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

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1

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

5

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7 **Abstract**

- 8 1. Seabirds which consume more than one prey type may adjust their foraging to
9 maintain provisioning rates for their chicks. How energetically effective are these
10 strategies, and what are the implications for the management of seabirds and their
11 marine habitat?
- 12 2. A multi-species functional response (MSFR) links consumption rates to the
13 availability of multiple prey, but fitting MSFRs to field data can be difficult, requiring
14 consumption measurements over a range of different prey abundances. Such
15 detailed data may be especially difficult to obtain in marine ecosystems.
- 16 3. We used annual time series data on chick provisioning for the common guillemot
17 (*Uria aalge*) together with abundance indices for its two main prey (lesser sandeel

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1 *Ammodytes marinus* and sprat *Sprattus sprattus*) to parameterize an MSFR for
2 parents provisioning chicks at a major North Sea colony from 1992-2005.

- 3 4. The fitted model reproduced changes in diet and consumption rate which were
4 consistent with changes in local prey abundance including a long-term decline in
5 sandeels.
- 6 5. The model predicted that energy intake by chicks would be more sensitive to
7 changes in sprat abundance than sandeel abundance. Guillemots appeared able to
8 adjust their foraging tactics over a wide range of prey abundances to maintain a
9 consistent energetic intake rate for chicks.
- 10 6. *Synthesis and applications:* Our results suggest guillemot chicks obtain adequate
11 calorific intake from their parents despite fluctuating prey abundances, conferring
12 some resilience in the face of environmental variation. The parameterized MSFR
13 can be used to estimate levels of severe prey shortage that compromise
14 provisioning. It also enables us to interpret predator consumption rates so that
15 these can be used as a metric of prey availability. Further, quantifying trophic links
16 between marine prey and apex predators is important and timely, because this
17 information is needed to support the development of multi-species models in which
18 the predators can be included. Such models are needed as tools to effectively
19 manage the marine ecosystem, taking into account the objectives of fishing,
20 conservation, and the need to maintain Good Environmental Status (GES).

21
22 Keywords: *Ammodytes marinus*; generalist; Good Environmental Status; indicator species;
23 MCMC; chick provisioning; predator prey interactions; seabird diet; *Sprattus sprattus*; *Uria*
24 *aalge*.

1 Introduction

2 Management of marine ecosystems should allow for sustainable fishing, and the
3 conservation of dependent species such as seabirds. Seabird populations may act as
4 indicators of the health of the ecosystem of which they are part, informing the
5 management of fisheries that impact their key prey (Boyd & Murray 2001; Frederiksen *et*
6 *al.* 2008; Hjernquist & Hjernquist 2010). If a seabird demographic rate such as breeding
7 success is to be used as an indicator, then we need to quantify the relationship between
8 that rate and the abundance of suitable prey (Cury *et al.* 2011). However, if the birds
9 exploit several sizes/species of fish, and if their response to changing prey fields is non-
10 linear, then it may be difficult to attribute changes in their vital rates to the abundance of
11 any one prey (Durant *et al.* 2009). To make inferences about the state of the prey
12 community, we need to understand the relationship between food intake by the predator,
13 and the abundance of multiple prey (Asseburg *et al.* 2006). This can be represented by the
14 predator's multi-species functional response (MSFR).

15
16 The simplest form of MSFR has the predator consuming prey in proportion to prey
17 abundance. However, predators may show preferences for some prey. Functional
18 responses may also 'saturate', reaching a maximum when prey is plentiful and
19 consumption is limited either by handling/digestion time (Jeschke, Kopp & Tollrian 2002) or
20 because 'sufficient' prey has been acquired so that further foraging effort is not justified.
21 Depending on what it is that limits consumption, this asymptotic intake rate may be more
22 appropriately represented in terms of energy, biomass, or a count of individual prey items.

23
24 As a result of preference alone, predator diets are expected to change composition as the
25 relative abundances of different prey types in the system change. However it is also
26 possible that preferences themselves change as a function of prey abundance, e.g. if

1 aggregated prey are preferentially targeted by the predator (Murdoch & Oaten 1975;
2 Chesson 1983; Yodzis 1994). Preference, switching and saturation can all be represented
3 by parameters in a mathematical model. By fitting data to estimate these parameters, we
4 can improve our understanding of the corresponding biological effects.

5
6 MSFRs are often difficult to determine for marine species. Sufficient data are needed to
7 represent a range of prey abundance for all prey types, and consumption may be difficult
8 to measure directly, leaving us to rely on diet composition estimates e.g. from faecal and
9 stomach samples (Rindorf & Gislason 2005; Matthiopoulos *et al.* 2008). Even where intake
10 rates can be quantified, these may exhibit skewed statistical distributions and be subject to
11 uncertainty in the identification of prey. Further, there are often problems in estimating the
12 abundance of prey at relevant scales in time and space, especially in marine systems
13 where the distribution of prey may be highly variable (Harbitz & Lindstrom 2001). This
14 problem is particularly acute for central-place foragers with restricted foraging ranges,
15 such as the small to medium sized seabirds which dominate the avian predator community
16 in Atlantic shelf seas. It is therefore important that analysis is carried out within a
17 framework that takes account of uncertainties in the raw data and in derived quantities
18 (such as prey abundance) that contribute to the final estimation of functional response
19 parameters.

20
21 We model chick provisioning for the common guillemot (*Uria aalge*) during the period 1992
22 to 2005 using data from a large North Sea breeding colony (the Isle of May, southeast
23 Scotland) and the associated foraging area for the birds at sea. This system provides an
24 unusually rich data set including time-series estimates of local prey abundance from trawl
25 surveys (IBTSWG 2010; Jensen *et al.* 2011) and detailed annual observations of the rate
26 at which chicks are provisioned (Wanless *et al.* 2005).

1
2 The guillemot is the most abundant seabird in the northwestern North Sea (Mitchell *et al.*
3 2004) breeding in colonies on cliffs or among boulders from late April to mid July. Unless
4 conditions are severe, one parent remains at the site to incubate the egg or brood the
5 chick while the mate is at sea feeding (Wanless *et al.* 2005). Parents bring back one prey
6 item, held lengthways in the bill for the chick making it relatively straightforward to study
7 prey consumption because an observer can identify feeding events and identify prey items
8 without causing disturbance. Prey consist mainly of small pelagic fish which at the Isle of
9 May are principally lesser sandeels *Ammodytes marinus* and sprats *Sprattus sprattus*
10 (Thaxter *et al.* 2009).

11
12 Sprat are small schooling clupeids associated with shallow waters such as the Firth of
13 Forth. The distribution of sprat is variable, as are fishery catches, making stock
14 assessments uncertain though acoustic and trawl survey data suggest an increasing trend
15 in abundance (Hawg 2011). Sandeels are an important forage species for predatory fish
16 and mammals (Frederiksen *et al.* 2004; Hammond & Grellier 2005; Kempf *et al.* 2010).
17 They bury in sediment during the winter but forage in the water column during spring and
18 summer, becoming accessible to foraging guillemots (Jensen, Wright & Munk 2003;
19 Thaxter *et al.* 2009; Embling *et al.* 2012). Due to shifts in environmental conditions (Arnott
20 & Ruxton 2002; Poloczanska *et al.* 2004) and changes in the level of industrial fishing for
21 sandeels including fishery closure (Wanless *et al.* 2007) sandeel abundance varied
22 substantially over the study period with some very low years during the later part of the
23 time series (ICES 2008a; ICES 2008b).

24
25 The objective of our study is to connect local forage fish abundance with changes in
26 seabird consumption. To this end, we use guillemot chick provisioning data together with

1 abundance estimates for sprat and sandeels to parameterize an MSFR, and predict
2 energetic provision for the chicks by the parent birds. We explore how parents can
3 maintain provisioning of chicks as the abundance of prey species changes, and show how
4 it is possible to suggest conditions in which they are likely to fail in these efforts. From a
5 conservation perspective, these results indicate how sensitive guillemots are to likely
6 changes in prey abundance and thus whether they could provide a useful indicator of
7 good ecosystem status (GES) (Durant *et al.* 2009). From the standpoint of marine
8 management, our findings highlight that to avoid adverse effects on predators, periods
9 when abundances of multiple prey species are low require a more precautionary
10 approach than periods when abundance is only reduced in one prey species..

11

12 **Materials and Methods**

13 To parameterize a functional response, two sets of contemporary data are needed:
14 consumption rates for each important prey, and estimates of the abundance of each prey
15 type at appropriate temporal and spatial scales (Smout & Lindstrom 2007; Matthiopoulos
16 *et al.* 2008). We used a series of analytical steps which are outlined in Figure 1. We used
17 direct observations of prey items provided for guillemot chicks to estimate consumption
18 rates and identify important prey items in the chick diets. Prey abundance was estimated
19 using IBTS survey data for sprat (Hawg 2011) and fisheries-based survey data for sandeel
20 (Jensen *et al.* 2011) both designed to estimate prey abundance at the scale of the ICES
21 statistical rectangle (1° Longitude by 0.5° Latitude, Figure 2). The combined availability of
22 data limited our study to the time period 1992-1994, 1996-2005. We fitted an MSFR using
23 Bayesian methods and used it to make predictions about the effectiveness of chick
24 provisioning under different regimes of prey abundance. The restricted number of data,
25 and the uncertainties in consumption rates and prey abundances were accounted for

1 within the Bayesian analysis, and reflected in the uncertainty in parameters and
2 predictions of the mode.

3 **1. Prey consumption by guillemot chicks**

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

13
14 Chick diets were dominated by sandeels and clupeids (> 95% of the total diet). It was
15 impossible to identify clupeid species from feeding watches, but examination of fish found
16 on ledges indicated all clupeids were sprat. Sprats were treated as a single size class. For
17 sandeels, it was possible for observers to distinguish four size classes in the field: 'small' S
18 (<8 cm), 'medium' M (8-11 cm), 'large' L (11-14 cm) and 'extra-large' XL (>14 cm).
19 Because very few small sandeels were brought in (<5% of items) this category was
20 excluded from analyses.

21 **2. Prey abundance**

22 During the chick-rearing period (late May to mid July) guillemots typically feed within 30
23 km of the Isle of May (Figure 2) (Thaxter *et al.* 2009). This area lies within ICES rectangle
24 41E7 (56.0°N to 56.5°N, 3°W to 2°W). For both sprat and sandeels, we first developed
25 spatial models using data from a larger North Sea area with the aim of borrowing strength

1 from the full data set to inform local estimates of abundance at the level of ICES
2 rectangle 41E7.

3

4 To estimate sprat abundance we made use of IBTS data collected using standardized
5 bottom trawl gear and methodology (IBTSWG 2010). CPUE count data for sprat were
6 available for ICES rectangles throughout the North Sea (Figure 2) for the first and third
7 quarters of the year. These data, and further details about the data collection protocols,
8 are publicly available through ICES (ICES 2012).

9

10 Catch data for fish are over-dispersed and zero-inflated. To account for this, we
11 parameterized a two-stage generalized additive model using the mgcv package in R
12 (Wood 2006). First, a presence-absence model was fitted. Predictions of this model
13 represent the probability P_x that sprats are present at location x . Then, a further model was
14 fitted to describe the abundance of the species A_x given that it is present. Candidate
15 covariates were the spatial co-ordinates of the trawl, year, water depth, quarter of the year,
16 and vessel identity. The final combination of covariates to include was decided in each
17 case on the basis of GCV score (Wood 2006). The two 'best' models were then used to
18 predict mean CPUE given by the product $A_x P_x$ (Wood 2006; Murase *et al.* 2009; Team
19 2011). We used data from the entire North Sea to generate a time series of predictions at
20 the Isle of May in ICES rectangle 41E7 (Figure 2). The original IBTS data were collected
21 consistently only in Quarter 1 (January - March) and 3 (July - September). The Quarter 3
22 hauls may contain young-of-the year, which are likely to be less important than adult sprat
23 as food for guillemot chicks, so we made predictions for Quarter 1 assuming these would
24 remain in the area, forming prey for the chicks in Quarter 2 (April – June).

25

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

$$10 \quad \ln(\hat{CPUE}_{r,q,y,GT}) = \alpha_{q,r} + \beta_{q,y} + \gamma_q \ln(GT) \quad (1)$$

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

22

23 Because the catchability of prey was unknown, the time series of CPUE estimates for both
 24 sandeels and sprats should be treated as indices of abundance rather than absolute

1 estimates of biomass. We tentatively assume these indices are directly proportional to
 2 prey abundance.

3

4 Further details about the estimation of fish abundance indices are given in supplementary
 5 material.

6

7 **3. Model fitting**

8 We used a general MSFR model

$$9 \quad c_i = \frac{(a_i n_i)^m}{1 + t \sum_j (a_j n_j)^m} \quad (2)$$

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

16

17 We fitted two models: in model (1) consumption rate was defined as the number of items
 18 consumed per hour and in model (2) consumption rate was quantified in terms of prey
 19 energetic content (kJ per chick per hour). The energy content of a prey item of average
 20 size was assumed constant for all years except for 2004, a year of unusually poor prey
 21 quality. For all years except 2004 we used values of 135.0 kJ for sprats and 15.1 kJ, 40.4
 22 kJ and 86.9 kJ for M, L and XL sandeels respectively. For 2004 we used 11.9 kJ for
 23 sprats, and 3.52 kJ, 17.5 kJ and 20 kJ for M, L and XL sandeels respectively (Wanless *et*
 24 *al.* 2005).

1

2 We assumed observations of prey delivery to chicks could be modeled as a Poisson
3 process, with the hourly rate of delivery predicted by the functional response in Equation 2
4 as c_i . To account for unidentified prey items, we assumed that for prey species i the
5 probability that it is identified is p_i and therefore the probability that it is not identified is $1-p_i$.
6 We were then able to fit the observed counts of identified species along with the counts of
7 unidentified items, and the prey-specific parameters p_i were estimated during the model-
8 fitting process, along with the parameters of the functional response itself.

9

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

14

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

20

21 We fitted the model using a Bayesian approach and Markov chain Monte Carlo (MCMC)
22 algorithm implemented with the freely available software WinBUGS (Lunn *et al.* 2000;
23 Smout *et al.* 2010). Code and further details are provided in supplementary material.

24

25 After fitting, models using prey items and prey energy as currency were compared and the
26 best model was chosen based on the Deviance Information Criterion (DIC). This quantity,

1 which can be readily calculated based on the output of the MCMC, is analogous to the
2 AIC in frequentist statistics (Spiegelhalter *et al.* 2002).

3 **4. Predictions**

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

6

7 **Results**

8 **1. Prey Consumption**

9

10 During the study, there were 767 hours of watches during which 14,938 prey items were
11 recorded. 27.6% were sandeel, 52.3% were sprat, and 21.1% were unidentified.

12

13 **2. Prey Abundance**

14 For sandeel, the GLM explained just below a third of the total observed variation in North
15 Sea CPUE in Quarter 2. For sprat, the chosen models for both the presence absence data
16 and the abundance data included the covariates *x*, *y*, *year*, *quarter*, and *vessel*. Deviance
17 Explained scores were 38.6% and 38.9% respectively. Indices of prey abundance for all
18 prey types are shown in Figure 3. The time series ended on a historic high for sprats. In
19 contrast, abundance indices for L and XL sandeels peaked at the start of the period, was
20 also high for L sandeels in 1997 and peaked again for M sandeels in 2000.

21 **3. Functional response models**

22 Using DIC, Model (2) was preferred (Table 1) and subsequent predictions were calculated
23 from this 'energy-based' model. Parameter estimates and 95% Bayesian credible intervals

1 are given in Table 2. The ‘currency’ for prey abundance is energy in kJ, and we give the
2 value of the parameter c_{max} which is the asymptotic consumption rate in these units.

3

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

7

8 **4. Predictions**

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

19

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

26

1 Variation in daily provisioning rates of chicks in response to prey abundance is shown in
2 Figure 6. Higher levels of sandeel consumption (left hand panel) are predicted only for
3 prey regimes that are relatively low in sprat and high in sandeel. Sprat consumption
4 (centre panel) remains high over a wide range of combinations of prey abundance. In
5 general, provisioning is consistent with observed rates (Wanless *et al.* 2005). Historical
6 prey abundances for sandeels range from approximately 2 to 100, and for sprat from 11 to
7 100; thus the main part of the 'area' representing combinations of prey availability falls
8 within these limits. The right-hand panel in Figure 6 represents the total daily energetic
9 value of prey items delivered to the chick, which appears to remain high over much of the
10 range covered by the historical data. The figure also suggests a region of particularly
11 sharp decline in this rate, mainly due to changes in sprat abundance. A solid line (with
12 95% Bayesian credible intervals shown as dotted lines) represents the contour below
13 which energy intake drops to $< 75\%$ of its maximum predicted value. Although this 'limit' is
14 presented for illustrative purposes, the approach highlights how MSFR can be used to
15 indicate levels of prey that result in energetic intakes above/below a target threshold.
16 Further work linking food intake to demographic rates is needed to estimate the level of
17 energetic provisioning that would represent a 'success threshold' for chick rearing
18 consistent with conservation objectives (Wanless *et al.* 2005; Cury *et al.* 2011).

19

20 **Discussion**

21

22 We parameterized an MSFR for guillemots provisioning their chicks, using Bayesian
23 methods. The fitted MSFR allows us to predict intake rates under dynamically shifting
24 conditions of prey abundance, offering potential benefits for the management of predators
25 and ecological communities. Where predation has an appreciable impact on prey, this can
26 be quantified, which is important where the aim is to manage fish stocks using an

1 ecosystem based approach that takes account of multi-species trophic interactions
2 (Lindstrom *et al.* 2009; Ripple & Beschta 2012). Where conservation of predator species
3 themselves is of interest then an MSFR can predict 'critical' levels of prey below which
4 predator intake rates are likely to drop substantially (Figure 6). This is valuable in itself,
5 and also should improve our understanding of observed empirical relationships between
6 predator life history and prey abundance (Testa *et al.* 1991; Boyd *et al.* 1994; Sydeman
7 1999; Furness & Tasker 2000; Mori & Boyd 2004). Thus a fitted MSFR has the potential to
8 improve inferences about the system based on using the predator as an indicator (Boyd &
9 Murray 2001; Durant *et al.* 2009; Cury *et al.* 2011).

10

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

21

22 The values of model parameters have ecological implications and can potentially improve
23 our understanding of predator-prey dynamics of Isle of May Guillemots. However, the
24 interpretation of the 'preference parameters' a_i is not straightforward. Prey abundances
25 were scaled to improve numerical performance, and our original CPUE estimates were
26 indices rather than direct estimates of prey abundance. According to our model, if all prey

1 were present in the system at historically high abundance levels, then sprat would be
2 the most important part of the chick diet. Of the sandeels, the medium-size category would
3 then appear to be 'preferred' over the larger sandeels. One possible explanation is that
4 parents carrying larger sandeels may be vulnerable to kleptoparasitism while in flight. It is
5 also likely that the larger sandeels are relatively scarce, even when they are (in historical
6 terms) at high levels.

7

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

13

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

18

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

1
2 If there is (as our model suggests) general consistency in chick energy intake over a wide
3 range of likely combinations of prey abundance, this implies guillemots are able to some
4 extent to maintain provisioning of their chicks despite changes in the abundance of their
5 key prey. This contrasts with other species e.g. black- legged kittiwakes (*Rissa tridactyla*),
6 which are very sensitive to changes in the abundance of one prey type, and is consistent
7 with the results of guillemot studies in other areas (Piatt *et al.* 2007; Wanless *et al.* 2007).
8 However, it should be noted that while parent birds may sometimes be able to maintain
9 their delivery rate by adjusting their foraging, they are not necessarily able to compensate
10 for changes in the energetic content of prey (Wanless *et al.* 2005). There may also be
11 'hidden costs' to the adaptable foraging strategies of parent birds. If parents make longer
12 trips to compensate for reduced prey abundance, they may spend less time guarding their
13 chick resulting in higher chick mortality (Ashbrook *et al.* 2008). Trade-offs between the
14 costs of different parental foraging strategies and reproductive success would be a fruitful
15 area for further investigation especially if informed by detailed data on the energetic
16 content of prey.

17
18 Our study suggests that energy intake of guillemot chicks may not be a particularly
19 sensitive indicator of fluctuating prey abundance. However, where diet and consumption
20 are regularly monitored (as at the Isle of May) there is also the potential to use these
21 records directly to indicate changing prey abundance and the state of the system. This
22 would ideally be done in combination with observations of other indicator species,
23 appropriate to the area (Wanless *et al.* 2007). Our model also suggests regimes of prey
24 abundance that allow for chick provisioning above a given threshold level, provided we are
25 able to estimate threshold levels for satisfactory energy intake (Figure 6). In order to do
26 this, we would need to develop the approach further to establish links between chick

1 provisioning rates, prey abundance, breeding success and possibly other demographic
2 rates. This could be a very fruitful direction for future work, and results could feed into
3 management strategies to support conservation efforts for sensitive species within
4 programs focused primarily on different objectives e.g. optimizing commercial fishing using
5 approaches based on Maximum Sustainable Yield (Mace 2001; Constable 2011). An
6 important advantage of our Bayesian methodology is that the uncertainty of model
7 predictions can be estimated robustly, allowing us to quantify the level of risk for
8 dependent species associated with a 'low prey' regime (Harwood & Stokes 2003).

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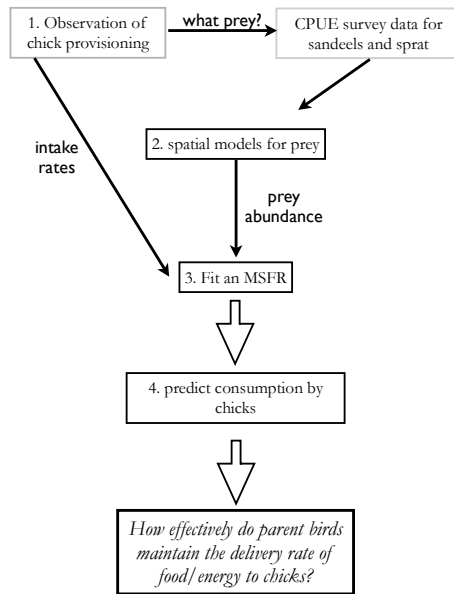
12 **Acknowledgements**

13

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15 by the FACTS project (www.facts-project.eu). The guillemot chick diet and provisioning data were collected
16 as part of CEH's Isle of May long-term study (IMLOTS) partly funded by JNCC.

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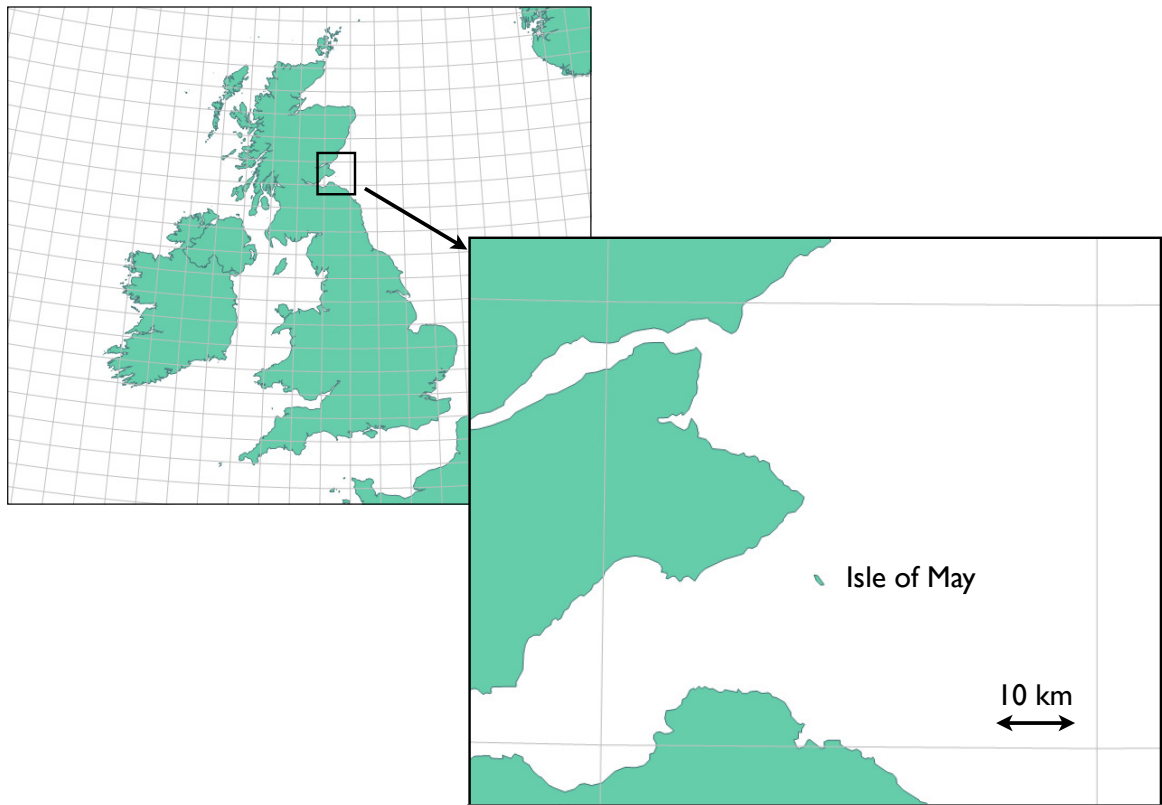
Figures



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Figure 1: Outline of the modeling steps involved in the analysis

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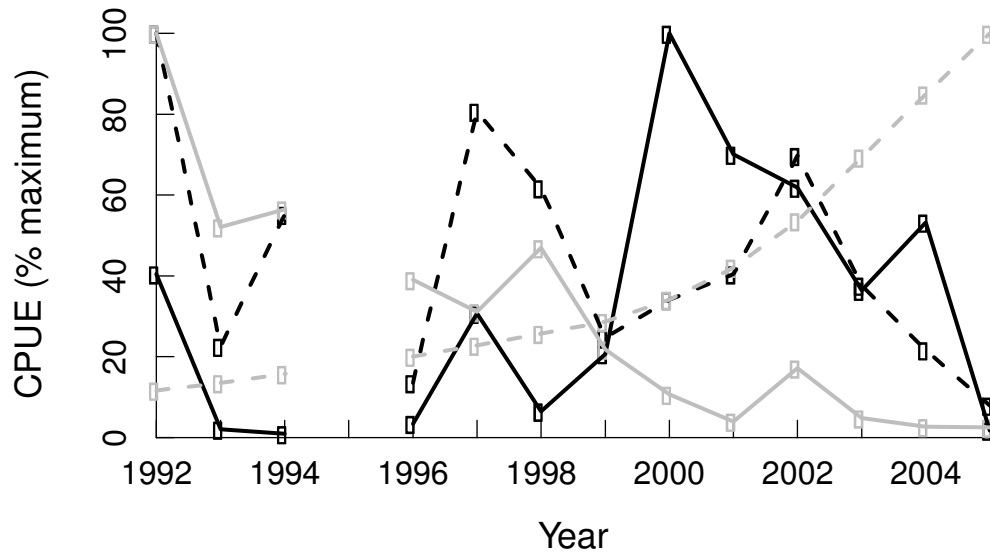
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14 Figure 2: A map of the UK showing ICES statistical rectangles. 41E7, the rectangle containing the Isle of May
15 study area, is shown in more detail.

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5 Figure 3: Prey abundance indices for the years 1992-2005 (no data available for 1995). Sprat (grey dashed

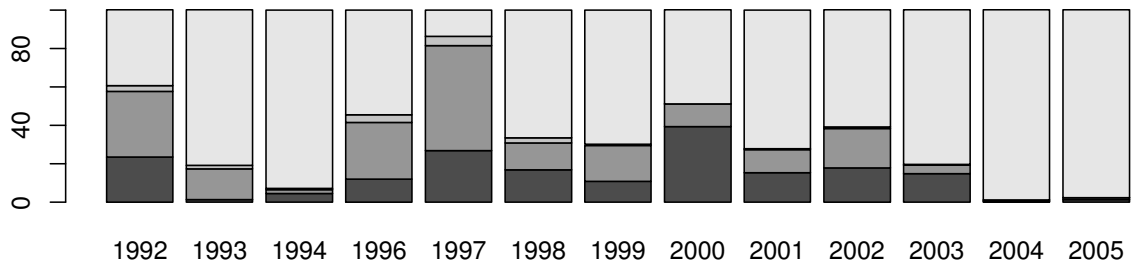
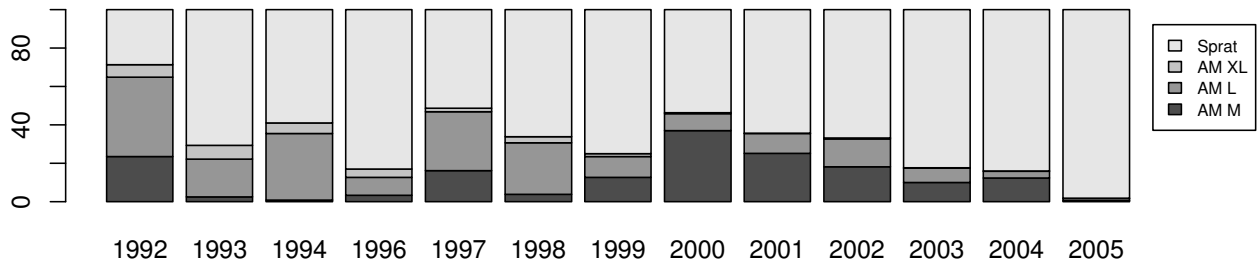
6 line); sandeels size class M (black line); L (black dashed line); XL (grey line).

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5 Figure 4: The composition of the diet of guillemot chicks during the years of the study (% by count).

6 Predictions from Model 2 are shown in the upper panel, and observed counts are represented in the lower
 7 panel. Greyscale represents (from light to dark) sprat, sandeel (AM) size XL, sandeel size L, and sandeel size
 8 M respectively.

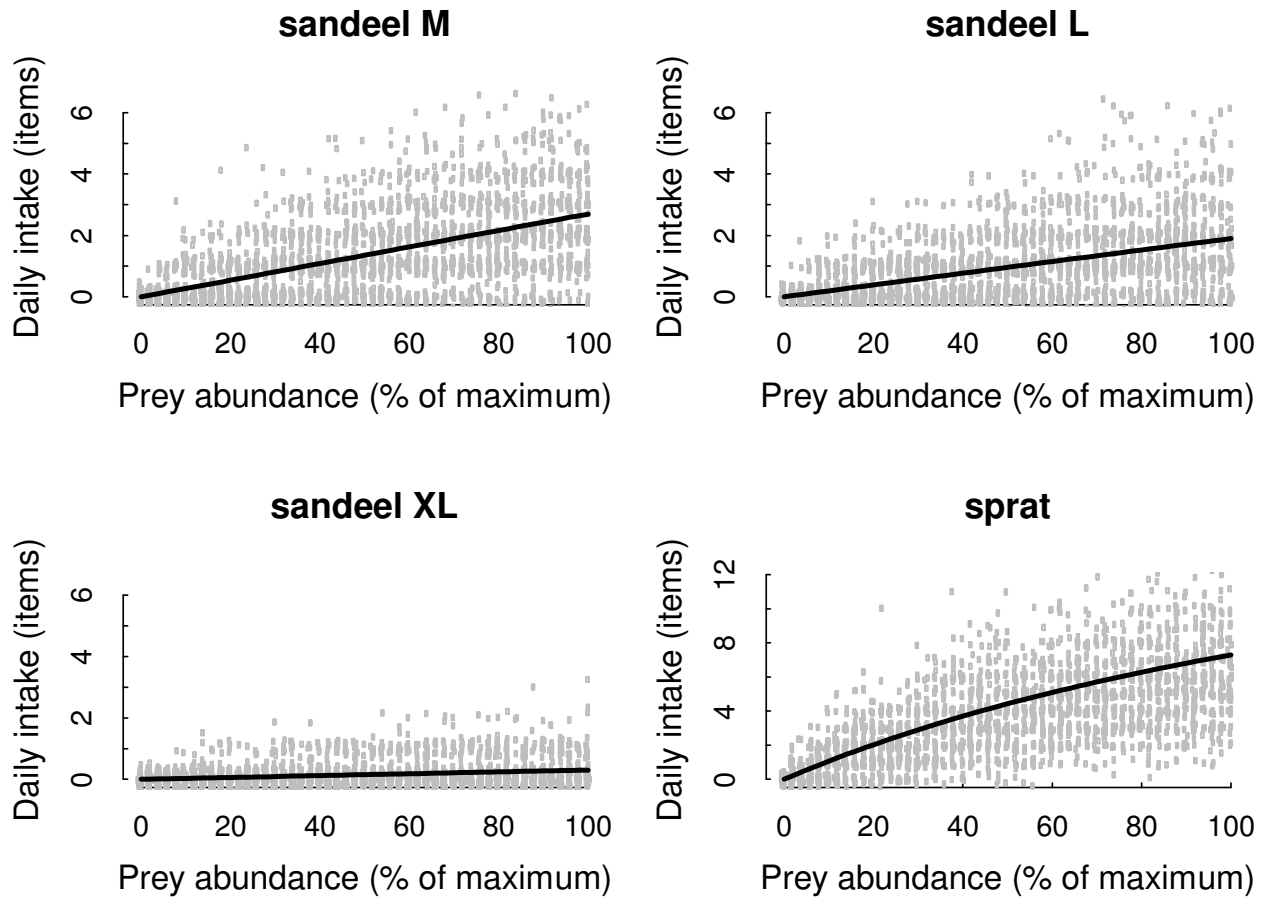
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2 Figure 4 Multi-species functional response of guillemots provisioning their chicks (Model 2) with two prey
 3 species sprat and sandeel. Bold curves show the functional response based on mean parameter estimates,
 4 while the points are simulated values based on 100 random parameter sets drawn from the Markov chain,
 5 with random Poisson sampling (for illustrative purposes noise is also added to the integer values to display
 6 points separately). Each curve represents the response of the birds to one target prey type, when the
 7 'other' prey in the system is at low levels.

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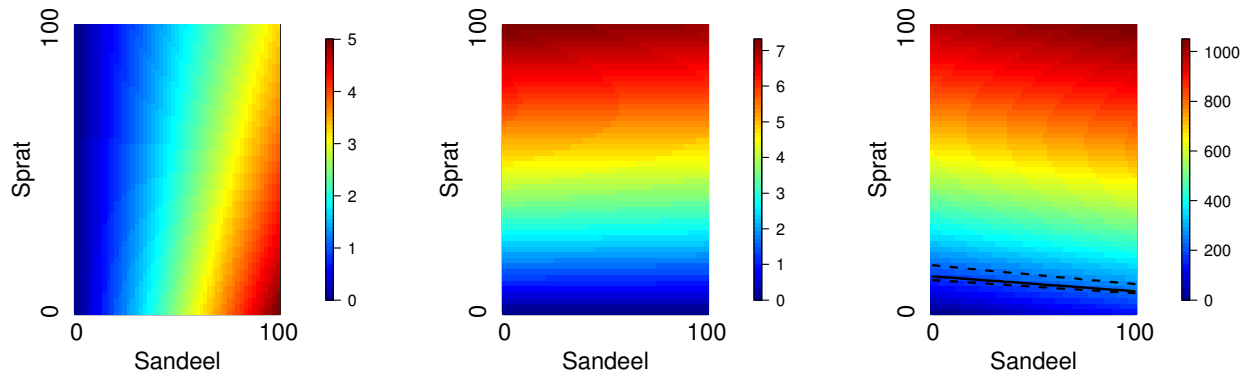
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2 Figure 6: Consumption surfaces. Surface colours indicate predicted consumption rates, in response to
 3 variation in both sprat and sandeel abundance. Abundances of all prey types vary from 0 to 100 where 100
 4 represents the historical maximum. *Left panel*: consumption rate of sandeel (items per day): surface
 5 colours indicate the net daily consumption rate of sandeel according to the colour scale. *Centre panel*:
 6 consumption of sprat (items per day). *Right panel*: net energetic intake by chicks (in kJ per day, including
 7 contributions from both sandeel and sprat). The solid line represents a contour at which net energy intake
 8 by chicks is at 75% of its maximum value (95% Bayesian CIs are shown as dotted lines). The area below the
 9 contour represents prey abundances for which chick provisioning rates fall below this level. All predictions
 10 are from Model 2.

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2 Table 1: Mathematical form of functional response Models 1 and 2 with associated DIC values. c_i represents
 3 the consumption rate for prey i , and n_i represents the abundance of prey i

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

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

3

	Parameter	Mean	95% CI
Preference	a_M	3.94×10^{-3}	$(3.01 \times 10^{-3}, 4.95 \times 10^{-3})$
	a_L	2.82×10^{-3}	$(2.16 \times 10^{-3}, 3.56 \times 10^{-3})$
	a_{XL}	4.41×10^{-4}	$(3.24 \times 10^{-4}, 5.73 \times 10^{-4})$
	a_{sprat}	1.66×10^{-2}	$(1.15 \times 10^{-2}, 2.32 \times 10^{-2})$
Switching parameter	m	1.00312	(1.000,1.012)
Maximum consumption rate	c_{max}	57.7 kJ h^{-1}	$(49.9, 70.43) \text{ kJ h}^{-1}$
Probability of identifying sprat	p_{sprat}	0.769	(0.758,0.779)
Probability of identifying sandeel	$P_{sandeel}$	0.844	(0.827,0.859)

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