

Combined spatial and tidal processes identify links between pelagic prey species and seabirds

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ABSTRACT: To gain further insight into the foraging behaviour of predator species, it is essential that interactions between predators, their prey and the surrounding environment are better understood. The primary purpose of this study was to determine the underlying processes, both physical and biological, driving variation in the times and locations of seabird foraging events. Using fine-scale simultaneous measurements of seabird abundance, prey density and oceanographic variability collected during an at-sea survey in the Firth of Forth region of the North Sea, zero-inflated negative binomial models were applied to identify the underlying processes driving foraging behaviour in 2 seabird species: the common guillemot *Uria aalge* and the black-legged kittiwake *Rissa tridactyla*. Both guillemot and kittiwake models showed consistency in their results; specific tidal states and thermal stratification levels explained observed increases in abundance. The secondary purpose of this study was to identify key oceanographic processes driving variability in prey density and determine if these were comparable to those underlying the behaviour of foraging seabirds. Log-transformations of 2 measures of prey density, $NASC-40-50_{MAX}$ and $NASC-50-70_{MAX}$, were modelled using generalised least squares. Similar tidal conditions and thermal stratification levels explained distributional patterns, suggesting that these processes act to increase prey availability, creating profitable foraging opportunities for predators to exploit. This has been termed the tidal coupling hypothesis and identifies that critical marine habitats occur not only at limited spatial locations but also within specific temporal intervals relating to the tidal cycle. Furthermore, by incorporating this oceanographic influence on foraging habitat, fine-scale predator–prey relationships were also identified. Foraging guillemots and kittiwakes displayed a Type II functional response to increasing values of $NASC-40-50_{MAX}$.

KEY WORDS: Predator–prey interaction · Physical–biological coupling · Spatio-temporal variability · Foraging ecology · Critical marine habitat · Trophic relationship

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INTRODUCTION

Heterogeneity throughout the marine environment has been well documented and is reflected not only through the distributional patterns of marine resources but also in the behaviour of the species that rely on such materials (Hooker & Gerber 2004, Worm et al. 2005). This results in the formation of distinct

feeding locations, where species from a number of trophic levels may aggregate (Sydeman et al. 2006). Such locations are vital for the successful transferral of energy up the food web and have therefore been termed critical marine habitats. These habitats may be subject to a specific set of environmental conditions, varying in both space and time (Wakefield et al. 2009, Scott et al. 2010).

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The observed patchiness of the marine environment is often predictable and driven by underlying physical processes that result in areas of increased primary productivity or plankton accumulation, which attract prey resources (Schneider 1982, Wolanski & Hamner 1988, Hyrenbach et al. 2000, Yen et al. 2006). Indeed, the association of seabirds with larger scale (>15 km) oceanographic features such as eddies and fronts has been well documented (Hunt et al. 1999, Louzao et al. 2006, Piatt et al. 2006, Bost et al. 2009). As spatial scale decreases, or within areas of increased productivity, prey may become more accessible through other interactions with the environment (Wakefield et al. 2009). However, currently the influence that finer-scale (<15 km) oceanographic variability has on seabird foraging behaviour is poorly understood, probably due to the complex and dynamic nature of the combined environmental and trophic interactions linking the two (Daunt et al. 2006, González-Solis & Shaffer 2009, Embling et al. 2012).

At larger spatial scales, interactions between seabirds and their prey have been prominent, and positive correlations are often found (Russell et al. 1992, Skov et al. 2000, Fauchald & Erikstad 2002). However, foraging activity at finer spatial scales tends to be more concentrated (Hamer et al. 2009), and subsequent predator–prey correlations should reflect this. Regardless, research has shown some contrasting results, and over fine scales, often only weak or even negative correlations are detected (Heinemann et al. 1989, Logerwell & Hargreaves 1996, Logerwell et al. 1998, Fauchald et al. 2000).

When seabirds concentrate their searching efforts at specific oceanographic features, any relationship with their prey would be limited within a small proportion of their potential range (Decker & Hunt 1996). Interactions would be subject to not only the spatial heterogeneity of the marine environment but also the tidal temporal variability of underlying driving processes, something recognised by only a handful of studies (Irons 1998, Holm & Burger 2002, Zamon 2003, Embling et al. 2012). Consequently, incorporating oceanographic variability (both spatially and temporally) into predator–prey studies of seabirds should provide further insight toward top predator foraging behaviour.

To be able to identify the characteristics of momentary predator–prey encounters, simultaneous measurements of predators, prey and oceanography are required (Schneider & Piatt 1986), an entity sparse within the literature (Tremblay et al. 2009). Furthermore, current survey designs and sampling regimes may not be appropriate for such studies. Aiming to

address this, the purpose of this study was 2-fold. First, expanding on recent work by Scott et al. (2010), we aim to further identify the underlying biological and physical processes driving predator–prey encounters across a region of the North Sea with a focus on determining tidal temporal variability in seabird foraging habitat. Secondly, we aim to also identify the oceanographic parameters driving both spatial and tidal temporal variability in prey density. We hypothesise that similar oceanographic parameters will drive variation in both seabird species and their prey and suggest that by incorporating these oceanographic parameters into fine-scale studies, the mechanistic relationships between seabird predators and their prey will become evident.

MATERIALS AND METHODS

Study area and species

The study area is located in the Firth of Forth region of the North Sea off the east coast of Scotland, UK (55.75° to 56.75°N and 0.45° to 2.70°W). The North Sea is a semi-enclosed shallow (<200 m deep) shelf sea where interactions between tidal currents, solar irradiation, wind patterns and bathymetry create a mosaic of mixed, stratified and frontal regions during the spring and summer months (Scott et al. 2006, Sharples 2008). This creates a diverse array of foraging habitats accessible to a range of seabird species, where neighbouring bird colonies at Bass rock and the Isle of May host in excess of 40 000, 26 000, 3000 and 3000 breeding pairs of gannets *Morus bassanus*, common guillemots *Uria aalge*, black-legged kittiwakes *Rissa tridactyla* and razor-bills *Alca torda*, respectively (Mavor et al. 2005). To determine the relative importance of a multitude of foraging habitats to different species, this study focuses on 2 seabird species with contrasting foraging behaviours. The common guillemot employs a pursuit dive strategy (Montevecchi et al. 2006), and the black-legged kittiwake is a surface feeder (Furness & Tasker 2000). These species primarily prey on sandeels *Ammodytes* spp. and clupeids such as herring *Clupea harengus* and sprat *Sprattus sprattus* (Furness & Tasker 2000, Daunt et al. 2006).

Data collection

Eight transects across the study area, approximately 10 km apart, were carried out during a 1-time

survey from 8 to 17 June 2003 by the RV ‘Pelagia’ (a 66 m Netherlands Institute for Sea Research vessel). The direction of these transects alternated by day, changing from an east-to-west direction to a west-to-east direction. Daily starting locations were dependent on the finishing location the day before and did not correspond to the beginning or end of transect lines. This allowed for time of day, location and a variety of habitat types to be randomly sampled (examples of habitat combinations, both spatially and temporally, are shown in Table 1). For further details on the methods than those provided, refer to Scott et al. (2010).

Seabird data

Foraging seabirds were recorded via standard strip transect techniques for ship-based seabird surveys in the North Sea (Tasker et al. 1984, Camphuysen et al. 2004). Continuous counts of seabirds were taken by a minimum of 2 trained observers from a platform approximately 20 m above sea level. Counts were taken at 5 min intervals within a radius of 300 m ahead and a strip 300 m to the side of the vessel with the best available light conditions. Each 5 min interval covered an average distance of 1.24 km. To distinguish feeding and foraging seabirds from non-feeding individuals, standard observational techniques (Ashmole 1971) were expanded on (Camphuysen & Garthe 2004). Birds that were associated with or attracted by the research vessel were not recorded.

Table 1. Various combinations of habitats sampled both spatially and temporally during the survey period. Morning (a.m.) is defined as 00:00 to 11:59 h and afternoon (p.m.) as 12:00 to 23:59 h. Low *ThermSTRAT* is greater than a temperature difference of 3.5 °C, and high *ThermSTRAT* is greater than or equal to a temperature difference of 3.5°C. Number of samples obtained at different stages of the tidal cycle at different times of the day in different habitat scenarios are shown

Tidal flag	<i>ThermSTRAT</i>				Total
	Low		High		
	a.m.	p.m.	a.m.	p.m.	
<i>Increasing ebb</i>	34	4	30	34	102
<i>Maximum ebb</i>	20	50	49	11	130
<i>Decreasing ebb</i>	31	66	45	28	170
<i>Increasing flood</i>	32	12	33	28	105
<i>Maximum flood</i>	61	17	45	33	156
<i>Decreasing flood</i>	23	7	78	30	138
Total	201	156	280	164	801

Prey acoustic data

Prey acoustic data were collected using the SIMRAD EK500 scientific echosounder (Bodholt et al. 1989). This operated at 3 frequencies (38, 120 and 200 kHz) and was configured to ping at each simultaneously every 1 s, with a pulse duration of 1 ms for each frequency. Data were logged from the echosounder to a personal computer with Myriax’s Echolog software. The echosounder was run simultaneously with a Scanfish (see below) during all seabird observations throughout daylight hours.

It is noted that the SIMRAD EK500 echosounder had not been calibrated for the survey. However, a sensitivity test carried out by Embling et al. (2012) showed that there were no adverse effects on the acoustic variables as a result of this.

Oceanographic data

Physical and biological characteristics of the entire water column were sampled via the Scanfish (*MKII 1250*, EIVA) carrying a Sea-Bird 911 CTD and Chelsea Instruments Aquatraka MKIII chlorophyll fluorometer. This equipment collected continuous vertical and horizontal information on temperature, salinity, density and fluorescence, resulting in a vertical spatial resolution of between 0.5 and 1 m to within 2 to 5 m of the seabed and surface and a horizontal resolution of less than 400 m.

The Aquaflo installed on the RV ‘Pelagia’ ran during the entire cruise and logged the following data at 1 min intervals: time, latitude, longitude, water depth (m), wind speed (knots) and direction (compass bearing), and sea surface temperature, salinity and fluorescence.

Data processing

For the continuous measurements from the Scanfish, Aquaflo and SIMRAD EK500 to be comparable to the 5 min bin observations of foraging seabirds, summaries of biological and physical characteristics of the water column were created for the same 5 min intervals.

Prey acoustic data

Prey acoustic data were analysed between 10 m of the surface and 0.5 m of the seabed to avoid the near-field effect of transducers and bottom pixels.

Data were sorted into 3 threshold groups (greater than –40 dB, –40 to –50 dB and –50 to –70 dB), each containing nautical area scattering coefficient (NASC) values at 5 min intervals for every 5 m change in depth through the water column (further details in Supplement 1 at www.int-res.com/articles/suppl/m479p203_supp.pdf). This provided an index of potential prey density, where NASC ($\text{m}^2 \text{nmi}^{-2}$) is proportional to density (MacLennan et al. 2002).

Threshold groups were roughly assigned multi-species groupings based on similarities in specific backscattering characteristics. Above –40 dB, backscatterings are expected to be from gadoid species such as cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*. Between –40 and –50 dB, NASC values represent the density of pelagic species such as herring and sprat. Below –50 dB to –70 dB, scatterings are likely to represent sandeels and larger zooplankton species (MacLennan & Simmonds 1992).

Corresponding to the time allocations of the 5 min bins, acoustic data in the 3 threshold groups were allocated bin identifications. This resulted in each bin containing 1 rotation of density measurements at depth. For each threshold group, in each bin, the maximum NASC value within the water column and the depth at which it occurred were extracted. This created 2 variables for each threshold group, NASC_{MAX} and $\text{Depth}_{\text{MaxNASC}}$.

Oceanographic data

Using the time allocations of the observational 5 min bins, physical data collected via the Scanfish and Aquaflow were sorted into corresponding 5 min bins. The following variables were included in the final analysis: potential tidal stratification h/U^3 , maximum sub-surface chlorophyll CHL_{MAX} , thermal stratification *ThermSTRAT*, density gradient *DenGRAD*, depth variation $SD(h)$, tidal flag *Tidal Flag*, wind speed *WindSPEED* and wind direction *WindDIR*. Time of day was excluded in preference of tidal flag, as temporal variations in the foraging behaviour of seabirds have been linked to specific phases of the tidal cycle (Irons 1998, Holm & Burger 2002, Daunt et al. 2006). Including time of day could mask such interactions. Brief outlines of oceanographic variables are given below (further details can be found in Scott et al. 2010).

Potential tidal stratification h/U^3 . In shallow (<200 m) tidal mixing seas, the tendency of the

water column to stratify can be quantified in the depth (h) divided by the mean tidal speed (U) cubed to give h/U^3 (Simpson & Hunter 1974, Sharples 2008, Scott et al. 2010). Small values indicate areas where the water column is likely to remain mixed throughout the year, whilst larger values represent areas likely to become thermally stratified in the summer months. Depth was taken from the British Geological Survey (BGS; www.bgs.ac.uk/products/digbath250/sample.html) and mean monthly depth mean tidal speed (for June 2003) from the POLPRED tidal prediction model (Proudman Oceanographic Laboratory, Natural Environment Research Council [NERC], UK) to give a tidal stratification index, $\log_{10}(h/U^3)$. The BGS depth data were used over *in situ* measurements to retain consistency with the outputs from the POLPRED tidal prediction model, which is run using BGS data.

Maximum sub-surface chlorophyll CHL_{MAX} . Chlorophyll samples taken from a range of depths and locations throughout the study region were used to calibrate the voltage output from the fluorometer on the Scanfish to give chlorophyll concentration CHL (mg m^{-3}). Using the formula $\text{CHL} = a \times \text{voltage}^b$, a calibration equation of CHL (mg m^{-3}) = $19.85 \times \text{voltage}^{1.91}$ (SE: $a = \pm 4.677$, $b = \pm 0.187$; $n = 70$) was yielded. CHL_{MAX} was then defined as the highest concentration of chlorophyll within each 5 min bin regardless of its position in the water column.

Thermal stratification *ThermSTRAT* and density gradient *DenGRAD*. Variation in stratification may arise through seasonal and daily fluctuations in solar radiation, wind-driven surface mixing and tidally driven bottom mixing (Fearnhead 1975). Using outputs from the Scanfish, due to the added influence of freshwater at the mouth of the Firth of Forth (see Scott et al. 2010), the mean temperatures above and below the pycnocline were calculated within each 5 min bin, the difference between the two giving an index of the level of thermal stratification in the water column. In contrast to potential tidal stratification h/U^3 , which is a modelling index (and only accounts for stratification relating to depth and tidal speed), thermal stratification is measured *in situ* and gives a measure representative of current conditions. Density gradient was taken as the difference in density across the width of the pycnocline. The depths of the top and bottom of the pycnocline were identified where the vertical density gradient dropped below 0.01 kg m^{-4} .

Depth variation SD(h). Using the depth data from the ship's Aquaflo output, the standard deviation in depth was taken for each 5 min bin. As slope would only be calculated in east-west or west-east directions, depth variation provides a more useful variable for the effects of changes in topography.

Tidal flag. A tidal flag index (a combination of tidal speeds and direction) was calculated from the POLPRED prediction model to give 6 different 2 h and 5 min categories of tidal state: *Increasing ebb* (0 to 85% of maximum current velocity), *Maximum ebb* (>85% of maximum current velocity), *Decreasing ebb* (0 to 85% of maximum current velocity), *Increasing flood* (0 to 85% of maximum current velocity), *Maximum flood* (>85% of maximum current velocity) and *Decreasing flood* (0 to 85% of maximum current velocity). Although individual locations were not sampled repeatedly on multiple tidal stages, because we travelled from less to more and from more to less stratified waters on alternate days, spatially similar oceanographic conditions (e.g. stratification levels) were sampled over a range of tidal conditions (Table 1).

Wind speed WindSPEED and direction WindDIR. Using the Aquaflo data set, the averaged wind speed and direction were taken for each 5 min bin, as recent studies have indicated that wind interacting with surface currents may create potential foraging habitats (B. E. Scott et al. unpubl.).

Data analysis

Data analysis was performed in R, version 2.13.0 (R Development Core Team 2011). All potential explanatory variables were screened using histograms, dot plots and scatter plots to determine distributions, extreme values and potential outliers. All prey $NASC_{MAX}$ variables and $SD(h)$ were log-transformed ($\log[NASC_{MAX} + 1]$; $\log[SD(h) + 1]$) due to non-normality in distributions and some extreme values.

Pair's plots, correlation coefficients and variance inflation factors (VIF) were used to identify any co-linear variables. If 2 variables were highly co-linear ($r > 0.7$ or $VIF > 3$), one of the co-linear variables was deleted from further analysis (Zuur et al. 2009). This was relevant for stratification indices of temperature (*ThermSTRAT*) and density and gradients in temperature and density (*DenGRAD*) across the pycnocline. To include a range of thermal and density variables that were not correlated, *ThermSTRAT* and *DenGRAD* were selected (further details in Scott et al. 2010).

Modelling variation in the abundance of seabirds in relation to prey and oceanography

The seabird survey produced count data suitable for a modelling framework based on generalised linear models (GLMs). Typically, spatial counts of flocking birds exhibit over-dispersion, caused by both large counts of individuals and zero inflation resulting from an excessive number of zero counts (Agarwal et al. 2002, Martin et al. 2005). Such an excess of zero counts may arise from several scenarios ranging from the low occurrence of species to a strong habitat preference that leads to many sites being unused. Ignoring such characteristics of a data set can lead to incorrect conclusions and, therefore, the use of classical GLMs is limited (Martin et al. 2005, Zeileis et al. 2008).

Variation in seabird abundance was modelled using a zero-inflated negative binomial (ZINB) model from the R package *pscl* (Jackman 2011). This accounted for an excess in zero values, whilst also allowing for further over-dispersion in the data set typical in seabird studies (Zipkin et al. 2010). The use of a negative binomial distribution over a Poisson distribution was better fitted to the data, and this was confirmed through a likelihood ratio test (Zuur et al. 2009).

ZINB models work using a 2-part modelling approach. First, the model uses presence/absence data to determine the probability of measuring a zero observation given specific habitat characteristics. Second, the influence of set explanatory variables on variation in abundance is determined by taking the positive abundance counts and the proportion of the zero counts not accounted for by the habitat characteristics in the first part of the model (Martin et al. 2005, Zuur et al. 2009). Therefore, the predicted abundance of seabirds is dependent, first, on the probability of a zero count and, second, on specific explanatory variables modelled in the count component of the model.

For the 2 seabird species modelled, variables initially included in the habitat part of the model were those stationary variables where potential seabird habitat may occur: h/U^3 , CHL_{MAX} and $\log SD(h)$. Explanatory variables in the count part of the model were those that vary on shorter time scales: *WindSPEED*, *WindDIR*, *Tidal Flag*, *DenGRAD*, *ThermSTRAT*, CHL_{MAX} , $\log NASC-40_{MAX}$, $\log NASC-40-50_{MAX}$, $\log NASC-50-70_{MAX}$, $Depth-40-50_{MaxNASC}$ and $Depth-50-70_{MaxNASC}$. CHL_{MAX} was included in both parts of the model, as variation may occur on different time scales (ranging from a few days to sea-

sonal fluctuations; Cloern 1991), influencing both the probability of a zero observation and variation in seabird abundance. *ThermSTRAT* and h/U^3 , although both representing indices of stratification, did not display signs of being correlated. In any case, they were used in separate parts of the model to determine their relative roles in influencing changes in seabird abundance of the probability of a zero observation, respectively. *Depth-40_{MaxNASC}* was not included in the analysis due to a high number of not-applicable measurements resulting from zero values of *NASC-40_{MAX}*.

Quadratic terms were included to model non-linear relationships. To avoid issues with convergence and over-fitting, biological reasoning and exploratory analysis through bi-variate scatter plots and basic generalised additive models determined if a quadratic term should be considered for an explanatory variable (Crawley 2007).

The most parsimonious model was selected through forwards and backwards stepwise selection using Akaike's information criterion (AIC) and likelihood ratio testing. Pearson residuals of the resulting models were extracted and plotted against the fitted values of the model, the response variable and all explanatory variables to identify any violation of model assumptions. Residuals were plotted through space to identify any spatial patterns indicating potential non-independence of observations. Fitted values were plotted against observed values to evaluate goodness of fit (Potts & Elith 2006). Finally, where extreme values were identified in the seabird response variables, models were fitted with both their inclusion and exclusion to determine their influence on results.

Modelling variation in prey density in relation to oceanographic parameters

Variation in prey density (*NASC_{MAX}*) was modelled for 2 threshold groups, -40 to -50 dB and -50 to -70 dB, using generalised least squares with restricted maximum likelihood estimation from the nlme package (Pinheiro et al. 2011). The best-fitting model was selected with maximum likelihood estimation through forwards and backwards stepwise selection using AIC alongside Bayesian information criteria and likelihood ratio testing. Explanatory variables included in the analysis were *Tidal Flag*, *DEN-GRAD*, *ThermSTRAT*, h/U^3 , *CHL_{MAX}* and *Log SD(h)*.

Log transformations of both prey response variables ($\log[NASC_{MAX} + 1]$) were used to deal with per-

sistent residual patterns violating assumptions of homogeneity, normality and independence. To account for spatial autocorrelation issues in the data set, a spatial correlation structure was incorporated into each of the models. Different structures were tested (exponential, Gaussian, linear, rational quadratic and spherical), and through the comparison of AIC values and visual inspection of semi-variograms, a rational quadratic structure was included in each of the models (Zuur et al. 2009).

Normalized residuals were extracted from each model and plotted against the fitted values, response variable and all explanatory variables to identify potential violation of model assumptions. Fitted values were plotted against observed values to evaluate goodness of fit.

RESULTS

Distributional patterns of the 2 seabird species and prey threshold groups are shown in relation to thermal stratification in Figs. 1 & 2, respectively (distributional patterns in relation to other oceanographic variables can be found in Supplements 2 & 3 at www.int-res.com/articles/suppl/m479p203_supp.pdf). Guillemot and kittiwake distributions appear restricted within specific ranges. Acoustic measurements from the -40 to -50 dB threshold group appear sparser and more patchily distributed than those from the -50 to -70 dB threshold group, which are distributed fairly evenly through the study area.

Of the 801 bins surveyed, foraging seabirds were observed in 396 (49%). Kittiwakes were found in 91 (11%) and guillemots in 363 (45%). The total number of individual observations by species was 488 kittiwakes and 3356 guillemots.

In contrast, acoustic values were all non-zero in all bins surveyed for the -50 to -70 dB threshold group and for 779 of the 801 bins surveyed (97%) for the -40 to -50 dB threshold group. The distributional patterns of all species (seabirds and prey) were characterized by a predominance of mainly small observational values, accompanied by a few very high values.

Seabirds, oceanography and prey

Results of the final models obtained for the guillemots and kittiwakes are presented in Tables 2 to 5 (see Supplement 4 at www.int-res.com/articles/

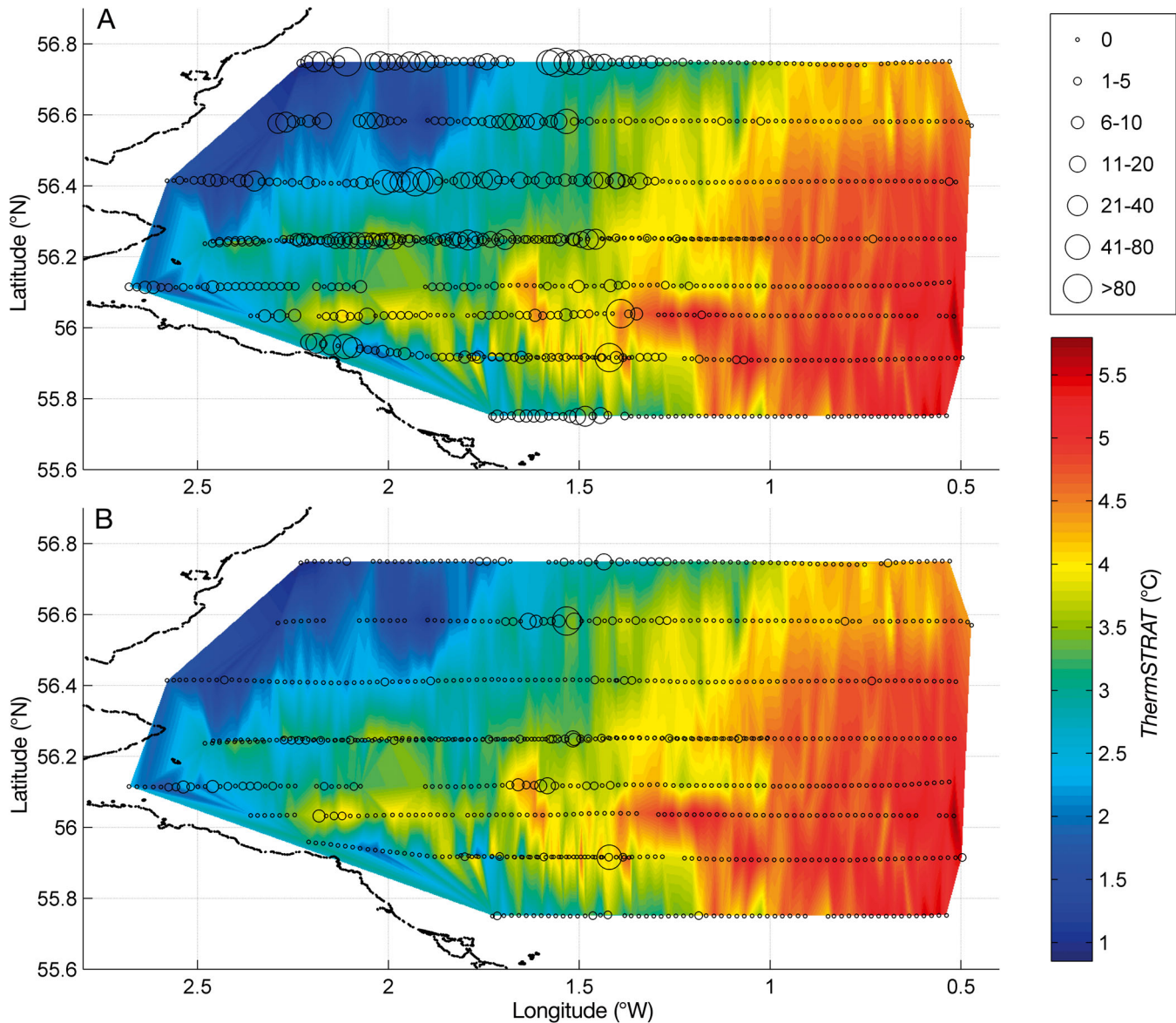


Fig. 1. *Uria aalge* and *Rissa tridactyla*. Distributions of the 2 seabird species in relation to thermal stratification. (A) Guillemots, (B) kittiwakes. Segregation between species is noted, with kittiwakes venturing further offshore in comparison to guillemots, which are restricted mainly to inshore waters. Observations of both species are characterised by many small observations accompanied with few large observations. Thermal stratification between the survey transects was calculated using a linear interpolation of the summary statistics for the 5 min bins

[suppl/m479p203_supp.pdf](#) for full model selection tables). Re-running models with the exclusion of extreme values produced similar relationships. Residual plots and goodness of fit, although deemed acceptable, were not perfect and, therefore, interpretation of the results should be treated with some degree of caution (discussed alongside the influence of extreme values and autocorrelation issues, deemed acceptable, in Supplement 5 at www.int-res.com/articles/suppl/m479p203_supp.pdf).

Guillemots

Both CHL_{MAX} and h/U^3 were retained in the habitat part of the guillemot model (Table 2). Excess zeros in the data set were attributed to areas of high h/U^3 and low CHL_{MAX} (Fig. 3).

The count component of the model retained several explanatory variables (Table 2). Most prominently, *ThermSTRAT* and *DenGRAD* explained spatial variations in abundance. Guillemot counts decreased

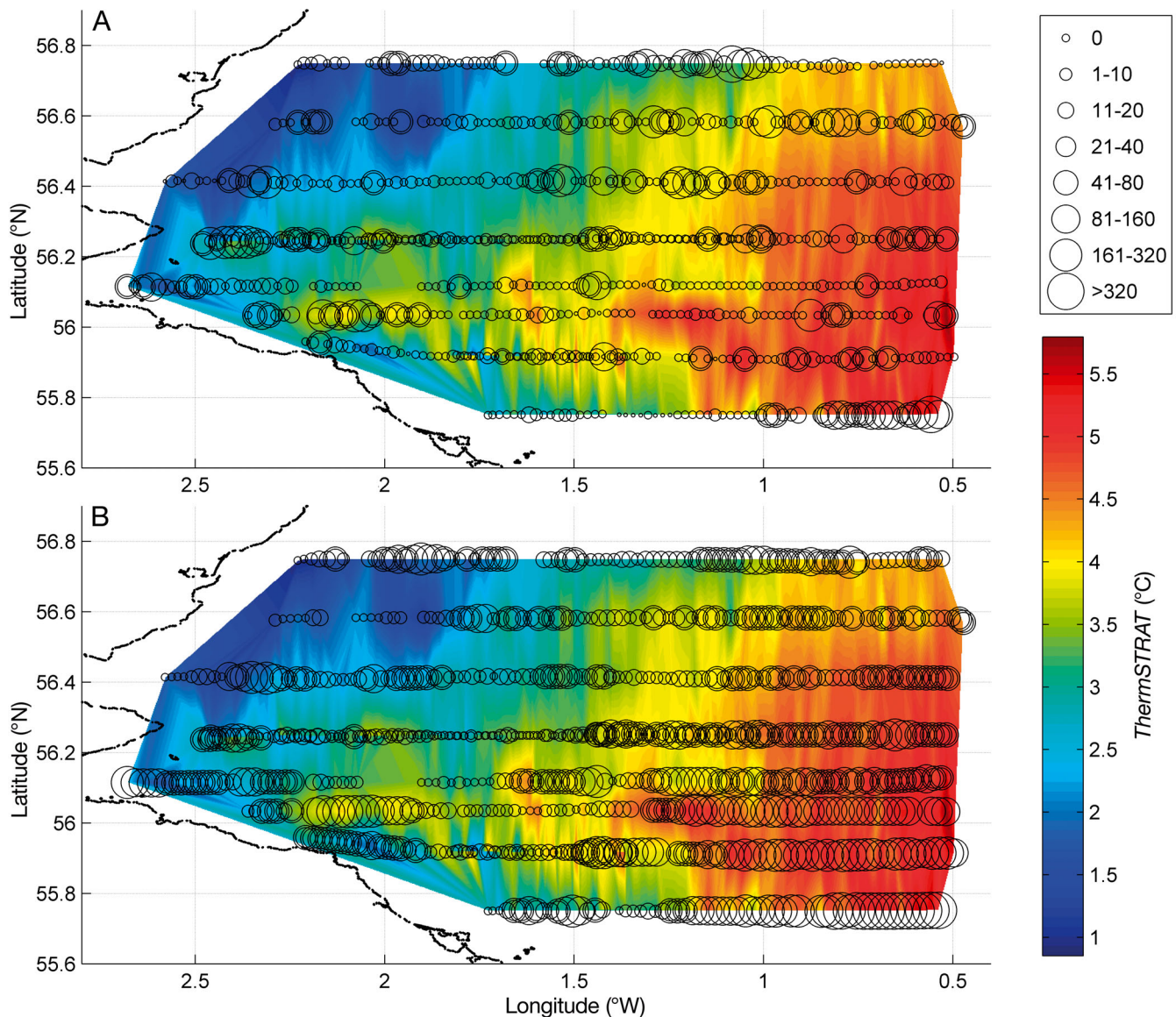


Fig. 2. Distributions of the 2 prey threshold groups are shown in relation to thermal stratification. (A) $NASC-40-50_{MAX}$, (B) $NASC-50-70_{MAX}$. An affiliation with more stratified waters is observed for both threshold groups. Thermal stratification between the survey transects was calculated using a linear interpolation of the summary statistics for the 5 min bins

with increasing thermal stratification ($p < 0.001$, $df = 1$; Table 2, Figs. 1 & 4), whilst a non-linear response to density gradient was evident ($p < 0.001$, $df = 2$; Table 2, Fig. 4).

There was also a strong influence of *Tidal Flag* ($p < 0.001$, $df = 5$; Table 2). Re-levelling the model showed that significant increases in foraging guillemots occurred on an increasing and maximum ebb tide (Table 3). Counts were lowest on the decreasing ebb and maximum flood tide.

A significant effect of *WindSPEED* on guillemot count was found. Increases corresponded to stronger winds ($p < 0.05$, $df = 1$; Table 2, Fig. 4). An influence

of *WindDIR* was also observed ($p < 0.05$, $df = 1$; Table 2). However, despite modelling a linear relationship, it is noted that wind direction is a circular variable. Results simply indicate that changes in wind direction influence expected guillemot counts and that a northerly wind direction (between 300° and 060°) may be important (Fig. 4).

Guillemots responded to 2 prey variables. First, there was an increase in bird counts with $\log NASC-40-50_{MAX}$ ($p < 0.05$, $df = 1$; Table 2). Against the back-transformed data, this occurred until a threshold point after which no further increase was observed (Fig. 4). This appears similar to that displayed by a

Table 2. *Uria aalge*. Explanatory variables retained by the habitat (π) and count (μ) part of the guillemot zero-inflated model. AIC: Akaike's information criterion. Significant values in **bold**

Dropped term	df	AIC	Likelihood ratio test χ^2	df	p
None	17	2864.593			
<i>Tidal Flag</i> from μ	12	2958.793	104.200	5	<0.001
<i>WindSPEED</i> from μ	16	2868.608	6.015	1	0.014
<i>WindDIR</i> from μ	16	2868.953	6.361	1	0.012
<i>ThermSTRAT</i> from μ	16	3013.869	151.280	1	<0.001
<i>Log NASC-40-50_{MAX}</i> from μ	16	2868.714	6.121	1	0.013
<i>DenGRAD²</i> from μ	15	2889.737	29.144	2	<0.001
<i>Depth-50-70_{MaxNASC}</i> from μ	16	2915.395	52.802	1	<0.001
<i>h/U³</i> from π	16	2873.568	10.975	1	0.001
<i>CHL_{MAX}</i> from π	16	2909.173	46.580	1	<0.001

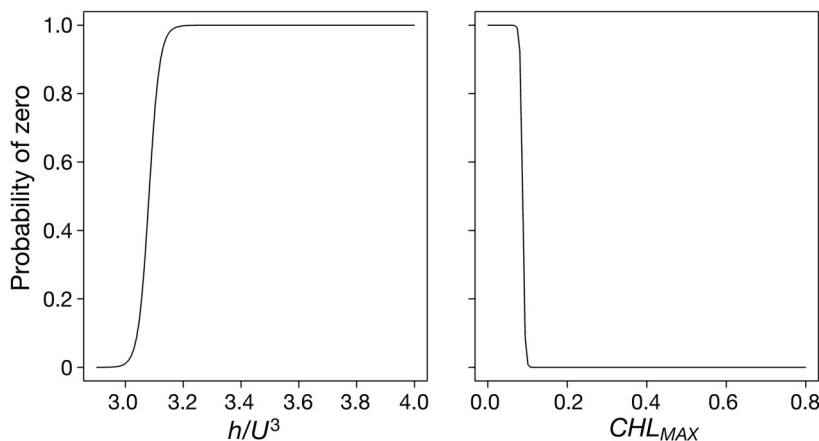


Fig. 3. *Uria aalge*. Probability of measuring a zero plotted against the habitat variables (x-axis) retained by the guillemot model. Both habitat variables show a threshold point, where the probability of measuring a zero value quickly changes from 0 to 1 (or vice versa). Graphs were produced with constants of *WindSPEED* = 10, *WindDIR* = 270, *ThermSTRAT* = 3, *DenGRAD* = 0.1, *Log NASC-40-50_{MAX}* = 3, *Depth-50-70_{MaxNASC}* = 42, *CHL_{MAX}* = 0.1 and *h/U³* = 3 for all variables not included in a plot

steep Type II functional response. Second, increased counts of guillemots were associated with deeper *Depth-50-70_{MaxNASC}* values ($p < 0.001$, $df = 1$; Table 2, Fig. 4).

Kittiwakes

A quadratic term to model non-linearity of *h/U³* was retained in the habitat component of the kittiwake model (Table 4, Fig. 5). Excess zero counts were associated with values of between 3.3 and 3.6.

The count component of the kittiwake model retained 3 explanatory variables (Table 4, Fig. 6). *ThermSTRAT* had a non-linear influence on kitti-

wake counts ($p < 0.001$, $df = 2$; Table 4, Fig. 6). Kittiwakes were associated with areas of higher thermal stratification than guillemots but not with areas of maximal stratification in the survey region (Fig. 1).

A significant effect of *Tidal Flag* was found ($p < 0.01$, $df = 5$; Table 4). Kittiwake counts were highest on an increasing and decreasing ebb and increasing flood tide (Table 5). Lowest counts were on the maximum ebb and flood tides.

There was an increase in bird counts with *Log NASC-40-50_{MAX}* occurred until a threshold point, after which no further increase was found ($p < 0.01$, $df = 1$; Table 4). Against the back-transformed data, this occurred until a threshold point, after which no further increase was found (Fig. 6). As observed with guillemots, this appears similar to that displayed by a Type II functional response.

Prey and oceanographic parameters

Results of the prey models are presented in Tables 6 & 7 (see Supplement 6 at www.int-res.com/articles/suppl/m479p203_supp.pdf for model selection tables). *Tidal Flag* and *ThermSTRAT* had a significant influence on both *Log NASC_{MAX}* variables.

Log NASC-40-50_{MAX} was highest on an increasing and maximum ebb tide (Table 6). Lowest measurements occurred on the increasing and maximum flood. The highest measurements of *Log NASC-50-70_{MAX}* corresponded to an increasing, maximum and decreasing ebb tide (Table 7). Significantly lower densities were associated with all stages of the flood tide.

Increases in both *Log NASC-40-50_{MAX}* and *Log NASC-50-70_{MAX}* corresponded to increased thermal stratification ($p < 0.01$, $df = 1$; Tables 6 & 7). Relationships were linear. However, Figs. 7 & 8 show that the highest measurements of *NASC-40-50_{MAX}* occurred where the level of stratification was characterized by a temperature difference of around 4°C, whereas the highest measurements of *NASC-50-70_{MAX}* corresponded to a temperature difference of around 5°C.

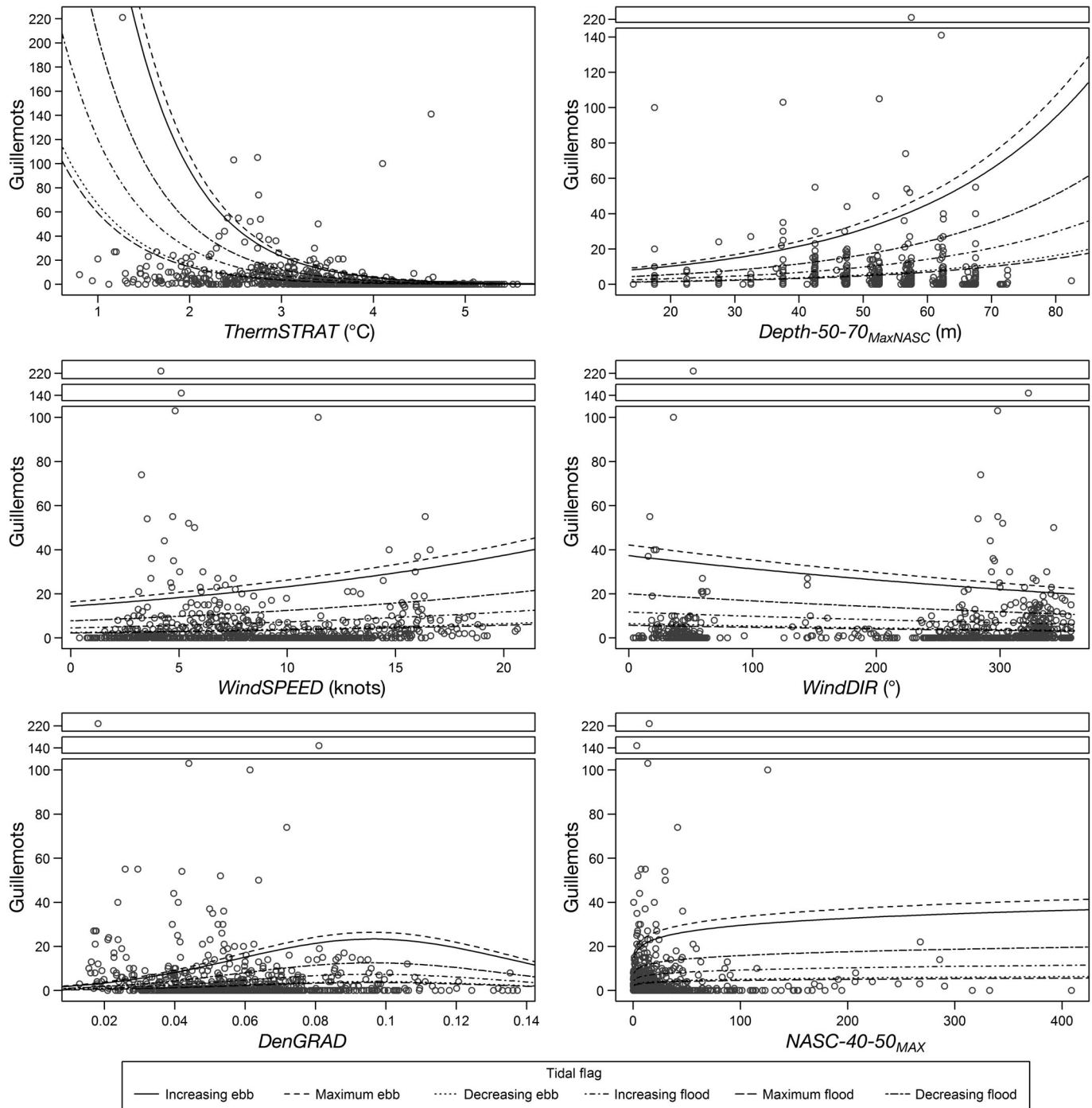


Fig. 4. *Uria aalge*. Fitted curves for each stage of the tide with the observed data from the count component of the zero-inflated negative binomial (ZINB) guillemot model. Each plot represents the effect of a specific explanatory variable (horizontal axis) on the expected guillemot count (vertical axis) given the inclusion of the other explanatory variables whilst assuming a ZINB distribution. Positive relationships are observed with *WindSPEED*, *Depth-50-70_{MaxNASC}* and *NASC-40-50_{MAX}*. A negative relationship is noted with both *ThermSTRAT* and *WindDIR*. A non-linear relationship is evident with *DenGRAD*, where an increase in the expected count is observed until a density gradient of around 0.09. Attention is drawn to the Type II functional response evident with *NASC-40-50_{MAX}*. Graphs were produced with constants of *WindSPEED* = 10, *WindDIR* = 270, *ThermSTRAT* = 3, *DenGRAD* = 0.1, *Log NASC-40-50_{MAX}* = 3, *Depth-50-70_{MaxNASC}* = 42, *CHL_{MAX}* = 0.5 and $h/U^3 = 3$ for all variables not included in a plot. *Log NASC-40-50_{MAX}* has been back-transformed to show the relationship of guillemot abundance with *NASC-40-50_{MAX}*. Note the varying axis and associated axis gaps between plots used to help display relationships over the entire range of tidal states

Table 3. *Uria aalge*. Parameter estimates, standard errors (SE) and p-values from the guillemot zero-inflated model. Significance levels are shown in relation to *Increasing ebb* (*Tidal Flag*). Significant values in **bold**

	Estimate	SE	p
Count coefficient			
<i>Increasing ebb</i>	2.291	0.616	<0.001
<i>Maximum ebb</i>	0.122	0.303	0.682
<i>Decreasing ebb</i>	-1.753	0.277	<0.001
<i>Increasing flood</i>	-1.158	0.297	<0.001
<i>Maximum flood</i>	-1.868	0.293	<0.001
<i>Decreasing flood</i>	-0.621	0.287	0.03
<i>WindSPEED</i>	0.048	0.02	0.015
<i>WindDIR</i>	-0.002	0.0007	0.012
<i>ThermSTRAT</i>	-1.400	0.117	<0.001
<i>DenGRAD</i>	0.636	0.146	<0.001
<i>DenGRAD</i> ²	-0.033	0.01	0.001
<i>Log NASC-40-50</i> _{MAX}	0.149	0.063	0.018
<i>Depth-50-70</i> _{MaxNASC}	0.037	0.005	<0.001
Habitat coefficient			
(Intercept)	-133.02	98.79	0.178
h/U^3	54.88	37.18	0.148
<i>CHL</i> _{MAX}	-360.91	235.17	0.178

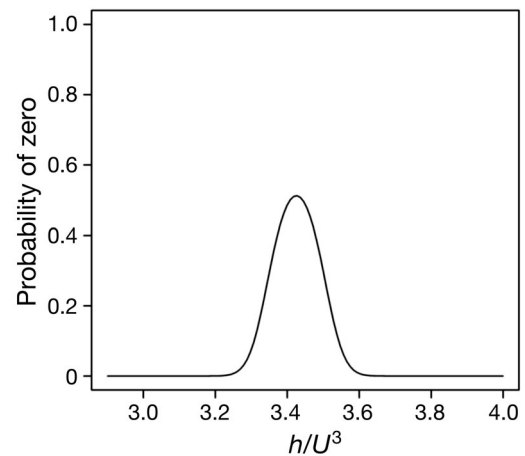


Fig. 5. *Rissa tridactyla*. Probability of measuring a zero plotted against the habitat variable retained by the kittiwake model. A specific range of h/U^3 values (3.3 to 3.6) increases the probability of obtaining a zero observation, suggesting that this range indicates unsuitable habitat and kittiwakes target regions with h/U^3 values above and below these values. This graph was produced using constants of $\text{Log NASC-40-50}_{\text{MAX}} = 4$ and $\text{ThermSTRAT} = 3$

Table 4. *Rissa tridactyla*. Explanatory variables retained by the habitat (π) and count (μ) part of the kittiwake zero-inflated model. AIC: Akaike's information criterion. Significant values in **bold**

Dropped term	df	AIC	Likelihood ratio test		
			χ^2	df	p
None	13	919.080			
<i>Tidal Flag</i> from μ	8	929.352	20.271	5	0.001
<i>Log NASC-40-50</i> _{MAX} from μ	12	925.768	8.687	1	0.003
<i>ThermSTRAT</i> ² from μ	11	932.522	17.441	2	<0.001
$(h/U^3)^2$ from π	11	921.188	6.108	2	0.047

DISCUSSION

The primary purpose of this study was to determine the underlying processes, both physical and biological, driving variation in the times and locations of seabird foraging events. Both guillemot and kittiwake models showed consistency in their results; *Tidal Flag* and *ThermSTRAT* explained observed variations. By incorporating this oceanographic influence on foraging habitat, we identified fine-scale predator–prey relationships where numbers of both foraging guillemots and kittiwakes varied in response to $\text{Log NASC-40-50}_{\text{MAX}}$.

The secondary purpose of this study was to identify key processes driving variability in prey density. Variation was explained by similar processes to the seabird models. Both *Tidal Flag* and *ThermSTRAT* explained the distributional patterns of prey density.

Seabirds and oceanography

The complexity of the marine environment creates a variety of habitats that species can exploit (Palacios et al. 2006). Guillemots and kittiwakes targeted different foraging habitats both spatially and temporally, supporting previous studies of segregated habitat use (Begg & Reid 1997, Pinaud & Weimerskirch 2007). This may result from either or both evolutionary differences in flight/diving ability and differing prey capture techniques or, on a more immediate ecological time scale, via competition and the need for niche separation. As both species responded to the same prey threshold group (and therefore appear to be targeting the same prey), we propose that the observed segregation results, at least in part, from differing prey capture techniques.

Spatial locations

The importance of tidal mixing and stratification in providing predictable and profitable foraging habitats to seabirds has been well documented (Begg & Reid 1997, Nel et al. 2001, Vlietstra et al.

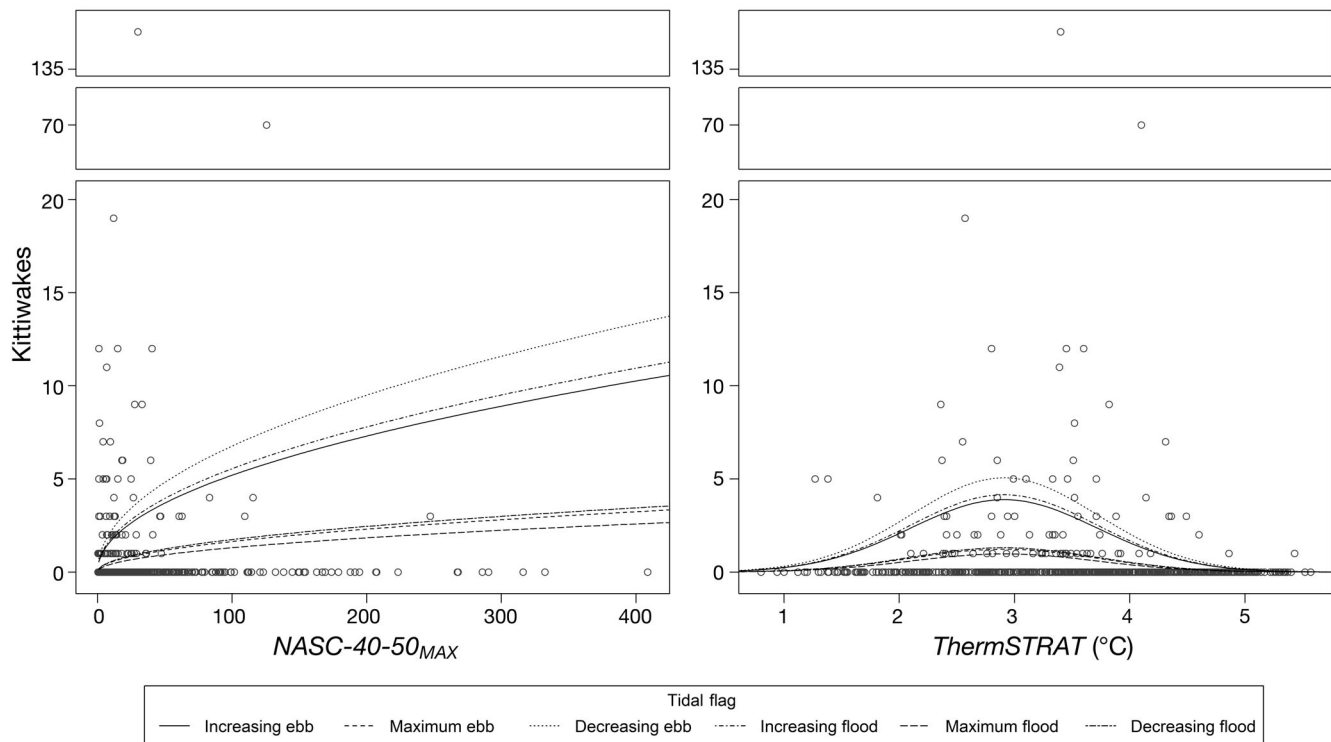


Fig. 6. *Rissa tridactyla*. Fitted curves for each stage of the tide from the count component of the zero-inflated negative binomial (ZINB) kittiwake model with the observed data. Each plot represents the effect of a specific explanatory variable (horizontal axis) on the expected kittiwake count (vertical axis) given the inclusion of the other explanatory variables whilst assuming a ZINB distribution. A non-linear relationship is evident with *ThermSTRAT*, where an optimal stratification level appears evident at around 3°C. A positive relationship in the form of a Type II functional response is noted with *NASC-40-50_MAX*. Graphs were produced with constants of $\text{Log NASC-40-50}_{\text{MAX}} = 4$, $\text{ThermSTRAT} = 3$ and $h/U^3 = 3.2$. $\text{Log NASC-40-50}_{\text{MAX}}$ has been back-transformed to show the relationship of kittiwake abundance with *NASC-40-50_MAX*. Note the vertical axis gaps to include 2 extreme values

2005, Ropert-Coudert et al. 2009). Our results support past work focused on the finer-scale processes that drive seabird foraging (Durazo et al. 1998, Skov & Durinck 2000, Scott et al. 2010, Embling et al. 2012). Furthermore, by concentrating on species with contrasting foraging capabilities, we have provided an insight into the importance of fine-scale water column structure in creating a variety of foraging habitats. A full discussion of the interpretation and meaning of these results can be found in Scott et al. (2010).

Additionally, sub-surface chlorophyll production was found to positively influence the presence of guillemots, suggesting that these patches create predictable spots of increased productivity that animals can exploit. This corresponds to a more in-depth study of the influence of these patches by Scott et al. (2010), where a full discussion of such results can be found.

Table 5. *Rissa tridactyla*. Parameter estimates, standard errors (SE) and p-values from the kittiwake zero-inflated model. Significance levels are shown in relation to *Increasing ebb* (Tidal Flag). Significant values in **bold**

	Estimate	SE	p
Count coefficient			
<i>Increasing ebb</i>	-7.060	1.656	<0.001
<i>Maximum ebb</i>	-1.154	0.643	0.073
<i>Decreasing ebb</i>	0.258	0.639	0.686
<i>Increasing flood</i>	0.062	0.659	0.925
<i>Maximum flood</i>	-1.377	0.646	0.033
<i>Decreasing flood</i>	-1.088	0.691	0.115
<i>ThermSTRAT</i>	4.442	1.106	<0.001
<i>ThermSTRAT</i> ²	-0.763	0.175	<0.001
<i>Log NASC-40-50_MAX</i>	0.489	0.161	0.002
Habitat coefficient			
(Intercept)	-1962.8	1232.5	0.111
h/U^3	1146.3	723.8	0.113
$(h/U^3)^2$	-167.3	106.2	0.115

Table 6. Parameter estimates, standard errors and p-values for the *Log NASC-40-50_{MAX}* model. Significance levels are shown in relation to *Increasing ebb* (Tidal Flag). Significant values in **bold**

Coefficient	Estimate	SE	p
<i>Increasing ebb</i>	1.437	0.485	0.003
<i>Maximum ebb</i>	−0.371	0.23	0.106
<i>Decreasing ebb</i>	−0.423	0.23	0.067
<i>Increasing flood</i>	−0.678	0.228	0.003
<i>Maximum flood</i>	−0.84	0.234	<0.001
<i>Decreasing flood</i>	−0.503	0.24	0.037
<i>ThermSTRAT</i>	0.466	0.11	<0.001

Table 7. Parameter estimates, standard errors and p-values for the *Log NASC-50-70_{MAX}* model. Significance levels are shown in relation to *Increasing ebb* (Tidal Flag). Significant values in **bold**

Coefficient	Estimate	SE	p
<i>Increasing ebb</i>	3.436	0.271	<0.001
<i>Maximum ebb</i>	0.056	0.12	0.636
<i>Decreasing ebb</i>	−0.007	0.117	0.956
<i>Increasing flood</i>	−0.358	0.12	0.001
<i>Maximum flood</i>	−0.359	0.117	0.002
<i>Decreasing flood</i>	−0.54	0.12	<0.001
<i>ThermSTRAT</i>	0.169	0.055	0.002

Tidal influences

Where we have primarily expanded on previous work is in addressing the potential impact of tidal temporal variability in the environment can have on seabird foraging behaviour and prey availability. In coastal waters, the abundance and accessibility of prey is often influenced by such effects (Nol & Gaskin 1987, Holm & Burger 2002). Our results are concurrent with such observations and point to specific tidal speeds and directions thought to influence prey behaviour and create foraging habitats which are exploited by both of the seabird species.

Guillemots. Foraging guillemots were well represented in the study area (being present in 45% of surveyed bins) and showed a strong positive association with increasing and maximum ebb tides. At short temporal scales, this is unlikely to stem from periods of increased productivity (Cloern 1991). However, rapid changes in fish and zooplankton densities and vertical distributions may result from changes in their behaviour at different speeds/directions of tidal currents (Franks 1992, Ross & Sharples 2007, 2008, C. B. Embling et al. unpubl.). Areas rich in zooplankton attract aggregations of fish, creating profitable foraging opportunities for predators. This has been termed the

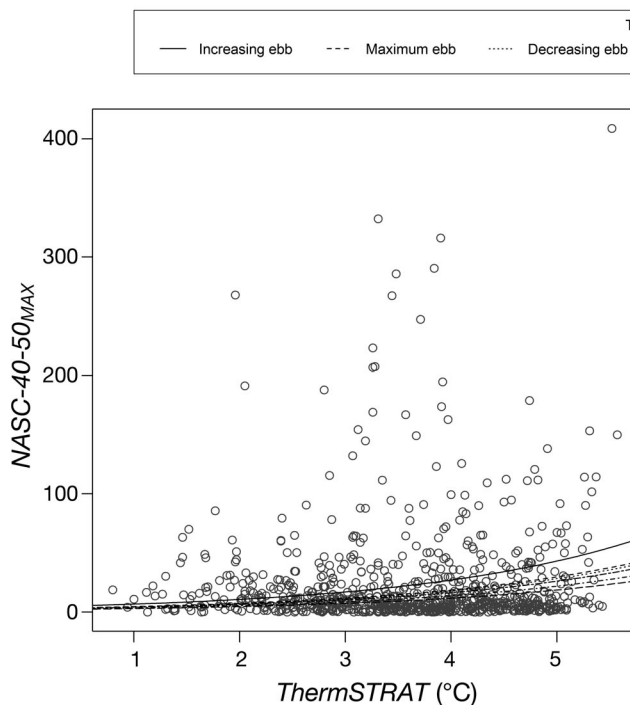


Fig. 7. Influence of thermal stratification on *NASC-40-50_{MAX}* (back-transformed) at each stage of the tide. An increase in *NASC-40-50_{MAX}* with thermal stratification is observed

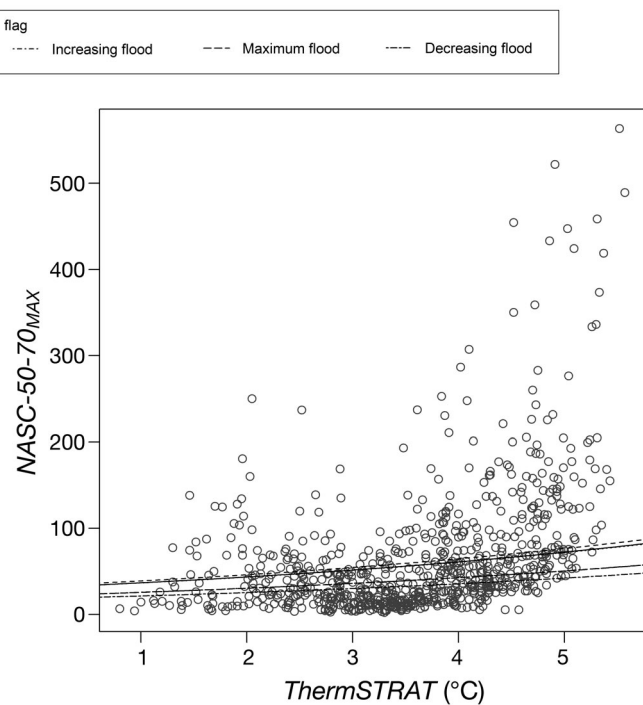


Fig. 8. Influence of thermal stratification on *NASC-50-70_{MAX}* (back-transformed) at each stage of the tide. An increase in *NASC-50-70_{MAX}* with thermal stratification is observed

tidal coupling hypothesis, where such opportunities occur only with specific tidal conditions (Zamon 2003). In this study, the density of both prey types increased only at ebb tides (Tables 6 & 7), suggesting a predictable change in behaviour across multiple trophic levels which includes an increase in prey capture by guillemots during these conditions. Counter-intuitively, increased numbers of foraging guillemots were found when the depth of prey was deeper (Fig. 4), suggesting that the changes in prey behaviour make it more worthwhile to dive deeper at ebbing tides even though deeper dives are more energetically costly than shallower dives (Langton et al. 2011).

Guillemots also associated with specific wind conditions. Strong winds can cause water column structure to break down, dispersing prey (Coyle et al. 1992, Becker & Bessinger 2003). A corresponding decrease in seabird foraging would therefore be expected. However, observed increases suggest that underlying processes are more complex. Increases in foraging guillemot abundances were associated with winds from the north. The main tidal axis in this region is north–south. Guillemots preferred the ebb tidal phase, when the tide runs to the north. Therefore the conditions at which guillemots were seen feeding in greater abundances occurred when tide and wind directions were opposed, a condition which can cause a higher degree of shear within the water column (Druon et al. 2001). This use of interactions between tidal currents, wind speed and wind direction by mobile predators has been noted in recent studies on gannets and storm petrels *Hydrobates pelagicus* in the Celtic Sea (B. E. Scott et al. unpubl.), where subsequent shear at the thermocline may create profitable foraging opportunities and therefore represents an area of research that should be investigated.

Kittiwakes. Associations of kittiwakes with particular tidal stages were not consistent with previous studies in this and other global locations. Irons (1998) found kittiwakes adjusted their foraging trips to coincide with a maximum flood or ebb tide in Alaska, a finding reiterated in a linked study to this one (explained in more detail below) focusing on only the areas of highest foraging densities (Embling et al. 2012). However, the observations of kittiwakes along transect lines in this study were lowest on the maximum flood and ebb tides. Several reasons may explain such disparate observations, which present very important considerations for the future design of at-sea surveys.

In contrast to guillemots, which are adapted to dive (Montevecchi et al. 2006, Langton et al. 2011), kittiwakes are surface feeders and need a food resource accessible in the top layer of the water column (Fur-

ness & Tasker 2000). Therefore, the locations at which kittiwakes can forage will be greatly limited compared to diving species such as guillemots. Also, given the comparatively small number of kittiwake observations (11% of surveyed bins versus 45% for guillemots) made during the survey, it may be that we were not in the right place at the right time often enough to sample foraging events. If optimal foraging conditions exist only for short periods in space and time, sampling out with this window of opportunity is more likely.

Fig. 1B shows that larger abundances of foraging kittiwakes were limited within a restricted region of the study area. However, corresponding values of h/U^3 for this region explained an excess of zero observations (Fig. 5), suggesting that these regions may only be profitable for kittiwakes with certain tidal conditions that we failed to adequately sample. To investigate the possibility of such a temporal influence, whilst also dealing with the issue of restricted areas of high abundance, Embling et al. (2012) sampled the same core foraging locations in space repeatedly on different phases of the tide. This allowed for tidal temporal interactions to be identified. Within hotspot locations, the mean number of birds per 5 min bin was 21.6 birds higher on the maximum ebb tide. This compared to just 1.6 birds during the maximum ebb tide across the transects that represent the study region as a whole, thus illustrating the influence restricted areas of high abundance can have on results. Taking the optimum values of h/U^3 for kittiwake foraging (3.5 to 3.6 as identified by Scott et al. 2010), of the 152 five min bins sampled in this survey within this h/U^3 range, only 10 (6.6%) were sampled on the ebb tide. Consequently, it becomes apparent that 93.4% of sampling in the right habitat was at the wrong time, possibly explaining why our results differ from previous studies.

Prey and oceanography

The extent to which spatial and tidal temporal oceanographic features are important to seabirds is dependent on the use of such features by their prey (Daunt et al. 2006, Stevick et al. 2008). In particular, variation in prey density is important for the foraging success of birds (Enstipp et al. 2007). We used acoustic measures sorted into rough multispecies groupings based on similarities in backscattering characteristics to provide an index of variation in potential prey density. Species identification is seen as a great

challenge in fisheries acoustics and is nearly impossible without trawl samples (MacLennan & Holliday 1996, Korneliussen & Ona 2002). Despite this, acoustics data even in the absence of trawls can provide a relative measure of multispecies prey distributions that can help to inform models of top predator distributions (Hazan et al. 2011), as is evident here.

Spatial locations

The importance of vertical thermal stratification as an indication of profitable foraging habitat is reiterated in the results from the prey models. Increased measurements of both threshold groups (representing pelagic species and large zooplankton) were found in areas of higher thermal stratification, suggesting that at these locations, mobile predators will find higher abundances of pelagic prey. However, during the summer months, primary production within such areas would be low due to seasonal nutrient depletion (Simpson et al. 1979). This would result in lower food supplies. Therefore, it is likely that increased densities result from more complex processes, possibly linked to regions where bi-weekly primary production within a strong thermocline supports a high level of secondary productivity (Sharples 2008).

Van der Kooij et al. (2008) found increased sandeel abundance in areas with increased vertical thermal stratification. A similar pattern was observed in herring (Maravelias 1997). Increased abundances corresponded to areas with a deep thermocline and transitional level of stratification. Low abundance was found at frontal regions. It was suggested that herring responded to a migration of zooplankton to deeper, more stratified waters during the summer. This link was later identified when aggregations of herring were shown to correspond to increased zooplankton abundance (Maravelias 2001). Given the association of our threshold groups with offshore, stratified waters (and acknowledging the rough species allocations), it appears that larger aggregations of multispecies groups of fish and zooplankton are found in more stratified waters, supporting the above studies.

Tidal influences

Acoustic prey measurements also varied on temporal scales, corresponding to particular tidal speeds and directions. Previous studies suggest that the

accumulation of zooplankton is often linked to times of the tidal cycle where current strength is increased (Aldredge & Hamner 1980, Ladd et al. 2005). We identified an increase in threshold group densities (expected to represent zooplankton and pelagic fish assemblages) during the ebb tide. This suggests that underlying processes associated with this phase of the tide act either to accumulate zooplankton or elicit changes in behaviour, which in turn attracts fish and, as suggested by the tidal coupling hypothesis, their predators (Zamon 2003).

Predator–prey interactions

When driven by transient processes such as those associated with tidal movements, encounters between predators and their prey will be short-lived. Aggregations often disperse over time periods of less than 1 to 2 h, echoing tidal phases (Durazo et al. 1998, Coyle et al. 1992). We have identified such a link emphasising the tidal temporal limitation on predator foraging. For successful foraging, predators should be not only in the right place but also at the right time.

Optimal foraging theory predicts that to exploit a patchy environment, predators should make decisions to maximise the net rate of energy intake during a foraging bout (Charnov 1976). Subsequently, a predator is expected to shift its movement in relation to its prey. However, empirical evidence of this is sparse. Fauchald (2009) accredited this to the ability of prey to avoid predation and counteract a predator's tracking ability. This results in the evolution of a hierarchical system, where uncorrelated small patches of predators and prey are nested within larger correlated patches. However, many of the studies concentrating on the spatial scales of predator–prey interactions have failed to incorporate the linked temporal and spatial variability of the environment in which such interactions are taking place (Logerwell et al. 1998, Fauchald et al. 2000). This may explain the lack of correlation found.

Foraging seabirds consistently coincide with the presence of their prey. However, prey presence is not necessarily indicative of foraging seabirds (Coyle et al. 1992, Swartzman & Hunt 2000), and it is important that the complex nature of the environment in which such interactions occur is acknowledged. In this study, by incorporating the influence of both spatial and tidal temporal variability in foraging habitat into predator–prey dynamics, we have identified fine-scale interactions between 2 seabird species and

their prey. We have provided evidence to suggest that both predator and a range of prey species predictably change behaviour with tidal speed and direction. We have also shown that in shallow sea areas, locations of higher stratification may play an important role in the predictability of the distribution of lower trophic levels.

Seabird abundance was, in part, driven by prey density. Prey capture rate increases with prey density (Enstipp et al. 2007) and, therefore, targeting areas with high prey densities should reduce energetic costs. Our results reflect this. Both species responded strongly to small increases in prey density, with a very steep Type II functional response curve rapidly approaching a threshold point (Figs. 4 & 6). Furthermore, guillemots preferentially foraged on tidal conditions associated with increased prey densities, suggesting that although it may be unnecessary to seek out the very highest prey densities, prey density is an important element in seabird foraging.

CONCLUSIONS

Seabirds spend in excess of 50% of their time foraging or feeding during the breeding season (Daunt et al. 2002). We have provided an insight toward some of the underlying tidally driven processes driving variation in foraging seabird abundance, identifying both potential spatial and tidal temporal critical marine habitats. Any localized disturbance within such habitats (including changes in tidal speeds) will have a disproportionate impact on associated populations and marine ecosystems (Crowder & Norse 2008, Hazan et al. 2011). Therefore, knowledge of the spatial and tidal temporal locations and mechanisms driving foraging behaviour at these sites is essential in seabird surveying and the planning of marine protected areas and renewable energy installations.

The short survey period (10 d) was a limitation of this study. Just as a predator has to be in the right place at the right time to capture its prey, sampling the occurrence of such events is subject to their ephemeral nature and ideally needs repetitive sampling of all trophic levels over tidal cycles in different seasons and years across a range of habitats. However, despite the limited amount of data collected, we have identified the fundamental importance of oceanographic and tidal variability, both spatially and temporally, in driving predator–prey interactions and defining critical seabird foraging habitat.

We suggest that transect versus repeated area surveys (e.g. Embling et al. 2012) provide varying degrees of information and inconsistencies between our kittiwake results versus those of Embling et al. (2012), suggesting that survey design and sampling regime can have a substantial influence on relationships detected. It is therefore pertinent that future sampling covers individual locations over a range of tidal conditions to be able to identify foraging habitats that are subject to tidal temporal variations. Subsequently, both researchers and managers of marine ecosystems are encouraged to design future surveys with consideration to both the temporal and spatial variability of the marine environment over a range of scales.

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LITERATURE CITED

- Agarwal DK, Gelfand AE, Citron-Pousty S (2002) Zero-inflated models with application to spatial count data. *Environ Ecol Stat* 9:341–355
- Allredge AL, Hamner WM (1980) Recurring aggregation of zooplankton by a tidal current. *Estuar Coast Mar Sci* 10: 31–37
- Ashmole NP (1971) Sea bird ecology and the marine environment. In: Farner DS, King JR (eds) *Avian biology*, Vol 1 Academic Press, New York, NY, p 223–286
- Becker BH, Beissinger SR (2003) Scale-dependent habitat selection by a nearshore seabird, the marbled murrelet, in a highly dynamic upwelling system. *Mar Ecol Prog Ser* 256:243–255
- Begg GS, Reid JB (1997) Spatial variation in seabird density at a shallow sea tidal mixing front in the Irish Sea. *ICES J Mar Sci* 54:552–565
- Bodholt H, Ness H, Solli H (1989) A new echo-sounder system. *Proc Inst Acoust* 11:123–130
- Bost CA, Cotté C, Bailleul F, Cherel Y and others (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J Mar Syst* 78:363–376

- Camphuysen CJ, Garthe S (2004) Recording foraging seabirds at sea: standardised recording and coding of foraging behaviour and multi species foraging associations. *Atl Seabirds* 6:1–32
- Camphuysen CJ, Fox AD, Leopold MF, Petersen IK (2004) Towards standardized seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms in the UK. Report No. COWRIE-BAM-02-2002, Royal Netherlands Institute for Sea Research, Texel
- Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor Popul Biol* 9:129–136
- Cloern JE (1991) Tidal stirring and phytoplankton bloom dynamics in an estuary. *J Mar Res* 49:203–221
- Coyle KO, Hunt GL Jr, Decker MB, Weingartner TJ (1992) Murre foraging, epibenthic sound scattering and tidal advection over a shoal near St. George Island, Bering Sea. *Mar Ecol Prog Ser* 83:1–14
- Crawley MJ (2007) *The R book*. John Wiley & Sons, Chichester
- Crowder L, Norse E (2008) Essential ecological insights for marine ecosystem-based management and marine spatial planning. *Mar Policy* 32:772–778
- Daunt F, Benvenuti S, Harris MP, Dall'Antonia L, Elston DA, Wanless S (2002) Foraging strategies of the black-legged kittiwake *Rissa tridactyla* at a North Sea colony: evidence for a maximum foraging range. *Mar Ecol Prog Ser* 245:239–247
- Daunt F, Wanless S, Peters G, Benvenuti S, Sharples J, Gremillet D, Scott B (2006) Impacts of oceanography on the foraging dynamics of seabirds in the North Sea. In: Boyd IL, Wanless S, Camphuysen CJ (eds) *Top predators in marine ecosystems: their role in monitoring and management*. Cambridge University Press, Cambridge, p 177–190
- Decker M, Hunt GL Jr (1996) Foraging by murrelets (*Uria* spp.) at tidal fronts surrounding the Pribilof Islands, Alaska, USA. *Mar Ecol Prog Ser* 139:1–10
- Dormann CF (2007) Effects of incorporating spatial autocorrelation into the analysis of species distribution data. *Glob Ecol Biogeogr* 16:129–138
- Druon JN, Langlois G, Le Fevre J (2001) Simulating vertical mixing in a shelf-break region: addition of a shear instability model, accounting for the overall effect of internal tides, on top of a one-dimensional turbulence closure mixed one layer model. *Cont Shelf Res* 21:423–454
- Durazo R, Harrison NM, Hill AE (1998) Seabird observations at a tidal mixing front in the Irish Sea. *Estuar Coast Shelf Sci* 47:153–164
- Embling CB, Illian J, Armstrong E, Van der Kooij J, Sharples J, Camphuysen CJ, Scott BE (2012) Investigating fine-scale spatio-temporal predator–prey patterns in dynamic marine ecosystems: a functional data analysis approach. *J Appl Ecol* 49:481–492
- Enstipp MR, Gremillet D, Jones DR (2007) Investigating the functional link between prey abundance and seabird predatory performance. *Mar Ecol Prog Ser* 331:267–279
- Fauchald P (2009) Spatial interaction between seabirds and prey: review and synthesis. *Mar Ecol Prog Ser* 391:139–151
- Fauchald P, Erikstad KE (2002) Scale-dependent predator–prey interactions: the aggregative response of seabirds to prey under variable prey abundance and patchiness. *Mar Ecol Prog Ser* 231:279–291
- Fauchald P, Erikstad K, Skarsfjord H (2000) Scale-dependent predator–prey interactions: the hierarchical spatial distribution of seabirds and prey. *Ecology* 81:773–783
- Fearnhead PG (1975) On the formation of fronts by tidal mixing around the British Isles. *Deep-Sea Res Oceanogr Abstr* 22:311–321
- Franks PJS (1992) Sink or swim: accumulation of biomass at fronts. *Mar Ecol Prog Ser* 82:1–12
- Furness RW, Tasker ML (2000) Seabird–fishery interactions: quantifying the sensitivity of seabirds to reduction in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Mar Ecol Prog Ser* 202:253–264
- González-Solís J, Shaffer SA (2009) Introduction and synthesis: spatial ecology of seabirds at sea. *Mar Ecol Prog Ser* 391:117–120
- Hamer KC, Humphreys EM, Magalhães MC, Garthe S and others (2009) Fine-scale foraging behaviour of a medium-ranging marine predator. *J Anim Ecol* 78:880–889
- Hazan EL, Nowacek DP, St. Laurent L, Halpin PN, Moretti DJ (2011) The relationship among oceanography, prey fields, and beaked whale foraging habitat in the tongue of the ocean. *PLoS ONE* 6:e19269
- Heinemann D, Hunt G, Everson I (1989) Relationships between the distributions of marine avian predators and their prey, *Euphasia superba*, in Bransfield Strait and southern Drake Passage, Antarctica. *Mar Ecol Prog Ser* 58:3–16
- Holm KJ, Burger AE (2002) Foraging behavior and resource partitioning by diving birds during winter in areas of strong tidal currents. *Waterbirds* 25:312–325
- Hooker SK, Gerber LR (2004) Marine reserves as a tool for ecosystem-based management: the potential importance of megafauna. *Bioscience* 54:27–39
- Hunt G Jr, Mehlum F, Russell R, Irons D, Decker M, Becker P (1999) Physical processes, prey abundance, and the foraging ecology of seabirds. In: Adams NJ, Slotow RH (eds) *Proc 22nd Int Ornithol Cong*, Durban. BirdLife South Africa, Johannesburg, p 2040–2056
- Hyrenbach KD, Forney KA, Dayton PK (2000) Marine protected areas and ocean basin management. *Aquat Conserv* 10:437–458
- Irons DB (1998) Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* 79:647–655
- Jackman S (2011) *pscl: classes and methods for R developed in the political science computational laboratory*, Stanford University. Department of Political Science, Stanford University. Stanford, CA. R package version 1.03.10, available at <http://pscl.stanford.edu/>
- Korneliussen RJ, Ona E (2002) An operational system for processing and visualizing multi-frequency acoustic data. *ICES J Mar Sci* 59:293–313
- Ladd C, Jahncke J, Hunt GL Jr, Coyle KO, Staben PJ (2005) Hydrographic features and seabird foraging in Aleutian passes. *Fish Oceanogr* 14:178–195
- Langton R, Davies IM, Scott BE (2011) Seabird conservation and tidal stream and wave power generation: information needs for predicting and managing potential impacts. *Mar Policy* 35:623–630
- Logerwell EA, Hargreaves NB (1996) The distribution of seabirds relative to their fish prey off Vancouver Island: opposing results at large and small spatial scales. *Fish Oceanogr* 5:163–175
- Logerwell E, Hewitt R, Demer D (1998) Scale-dependent spatial variance patterns and correlations of seabirds and

- prey in the southeastern Bering Sea as revealed by spectral analysis. *Ecography* 21:212–223
- Louzao M, Hyrenbach KD, Arcos JM, Abelló P, Sola LG, Oro D (2006) Oceanographic habitat of an endangered Mediterranean procellariiform: implications for marine protected areas. *Ecol Appl* 16:1683–1695
- MacLennan DN, Holliday DV (1996) Fisheries and plankton acoustics: past, present, and future. *ICES J Mar Sci* 53: 513–516
- MacLennan DN, Simmonds EJ (1992) *Fisheries acoustics*. Chapman & Hall, London
- MacLennan DN, Fernandes PG, Dalen J (2002) A consistent approach to definitions and symbols in fisheries acoustics. *ICES J Mar Sci* 59:365–369
- Maravelias CD (1997) Trends in the abundance and geographic distribution of North Sea herring in relation to environmental factors. *Mar Ecol Prog Ser* 159:151–164
- Maravelias CD (2001) Habitat associations of Atlantic herring in the Shetland area: influence of spatial scale and geographic segmentation. *Fish Oceanogr* 10:259–267
- Martin TG, Wintle BA, Rhodes JR, Kuhnert PM and others (2005) Zero tolerance ecology: improving ecological inference by modeling the source of zero observations. *Ecol Lett* 8:1235–1246
- Mavor RA, Parsons M, Heubeck M, Schmitt S (2005) Seabird numbers and breeding success in Britain and Ireland, 2004. UK Nature Conservation, No. 29, Joint Nature Conservation Committee, Peterborough
- Montevecchi WA, Garthe S, Davoren GK (2006) Biophysical influences on seabird trophic assessments. In: Boyd IL, Wanless S, Camphuysen CJ (eds) *Top predators in marine ecosystems: their role in monitoring and management*. Cambridge University Press, Cambridge, p 118–130
- Nel DE, Lutjeharms JRE, Pakhomov EA, Ansorge IJ, Ryan PG, Klages NTW (2001) Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian Ocean. *Mar Ecol Prog Ser* 217:15–26
- Nol E, Gaskin DE (1987) Distribution and movements of black guillemots (*Cephus grylle*) in coastal waters of the southwestern Bay of Fundy, Canada. *Can J Zool* 65: 2682–2689
- Palacios D, Bograd S, Foley D, Schwing F (2006) Oceanographic characteristics of biological hot spots in the North Pacific: a remote sensing perspective. *Deep-Sea Res II* 53:250–269
- Piatt JF, Wetzel J, Bell K, Degange AR and others (2006) Predictable hotspots and foraging habitat of the endangered short-tailed albatross (*Phoebastria albatrus*) in the North Pacific: implications for conservation. *Deep-Sea Res II* 53:387–398
- Pinaud D, Weimerskirch H (2007) At-sea distribution and scale dependent foraging behavior of petrels and albatrosses: a comparative study. *J Anim Ecol* 76:9–19
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2011) nlme: linear and nonlinear mixed effects models. R package version 3.1-102. R Foundation for Statistical Computing, Vienna
- Potts JM, Elith J (2006) Comparing species abundance models. *Ecol Model* 199:153–163
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ropert-Coudert Y, Kato A, Chiaradia A (2009) Impact of small-scale environmental perturbations on local marine food resources: a case study of a predator, the little penguin. *Proc R Soc Lond B Biol Sci* 276:4105–4109
- Ross ON, Sharples J (2007) Phytoplankton motility and the competition for nutrients in the thermocline. *Mar Ecol Prog Ser* 347:21–38
- Ross ON, Sharples J (2008) Swimming for survival: a role of phytoplankton motility in a stratified turbulent environment. *J Mar Syst* 70:248–262
- Russell RW, Hunt GL Jr, Coyle KO, Cooney RT (1992) Foraging in a fractal environment: spatial patterns in a marine predator prey system. *Landscape Ecol* 7:195–209
- Schneider D (1982) Fronts and seabird aggregations in the southeastern Bering Sea. *Mar Ecol Prog Ser* 10:101–103
- Schneider DC, Piatt JF (1986) Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. *Mar Ecol Prog Ser* 32:237–246
- Scott B, Sharples J, Wanless S, Ross ON, Frederiksen M, Daunt F (2006) The use of biologically meaningful oceanographic indices to separate the effects of climate and fisheries on seabird breeding success. In: Boyd IL, Wanless S, Camphuysen CJ (eds) *Top predators in marine ecosystems: their role in monitoring and management*. Cambridge University Press, Cambridge, p 46–62
- Scott BE, Sharples J, Ross ON, Wang J, Pierce GJ, Camphuysen CJ (2010) Sub-surface hotspots in shallow seas: fine-scale limited locations of top predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll. *Mar Ecol Prog Ser* 408:207–226
- Sharples J (2008) Potential impacts of the spring-neap tidal cycle on shelf sea primary production. *J Plankton Res* 30: 183–197
- Simpson JH, Hunter JR (1974) Fronts in the Irish Sea. *Nature* 250:404–406
- Simpson J, Edelsten D, Edwards A, Morris N, Tett P (1979) The Islay front: physical structure and phytoplankton distribution. *Estuar Coast Mar Sci* 9:713–726
- Skov H, Durinck J (2000) Seabird distribution in relation to hydrography in the Skagerrak. *Cont Shelf Res* 20: 169–187
- Skov H, Durinck J, Andell P (2000) Associations between wintering avian predators and schooling fish in the Skagerrak-Kattegat suggest reliance on predictable aggregations of herring *Clupea harengus*. *J Avian Biol* 31: 135–143
- Stevick PT, Incze LS, Kraus SD, Rosen S, Wolff N, Baukus A (2008) Trophic relationships and oceanography on and around a small offshore bank. *Mar Ecol Prog Ser* 363: 15–28
- Swartzman G, Hunt G (2000) Spatial association between murre (*Uria* spp.), puffins (*Fratercula* spp.) and fish shoals near Pribilof Islands, Alaska. *Mar Ecol Prog Ser* 206:297–309
- Sydeman W, Brodeur R, Grimes C, Bychkov A, Mckinnell S (2006) Marine habitat 'hotspots' and their use by migratory species and top predators in the North Pacific Ocean: introduction. *Deep-Sea Res II* 53:247–249
- Tasker ML, Jones PH, Dixon T, Blake BF (1984) Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. *Auk* 101:567–577
- Tremblay Y, Bertrand S, Henry RW, Kappes MA, Costa DA, Shaffer SP (2009) Analytical approaches to investigating seabird–environment interactions: a review. *Mar Ecol Prog Ser* 391:153–163

- Van der Kooij J, Scott BE, Mackinson S (2008) The effects of environmental factors on daytime sandeel distribution and abundance on the Dogger Bank. *J Sea Res* 60:201–209
- Vlietstra LS, Coyle KO, Kachel LNB, Hunt GL Jr (2005) Tidal front affects the size of prey used by a top marine predator, the short-tailed shearwater (*Puffinus tenuirostris*). *Fish Oceanogr* 14:196–211
- Wakefield ED, Phillips RA, Matthiopoulos J (2009) Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Mar Ecol Prog Ser* 391:165–182
- Wolanski E, Hamner WM (1988) Topographically controlled fronts in the ocean and their biological influence. *Science* 241:177–181
- Worm B, Sandow M, Oschlies A, Lotze HK, Myers RA (2005) Global patterns of predator diversity in the open oceans. *Science* 309:1365–1369
- Yen P, Sydeman W, Bograd S, Hyrenbach K (2006) Spring-time distributions of migratory marine birds in the southern California Current: oceanic eddy associations and coastal habitat hotspots over 17 years. *Deep-Sea Res II* 53:399–418
- Zamon JE (2003) Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelago depend on flooding tidal currents. *Mar Ecol Prog Ser* 261:243–255
- Zeileis A, Kleiber C, Jackman S (2008) Regression models for count data in R. *J Stat Softw* 27:1–25
- Zipkin EF, Gardner B, Gilbert AT, O'Connell AF Jr, Royle JA, Silverman ED (2010) Distribution patterns of wintering sea ducks in relation to the North Atlantic Oscillation and local environmental characteristics. *Oecologia* 163: 893–902
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer Verlag, New York, NY

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