was estimated using International Bottom Trawl Survey (IBTS) data for sprat (ICES 2012) and fisheries-based survey data for sandeel (Jensen *et al.* 2011) both designed to estimate prey abundance at the scale of the statistical rectangle (1°Longitude by 0·5°Latitude, Fig. 2, as defined by ICES the International Council for the Exploration of the Sea). The combined availability of data limited our study to the time period 1992–1994, 1996–2005. We fitted an MSFR using Bayesian methods and used it to make predictions about the effectiveness of chick provisioning under different regimes of prey abundance. The restricted number of data and the uncertainties in consumption rates and prey abundances were accounted for within the Bayesian analysis and reflected in the uncertainty in parameters and predictions of the model.

PREY CONSUMPTION BY GUILLEMOT CHICKS

Chick provisioning rates and diets were recorded using standardized methods (Wilson, Daunt & Wanless 2004). Breeding sites were observed for a minimum of 2 h with observation periods covering all hours of daylight. When a parent delivered a food item, the time, prey species and size were recorded. Because the time elapsing between an adult returning to the site and feeding the chick is very short (typically <5 s) and two guillemots occasionally arrive simultaneously, it was not always possible for the observer to identify the prey species and/or size. Thus, it was necessary to take account of 'unidentified' prey which might be either sprats or sandeels (see below under 'model fitting').

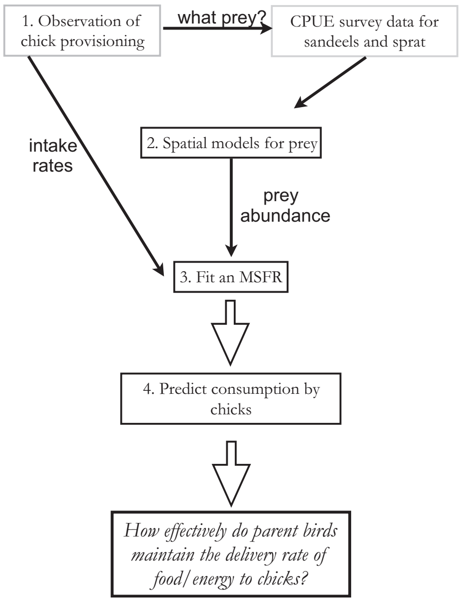

Fig. 1. Outline of the modelling steps involved in the analysis.

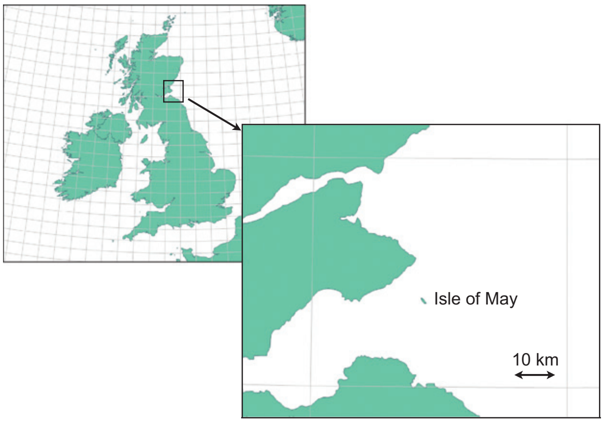

Fig. 2. A map of the UK showing ICES statistical rectangle. 41E7, the rectangle containing the Isle of May study area, is shown in more detail.

Chick diets were dominated by sandeels and clupeids (>95% of the total diet). It was impossible to identify clupeid species from feeding watches, but examination of fish found on ledges indicated all clupeids were sprats. Sprats were treated as a single size class. For sandeels, it was possible for observers to distinguish four size classes in the field: 'small' S (<8 cm), 'medium' M (8–11 cm), 'large' L (11–14 cm) and 'extra-large' XL (>14 cm). Because very few small sandeels were brought in (<5% of items), this category was excluded from analyses.

Further details are given in Appendix S1 (Supporting information).

PREY ABUNDANCE

During the chick-rearing period (late May to mid-July), guillemots typically feed within 30 km of the Isle of May (Fig. 2) (Thaxter *et al.* 2009). This area lies within ICES rectangle 41E7 (56·0°N to 56·5°N, 3°W to 2°W). For both sprats and sandeels, we first developed spatial models using data from a larger North Sea area with the aim of borrowing strength from the full data set to inform local estimates of abundance at the level of ICES rectangle 41E7.

To estimate sprat abundance, we made use of IBTS data collected using standardized bottom trawl gear and methodology (ICES 2010). Catch per unit effort (CPUE) data for sprat were available for ICES rectangles throughout the North Sea (Fig. 2) for the first and third quarters of the year. These data, and further details about the data collection protocols, are publicly available through ICES (ICES 2010).

Catch data for fish are over-dispersed and zero-inflated. To account for this, we parameterized a two-stage generalized additive model using the mgcv package in R (Wood 2006). First, a presence/absence model was fitted. Predictions of this model represent the probability P_x that sprats are present at location x. Then, a further model was fitted to describe the abundance of the species A_x given that it is present. Candidate covariates were the spatial coordinates of the trawl, year, water depth, quarter of the year and vessel identity. The final combination of covariates to include was decided in each case on the basis of Generalized Cross Validation score (Wood 2006). The two 'best' models were then used to predict mean CPUE given by the product A_xP_x (Wood 2006; Murase *et al.* 2009). We used data from the entire North Sea to generate a time series of predictions at the Isle of May in ICES rectangle 41E7 (Fig. 2). The original IBTS data were collected consistently only in Quarter 1 (January–March) and 3 (July–September). The Quarter 3 hauls may contain young-of-the year, which are likely to be less important than adult sprat as food for guillemot chicks, so we made predictions for Quarter 1 assuming these would remain in the area, forming prey for the chicks in Quarter 2 (April–June).

The North Sea sandeel fishing mainly takes place in April to August. We expect that sandeel catches, appropriately corrected for effort, will more closely represent the abundance of sandeels relevant to seabird foraging than continuous plankton recorder data which is based on larval abundance and is therefore only indirectly related to the abundance of adult sandeels (Frederiksen *et al.* 2008). We fitted a generalized linear model (GLM) for sandeel abundance (represented by daily catch rates, the data being CPUE based on Danish logbook records) for the North Sea area corresponding to a single sandeel stock [sandeel stock assessment unit 4 (Jensen *et al.* 2011)]. Covariates were space, time and vessel size. For a vessel of gross tonnage GT,

$$\ln(\widehat{CPUE}_{r,q,y,\mathrm{GT}}) = \alpha_{q,r} + \beta_{q,y} + \gamma_q \ln(\mathrm{GT}) \qquad \text{eqn 1}$$

Indices r, q and y denote statistical rectangle, quarter and year, respectively. α accounts for the average quarterly spatial distribution of CPUEs. This is time-invariant and considerably reduces the number of parameters to be estimated. This should be a reasonable assumption within a given subpopulation, given that sandeels are closely associated with sediment and depth, abiotic factors that are also time-invariant. β accounts for yearly differences in the North Sea average quarterly CPUE, and γ accounts for increased CPUE with vessel size. A standard vessel size of 200 GT was used to predict the CPUE for ICES statistical rectangle 41E7. The abundance of sandeels in the 3 main size classes (M, L and XL) was based on the predicted CPUE values, and the observed relative abundance of sandeels in each size class in samples taken from the commercial fishery in the Firth of Forth.

The time series of CPUE estimates for both sandeels and sprats should be treated as indices of abundance, rather than absolute estimates of biomass, because the catchability of prey was unknown. We tentatively assume these indices are directly proportional to prey abundance.

Further details about the estimation of fish abundance indices are given in Appendix S2 (Supporting information).

MODEL FITTING

We used a general MSFR model:

$$c_i = \frac{(a_i n_i)^m}{1 + t\sum_j (a_j n_j)^m} \qquad \text{eqn 2}$$

where c_i is consumption rate of prey type i (measured in 'items' or 'energetic value' per unit time), n_i is abundance of prey type i, and a_i, m and t are constants to be estimated by fitting to the data, which we refer to here as preference, switching parameter and handling time respectively. According to the values of these parameters, a Type 1, 2 or 3 functional response is obtained (Holling 1959). The asymptotic maximum consumption rate for all prey types is $c_{\max} = 1/t$ (Murdoch & Oaten 1975).

We fitted two models: in model (A), consumption rate was defined as the number of items consumed per hour and in model (B), consumption rate was quantified in terms of prey energetic content (kJ per chick per hour). The energy content of a prey item of average size was assumed constant for all years except for 2004, a year of unusually poor prey quality. For all years except 2004, we used values of 135·0 kJ for sprats and 15·1 kJ, 40·4 kJ and 86·9 kJ for M, L and XL sandeels, respectively. For 2004, we used 11·9 kJ for sprats and 3·52 kJ, 17·5 kJ and 20 kJ for M, L and XL sandeels, respectively (Wanless *et al.* 2005).

We assumed observations of prey delivery to chicks could be modelled as a Poisson process, with the hourly rate of delivery predicted by the functional response in eqn 2 as c_i. To account for unidentified prey items, we assumed that for prey species i, the probability that it is identified is P_i and therefore the probability that it is not identified is $1\text{-}P_i$. We were then able to fit the observed counts of identified species along with the counts of unidentified items, and the prey-specific parameters P_i were estimated during the model-fitting process, along with the parameters of the functional response itself.

Prey abundance estimates were subject to uncertainty. This was represented by sampling prey abundances from lognormal distributions with parameters set according to the estimated means and standard deviations from the predictions of the generalized additive model and GLM models for prey.

In eqn (2), the parameter a directly scales prey abundance, and therefore, the units in which n is measured are essentially arbitrary because changes to units will be 'absorbed' by changes in the estimate of a. For convenience in visualizing the results, and to improve computational performance during model fitting, all prey abundances were scaled with respect to their historical maximum so that the highest value for each prey type was 100.

We fitted the model using a Bayesian approach and Markov chain Monte Carlo (MCMC) algorithm implemented with the freely available software WinBUGS (Lunn *et al.* 2000; Smout *et al.* 2010).

After fitting, models using prey items and prey energy as currency were compared and the best model was chosen based on the Deviance Information Criterion (DIC). This quantity, which can be readily calculated based on the output of the MCMC, is analogous to the AIC in frequentist statistics (Spiegelhalter *et al.* 2002).

PREDICTIONS

The selected best model was then used to predict consumption rates under different regimes of prey availability.

Further details about the MSFR modelling are provided in Appendix S3 (Supporting information), and WinBUGS code is given in Appendix S4 (Supporting information).

Results

PREY CONSUMPTION

During the study, there were 767 h of watches during which 14 938 prey items were recorded. 27·6% were sandeels, 52·3% were sprats, and 21·1% were unidentified.

PREY ABUNDANCE

For sandeels, the GLM explained just below a third of the total observed variation in North Sea CPUE in Quarter 2. For sprats, the chosen models for both the presence absence data and the abundance data included the covariates *x, y, year, quarter* and *vessel*. Deviance Explained scores were 38·6% and 38·9%, respectively. Indices of prey abundance for all prey types are shown in Fig. 3. The time series ended on a historic high for sprats. In contrast, abundance indices for L and XL sandeels peaked at the start of the period, were also high for L sandeels in 1997 and peaked again for M sandeels in 2000.

FUNCTIONAL RESPONSE MODELS

Using DIC, Model (B) was preferred (Table 1) and subsequent predictions were calculated from this energy-based model. Parameter estimates and 95% Bayesian credible intervals are given in Table 2. The ‘currency’ for prey abundance is energy in kJ, and we give the value of the parameter $c_{\max}$ which is the asymptotic consumption rate in these units.

The probabilities of correctly identifying sprat and sandeel are high but appear distinct from one another based on the 95% credible intervals (Table 2), justifying the separate estimation of these parameters in order to improve predictions.

PREDICTIONS

The species and sizes of prey varied substantially over the study (Fig. 4, lower panel). Sprats were predominant in most years; only in 1992 and 1997 did sandeels make up more than 50% of the prey items. Model predictions based on the prey abundance estimates (Fig. 3) are shown in the upper panel of Fig. 4. In general, the model predicted diet composition well, and in most cases, it captured the contrasting sandeel-dominated and sprat-dominated diets (Fig. 4). However, predictions are less satisfactory for years 1994, 1996 and 1997. In particular, the predicted high consumption of L sandeels in 1994 is not consistent with observations in the field (this prey category made up <5% of consumed items). The fit of the model might be improved if estimates of prey energy content were available for each year of the study, so that any variation in prey ‘value’ could be fully taken into account.

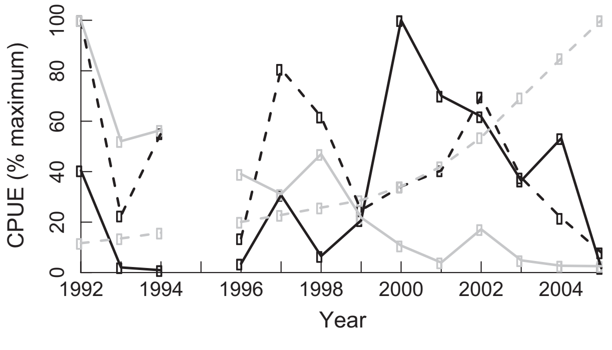

Fig. 3. Prey abundance indices for the years 1992–2005 (no data available for 1995). Sprat (grey dashed line); sandeel size class M (black line); L (black dashed line); XL (grey line).

Relationships between prey consumption rates for sprats and sandeels were predicted for different levels of prey abundance (Fig. 5). Abundance for each prey type is allowed to vary between 0 and 100, while the levels of ‘competing’ prey are held at historical low values (Fig. 3). The scatter in predicted consumption rates is based on parameter uncertainty and random Poisson sampling where the Poisson rate parameter is predicted from the MSFR.

Variation in daily provisioning rates of chicks in response to prey abundance is shown in Fig. 6. Higher levels of sandeel consumption (left hand panel) are predicted only for prey regimes that are relatively low in sprats and high in sandeels. Sprat consumption (centre panel) remains high over a wide range of combinations of prey abundance. In general, provisioning is consistent with observed rates (Wanless *et al.* 2005). Historical prey abundances for sandeel range from approximately 2 to 100, and for sprat from 11 to 100; thus, the main part of the area representing combinations of prey availability falls within these limits. The right-hand panel in Fig. 6 represents the total daily energetic value of prey items delivered to the chick, which appears to remain high over much of the range covered by the historical data. The figure also suggests a region of particularly sharp decline in this rate, mainly due to changes in sprat abundance. A solid line (with 95% Bayesian credible intervals shown as dotted lines) represents the contour below which energy intake drops to <75% of its maximum predicted value. Although this threshold is presented for illustrative purposes, the approach highlights how MSFR can be used to indicate levels of prey that result in energetic intakes above or below a target threshold. Further work linking food intake to demographic rates is needed to estimate the level of energetic provisioning that would represent a ‘success threshold’ for chick rearing consistent with conservation objectives (Wanless *et al.* 2005; Cury *et al.* 2011).

Discussion

Using Bayesian methods, we parameterized an MSFR for guillemots provisioning their chicks. The fitted MSFR allows us to predict intake rates under dynamically shifting conditions of prey abundance, offering potential benefits for the management of predators and ecological communities. Where predation has an appreciable impact on prey, this can be quantified, which is important where the aim is to manage fish stocks using an ecosystem-based approach that takes account of multi-species trophic

Table 1. Mathematical form of functional response Models A and B with associated Deviance Information Criterion (DIC) values. c_i represents the consumption rate for prey *i*, and n_i represents the abundance of prey *i*

	Equation	Estimated Parameters	DIC
1	$c_i = \frac{(a_i n_i)^m}{1 + t\sum_j (a_j n_j)^m}$	For each prey type: Attack rate *a* Common handling time *t* Switching parameter *m* (6 in total)	6165
2	$c_i = \frac{1}{\varepsilon_i}\left(\frac{(a_i \varepsilon_i n_i)^m}{1 + t\sum_j (a_j \varepsilon_j n_j)^m}\right)$	For each prey type: Attack rate *a* Common handling time *t* Switching parameter *m* (6 in total)	6138
	where ε_i is the energetic content of prey item in kJ		

Table 2. Parameter estimates for Model B (where consumption rate is quantified in terms of energy). 95% Bayesian credible intervals are calculated from the Markov chain.

	Parameter	Mean	95% CI
Preference	a_{M}	$3{\cdot}94 \times 10^{-3}$	$(3{\cdot}01 \times 10^{-3}, 4{\cdot}95 \times 10^{-3})$
	a_{L}	$2{\cdot}82 \times 10^{-3}$	$(2{\cdot}16 \times 10^{-3}, 3{\cdot}56 \times 10^{-3})$
	a_{XL}	$4{\cdot}41 \times 10^{-4}$	$(3{\cdot}24 \times 10^{-4}, 5{\cdot}73 \times 10^{-4})$
	a_{sprat}	$1{\cdot}66 \times 10^{-2}$	$(1{\cdot}15 \times 10^{-2}, 2{\cdot}32 \times 10^{-2})$
Switching parameter	m	1·00312	(1·000,1·012)
Maximum consumption rate	$c_{\max}$	57·7 kJ h^{-1}	(49·9, 70·43) kJ h^{-1}
Probability of identifying sprat	P_{sprat}	0·769	(0·758, 0·779)
Probability of identifying sandeel	P_{sandeel}	0·844	(0·827, 0·859)

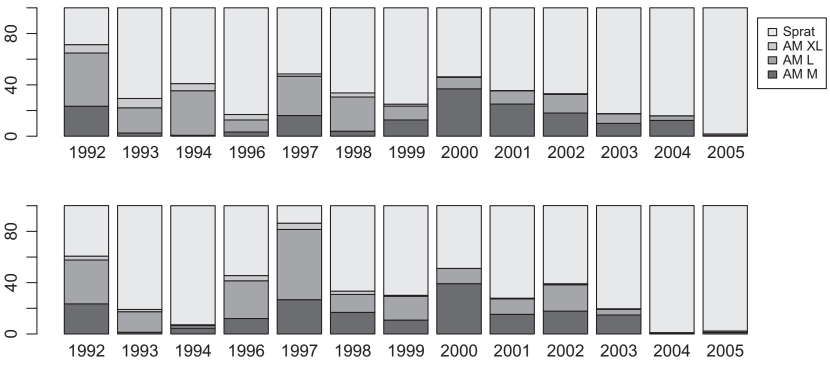

Fig. 4. The composition of the diet of guillemot chicks during the years of the study (% by count). Predictions from Model B are shown in the upper panel, and observed counts are represented in the lower panel. Greyscale represents (from light to dark) sprat, sandeel (AM) size XL, sandeel size L and sandeel size M.

interactions (Lindstrom *et al.* 2009; Ripple & Beschta 2012). Where conservation of predator species themselves is of interest, then an MSFR can predict 'critical' levels of prey below which predator intake rates are likely to drop substantially (Fig. 6). This is valuable in itself and also should improve our understanding of observed empirical relationships between predator life history and prey abundance (Testa *et al.* 1991; Boyd *et al.* 1994; Sydeman 1999; Furness & Tasker 2000; Mori & Boyd 2004). Thus, a fitted MSFR has the potential to improve inferences about the system based on using the predator as an indicator (Boyd & Murray 2001; Durant *et al.* 2009; Cury *et al.* 2011).

A difficulty in fitting MSFRs to field data is in estimating prey abundances that reflect the true availability of prey to predators. Our CPUE data were collected with a focus on understanding fish populations and estimated abundance at the scale of the ICES statistical rectangle (approximately 40 square miles). Fortuitously, this scale accords well with the foraging range of guillemots during the chick period (Cairns, Bredin & Montevecchi 1987; Thaxter *et al.* 2009). Although within this area, birds exploit patchily distributed resources (Wanless, Morris & Harris 1988; Thaxter *et al.* 2009), nevertheless we were able to find a general relationship between prey consumed by the chicks and broader-scale prey availability. This

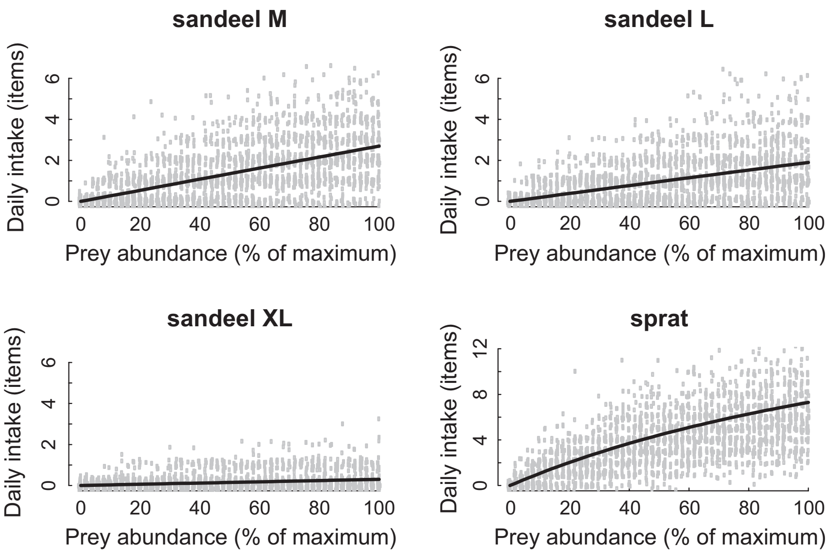

Fig. 5. Multi-species functional response of guillemots provisioning their chicks (Model B) with two prey species: sprat and sandeel. Bold curves show the functional response based on mean parameter estimates, while the points are simulated values based on 100 random parameter sets drawn from the Markov chain, with random Poisson sampling (for illustrative purposes, noise is also added to the integer values to display points separately). Each curve represents the response of the birds to one target prey type, when the other prey in the system are at low levels.

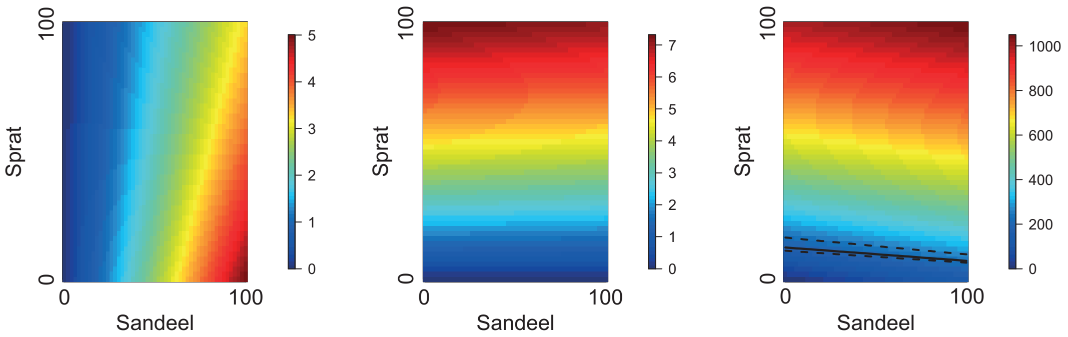

Fig. 6. Consumption surfaces. Surface colours indicate predicted consumption rates, in response to variation in both sprat and sandeel abundance. Abundances of all prey types vary from 0 to 100 where 100 represents the historical maximum. *Left panel*: consumption rate of sandeel (items per day): surface colours indicate the net daily consumption rate of sandeel according to the colour scale. *Centre panel*: consumption of sprat (items per day). *Right panel*: net energetic intake by chicks (in kJ per day, including contributions from both sandeel and sprat). The solid line represents a contour at which net energy intake by chicks is at 75% of its maximum value (95% Bayesian CIs are shown as dotted lines). The area below the contour represents prey abundances for which chick provisioning rates fall below this level. All predictions are from Model B.

result is encouraging, offering the potential to link fisheries management with the conservation of North Sea guillemot populations.

The values of model parameters have ecological implications and can potentially improve our understanding of predator–prey dynamics of Isle of May guillemots. However, the interpretation of the 'preference parameters' a_i is not straightforward. Prey abundances were scaled to improve numerical performance, and our original CPUE estimates were indices rather than direct estimates of prey abundance. According to our model, if all prey were present in the system at historically high abundance levels, then sprat would be the most important part of the chick diet. Of the sandeels, the medium-size category would then appear to be 'preferred' over the larger sandeels. One possible explanation is that parents carrying larger sandeels may be vulnerable to kleptoparasitism while in flight. It is also likely that the larger sandeels are relatively scarce, even when they are (in historical terms) at high levels.

Based on our parameter estimates, there is no support for prey switching by the guillemots because we estimate values of $m \sim 1$. To avoid possible confusion, what is meant by 'switching' here is not a change in diet, but a change in preference for particular prey (Chesson 1983). Consumption by chicks saturates, suggesting a Type 2 MSFR is appropriate given the spatial and temporal scale of our data.

Based on model selection, the best 'currency' for the estimation of consumption rates is energetic (rather than counts of prey items, or biomass). This suggests that the common parameter $c_{\max}$ (a 'sufficiently high' level of provisioning by the parent birds) is most usefully measured in terms of energy, and intuitively this seems reasonable.

Although sandeels have often been assumed to be the key prey for North Sea seabirds, energy intake by young guillemots appears to be more sensitive to variation in sprat abundance than sandeel abundance over the historically observed ranges of abundance (Fig. 6). At high sprat abundance, low sandeel abundance is well tolerated, having little effect on energy consumption. Only at low sprat abundance does the additional effect of low sandeel abundance become important. It is interesting to note the role of sprat as a key forage fish for seabird populations in another North East Atlantic system, the Baltic (Hjernquist & Hjernquist 2010; Kadin *et al*. 2012).

If there is (as our model suggests) general consistency in chick energy intake over a wide range of likely combinations of prey abundance, this implies guillemots are able to some extent to maintain provisioning of their chicks despite changes in the abundance of their key prey. This contrasts with other species, for example, black-legged kittiwakes *Rissa tridactyla*, which are very sensitive to changes in the abundance of one prey type, and is consistent with the results of guillemot studies in other areas (Piatt *et al*. 2007; Wanless *et al*. 2007). However, it should be noted that while parent birds may sometimes be able to maintain their delivery rate by adjusting their foraging, they are not necessarily able to compensate for changes in the energetic content of prey (Wanless *et al*. 2005). There may also be hidden costs to the adaptable foraging strategies of parent birds. If parents make longer trips to compensate for reduced prey abundance, they may spend less time guarding their chick resulting in higher chick mortality (Ashbrook *et al*. 2008). Trade-offs between the costs of different parental foraging strategies and reproductive success would be a fruitful area for further investigation especially if informed by detailed data on the energetic content of prey.

Our study suggests that energy intake of guillemot chicks may not be a particularly sensitive indicator of fluctuating prey abundance. However, where diet and consumption are regularly monitored (as at the Isle of May), there is also the potential to use these records directly to indicate changing prey abundance and the state of the system. This would ideally be done in combination with observations of other indicator species, appropriate to the area (Wanless *et al*. 2007). Our model also suggests regimes of prey abundance that allow for chick provisioning above a given threshold level, provided we are able to estimate threshold levels for satisfactory energy intake (Fig. 6). In order to do this, we would need to develop the approach further to establish links between chick provisioning rates, prey abundance, breeding success and possibly other demographic rates. This could be a very fruitful direction for future work, and results could feed into management strategies to support conservation efforts for sensitive species within programmes focussed primarily on different objectives, for example optimizing commercial fishing using approaches based on maximum sustainable yield (Mace 2001; Constable 2011). An important advantage of our Bayesian methodology is that the uncertainty of model predictions can be estimated robustly, allowing us to quantify the level of risk for dependent species associated with a low prey regime (Harwood & Stokes 2003).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Prey consumption: observations and data.

Appendix S2. Estimating prey Abundance Indices.

Appendix S3. Fitting the multi-species functional response.

Appendix S4. WinBUGS code.