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The diet of Common Guillemot (*Uria aalge*) chicks at colonies in the UK, 2006–2011: evidence for changing prey communities in the North Sea

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Local differences in feeding conditions have been suggested as a cause of regional variation in seabird demography but multi-colony comparisons of diet are rare. In UK waters the main fish eaten by seabirds during the breeding season belong to three families: Ammodytidae, Clupeidae and Gadidae. Climate change and fishing are affecting these fish stocks and so probably impact indirectly on predators such as seabirds. We used standardized observations of prey brought in for chicks to make the first integrated assessment of the diet of Common Guillemot *Uria aalge* chicks at a UK scale. Chick diet varied markedly among the 23 colonies sampled between 2006 and 2011. Sandeels (Ammodytidae), probably Lesser Sandeels *Ammodytes marinus*, were the commonest prey. Their contribution to the diet varied both latitudinally and among marine regions, with the proportion tending to be significantly higher for a given latitude on the west coast than on the east coast. The non-sandeel component of the diet showed latitudinal changes, with small clupeids, probably Sprats *Sprattus sprattus*, predominant at southern colonies and juvenile gadids the main alternative in the north. Comparison of our contemporary Guillemot chick diet with data collected 15–30 years earlier suggests that the proportion of sandeel eaten has decreased at colonies bordering the North Sea. No significant change was apparent in Atlantic colonies but historical data available were very limited. The early years of our study coincided with a population explosion of Snake Pipefish *Entelurus aequoreus* in the Northeast Atlantic and North Sea. Pipefish were recorded in Guillemot chick diet at several northern and northwestern colonies in 2006 and 2007 but have been absent since 2009. Spatial and temporal variation in chick diet accorded broadly with patterns expected as a result of rising sea temperatures and impacts of fishing. Guillemot chick diet could potentially be a useful indicator of changes in the distribution and abundance of forage fish.

Keywords: climate change, forage fish, multi-colony comparison, Northeast Atlantic, North Sea, Sandeel, Snake Pipefish, Sprat.

Studies investigating aspects of seabird demography at multi-colony scales are becoming increasingly common in the Northeast Atlantic (e.g. Grosbois *et al.* 2009, Cook *et al.* 2011, Lahoz-Monfort *et al.* 2011). However, multi-colony comparisons of diet remain rare despite the fact that local differences in feeding conditions are often cited as being a likely cause of regional variation in breeding success (Frederiksen *et al.* 2005, Mitchell & Daunt 2010). In British waters, sandeels, predominantly Lesser Sandeels *Ammodytes marinus*, are thought

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to be the main forage fish for seabirds (Mitchell *et al.* 2004). Sandeels are also the target of a major industrial fishery in the North Sea and, particularly where fishing occurs close to seabird colonies, there has been concern that this has a negative impact on seabird breeding (Furness 2002). A *c.* 100km zone out from the coast of eastern Scotland and northeast England was therefore closed to commercial sandeel fishing in 2000 with the aim of reducing adverse effects on top predators (Daunt *et al.* 2008). Although there is evidence of an improvement in breeding success of Black-legged Kittiwakes *Rissa tridactyla*, similar benefits of the fishery closure have not been demonstrated in other seabird species such as Common Guillemot *Uria aalge* and Atlantic Puffin *Fratercula arctica* (Frederiksen *et al.* 2008).

In addition to fishery effects, climatic changes in the waters around the UK are also thought to be affecting fish species, with Lesser Sandeel being identified as at particular risk due it its specialized habitat requirements and limited capacity to shift distribution (Heath *et al.* 2012). Conversely, Sprat *Sprattus sprattus*, another important prey species for some seabirds, is thought to be increasing (ICES 2012), and new prey species, e.g. Snake Pipefish *Entelurus aequoreus*, have started to be recorded in seabird diet (Harris *et al.* 2007).

Given the speed and magnitude of changes in fisheries and climate there is a need for an up-to-date assessment of the diet of seabirds to establish a baseline against which to measure subsequent changes. In practice, collecting dietary data is often challenging due to the difficulty of obtaining samples from cliff-nesting birds, particularly species such as Black-legged Kittiwakes that regurgitate prey for their chicks. However, auks and terns carry items back to the offspring in the bill, enabling prey to be recorded during the chick period.

Common Guillemots (hereafter Guillemot) were the most abundant seabird in the UK in the early 2000s (Mitchell *et al.* 2004). However, numbers at many colonies have since declined (JNCC 2012a, Wanless & Harris 2012) and population trends at east and west coast colonies have differed (Cook *et al.* 2011). Adults feeding chicks bring back a single fish held lengthwise in the bill, which makes identifying prey straightforward compared with species such as Atlantic Puffin and Razorbill *Alca torda* that frequently return with loads containing many fish. The literature suggests that in the UK, Guillemots normally feed their chicks on fish from three families: Ammodytidae (sandeels: mainly Lesser Sandeels), Clupeidae (mainly Sprats or young Atlantic Herring *Clupea harengus*) and Gadidae (mainly young Whiting *Merlangius merlangus*, Saithe *Pollachius virens* or Cod *Gadus morhua*) (Mitchell *et al.* 2004). However, in many cases the evidence for this is based on data collected more than a decade ago, primarily from North Sea colonies (Bradstreet & Brown 1985, Wanless *et al.* 1998, Furness & Tasker 2000, but see Hatchwell 1991). Knowledge of chick diet at colonies in western Britain remains limited but recent studies in the North Sea have suggested that reliance on sandeels has decreased (Wanless *et al.* 2005, Heubeck 2009). The aims of our study were therefore to (1) map the contemporary diet of Guillemot chicks at colonies around the UK; (2) test for spatial patterns in these data; (3) compare current diet with data available for earlier years; and (4) discuss spatial and temporal differences in Guillemot chick diet in relation to changes in forage fish abundance due to fisheries and climate.

METHODS

Data collection

Prior to each breeding season in 2006–2011, protocols for collecting standardized data on Guillemot chick diet were sent to researchers known to be carrying out work on the species, and individuals either likely to be visiting breeding colonies or with responsibility for managing seabird reserves around the coast of the British Isles (Fig. 1). Observers were asked to find a safe vantage point from where they could watch at least 50 pairs of Guillemots, preferably from a distance of <30 m. They were encouraged to spread checks throughout the day and to cover as much of the chick-rearing period as possible (typically from late May until late July) to minimize any potential bias associated with temporal changes in prey delivered. Data collection involved scanning Guillemots flying in towards the colony, either with the naked eye or with binoculars, identifying those carrying fish, and following them until they arrived back at their breeding site. Observers were requested to classify prey initially into one of five categories using body shape and/or colour as criteria: sandeel, clupeid, gadid, other known prey, e.g. pipefish or unknown (items that were not definitely identified usually because they were not seen clearly

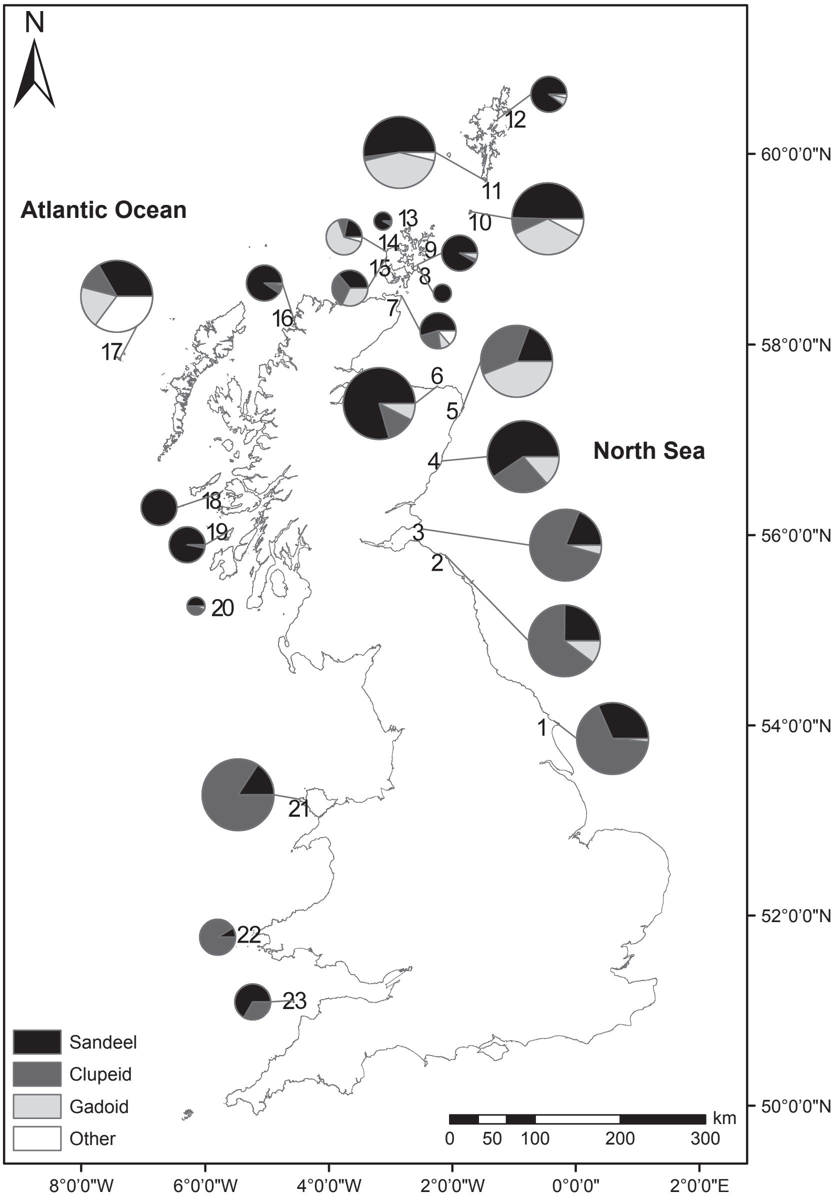

Figure 1. Proportions of different prey types fed to Common Guillemot chicks at 23 colonies where chick diet was monitored during at least one season between 2006 and 2011. Colony names and regions are given in Table 1. Colonies where the total sample size was <20 prey items, 20–100 prey items and >100 prey items are indicated by small, medium and large symbols, respectively.

enough). Unknown prey were excluded from subsequent analyses but, as far as we could tell, this did not result in the omission of any major prey types. The overall frequency of observations classed as 'unknown' was 3% (845 prey items in total) and varied from 0% at Burravoe, Colonsay, Duncansby and Lunga, to 47% ($n = 22$) at Row Head. Guillemots also return to the breeding colony with display fish that are held prominently in the bill and thus are potentially easier to identify than those fed to chicks, which are quickly swallowed. Observers were asked to ignore display fish, as they can differ from those brought in for chicks (Harris & Wanless 1985).

We considered two alternative geographical groupings of colonies. The first used biogeographical divisions as defined by OSPAR (2010) that are based on the differing hydro-biological conditions in

Table 1. Totals of identified prey items (sandeels, clupeids, gadids and other prey species) fed to Common Guillemot chicks at 23 UK colonies, 2006–2011. The number of years that observations were made and the sampling effort (number of days of diet data recorded) are also shown. Colony locations are shown in Fig. 1. Region 1 follows the OSPAR divisions and Region 2 follows the Regional Seas Monitoring Regions, with the exception of St Kilda, which was placed in a separate region instead of being included in the Scottish Continental Shelf.

Colony number	Colony	Region 1 (OSPAR)	Region 2 (Regional Seas Monitoring Regions)	No. of years sampled	Total sampling effort (days)	Total no. of identified prey items
1	Bempton	East coast	Northern North Sea	4	24	481
2	St Abbs	East coast	Northern North Sea	1	3	794
3	Isle of May	East coast	Northern North Sea	6	211	5106
4	Fowlsheugh	East coast	Northern North Sea	4	27	1675
5	Bullers of Buchan	East coast	Northern North Sea	1	5	356
6	Troup Head	East coast	Northern North Sea	1	5	413
7	Duncansby Head	East coast	Scottish Continental Shelf	1	2	22
8	Gultak	East coast	Scottish Continental Shelf	1	2	4
9	Mull Head	East coast	Scottish Continental Shelf	2	10	71
10	Fair Isle	East coast	Scottish Continental Shelf	1	4	446
11	Sumburgh Head	East coast	Scottish Continental Shelf	6	81	1660
12	Burravoe	East coast	Scottish Continental Shelf	1	2	30
13	Fowl Craig	East coast	Scottish Continental Shelf	1	5	13
14	Marwick Head	East coast	Scottish Continental Shelf	2	12	46
15	Row Head	East coast	Scottish Continental Shelf	1	2	25
16	Handa Island	West coast	Minches and Western Scotland	2	11	52
17	St Kilda	West coast	St Kilda	3	18	111
18	Lunga	West coast	Minches and Western Scotland	1	2	35
19	Colonsay	West coast	Minches and Western Scotland	1	2	35
20	Rathlin Island	West coast	Minches and Western Scotland	1	12	14
21	South Stack	West coast	Irish Sea	1	14	115
22	Ramsey Island	West coast	Irish Sea	1	4	23
23	Lundy Island	West coast	Celtic Sea	2	10	27
	Totals			45	468	11 554

Atlantic and North Sea waters. We therefore set a longitudinal boundary at 4°W and categorized colonies east of this boundary (including those in Orkney and Shetland) as East Coast and within the North Sea region, whereas those to the west of the boundary were categorized as West Coast and within the Atlantic region (Table 1). This division also accords with the two Ecological Assessment Areas identified for Guillemots on the basis of recent trends in abundance (Cook *et al.* 2011). For the second grouping, we used the Regional Seas Monitoring Regions (Connor *et al.* 2006), with the exception that St Kilda was placed in a separate region instead of being included with Orkney and Shetland in the Scottish Continental Shelf (Table 1).

Data analysis

A binomial generalized linear mixed model (GLMM) with a logit link was used to model the proportion of the total number of prey items recorded on each date at each colony that was sandeels. Within the model the dispersion parameter was estimated, with colony and the combination of year with colony as random effects. The random effects were necessary to ensure that variation other than observation error was included in the analysis and correlations in the data were properly accounted for. The fixed effects tested were linear effects of Julian date (1 = 1 January), year, latitude and region. As latitude and region vary between, rather than within, colonies, the choice between a model containing the divisions based on the Regional Seas Monitoring Regions and one containing both latitude and OSPAR region was made on the basis of which model explained more of the variation between colonies (i.e. had the smaller variance component for colonies). To investigate the importance of alternative prey to sandeels, a binomial GLMM with logit link was fitted to the proportion of clupeids in the total of items excluding sandeels. As in the sandeel model, colony and year within colony were identified as random effects. For both the sandeel and the clupeid models, parameter estimates given are slopes on the logit transformed scale.

The fitted proportion of sandeels in each region (Fig. 2a) and the fitted effect of latitude on the proportion of clupeids in non-sandeel prey (Fig. 2b) were formed for a notional colony and year (with zero random effects) for Julian date 175, the median date that data were recorded. These values are not the same as the population average values, as in a generalized linear model with a non-linear link function, making a prediction conditional on the average value of a covariate is not equivalent to taking the average of the predictions for all observed values of the covariate (Lane & Nelder 1982).

To investigate whether Guillemot chick diet had changed over a longer timescale (range 15–30 years) we used binomial tests to compare the proportions of sandeels recorded at four colonies for which there was previously published data (Isle of May, Fair Isle and Sumburgh Head on the East Coast and Canna on the West Coast). Canna was not included in our main analyses investigating spatial differences in contemporary Guillemot chick diet because the sampling method differed from the one we advocated, with fish being collected from the ledges during chick-ringing rather than by observations. However, because historical data were not available for any of our West Coast colonies, we used data for Canna in the temporal comparison, as in this case we were comparing changes within rather than among colonies. Sample sizes for contemporary data for the Isle of May, Fair Isle and Sumburgh Head are given in Table 1. Sixty-two samples were collected on Canna in 2006–2007 (Swann *et al.* 2008). Previous data for Sumburgh Head were collected in 1990–91 (n = 1124 items; Uttley *et al.* 1994); Fair Isle in 1985–87 (n = 2841; del Nevo 1990); Isle of May in 1981–84 (n = 2994; Harris & Wanless 1985); and Canna in the 1980s (n = 345; Swann *et al.* 2008).

Finally, to assess temporal changes in Guillemot chick diet in more detail, we analysed data collected annually at the Isle of May between 1982 and 2011. At this colony, prey delivered to the

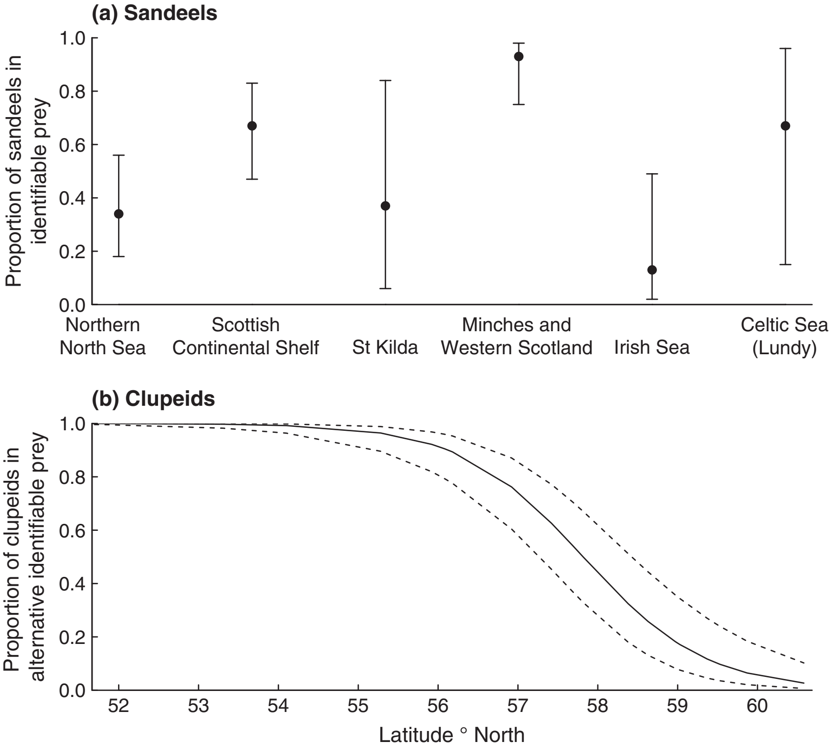

Figure 2. Fitted relationships between (a) Regional Seas Monitoring Regions and the proportion of sandeels and (b) latitude and the proportion of clupeids in Common Guillemot chick diet for the 23 colonies shown in Fig. 1. Error bars in (a) and dotted lines in (b) represent 95% confidence intervals.

chicks were recorded almost daily throughout the entire chick-rearing period such that the mean ± se number of fish observed each year was 1017 ± 7. Of 139 clupeids collected from the breeding ledges during ringing over the study period, 128 (93%) were identified as Sprats and 11 (7%) as juvenile Atlantic Herring. We therefore assumed that the clupeid component of the diet was largely made up of Sprats. For each year we estimated the proportion (by number) of sandeels in chick diet and the proportion of the non-sandeel component made up of Sprats or gadids. Logistic regression with an estimated dispersion parameter was used to test the trend in the proportion of sandeels.

All statistical analyses were carried out using GenStat for Windows (VSN International 2011) and all GLMM results are quoted on the logit transformed scale ± se.

RESULTS

In total, 11 554 prey items were recorded at 23 colonies between 2006 and 2011 (Table 1). The predominant prey type varied, with sandeels the commonest at 15 colonies (65%), clupeids at five (22%) and gadids at two (9%) (Fig. 1). 'Other' prey made up only 1.2% of items, most of which were pipefish (136 records, 96% of the category) and came mainly from the more northerly colonies (St Kilda, Duncansby Head, Marwick Head, Fair Isle and Sumburgh Head) and the earlier part of the sampling period (2006–2009). St Kilda was the only colony at which 'other' prey, all consisting of pipefish, was the commonest prey type (35%, $n = 39$). Additional items were squid (five records at two colonies 2010–2011) and one Cottidae in 2011.

There were significant differences in diet composition both among colonies and among years within colonies. However, for the nine colonies for which we had data for multiple years, variation in the proportions of sandeel and clupeid (as indicated by the variance components) was greater among colonies than among years within colonies (GLMM including random effects only, sandeel: among colonies variance component = 1.408, years within colonies = 0.360; clupeid: among colonies = 6.841, year within colonies = 1.546). In addition, the fixed effect for year was not significant if added to the final model for all colonies ($F_{5,16} = 3.33$, $P = 0.66$ for the sandeel model with Regional Seas Monitoring Regions and $F_{5,20} = 1.06$, $P = 0.41$ for the non-sandeel prey model), indicating that there were no consistent differences across colonies between particular years.

After including date ($F_{1,421} = 23.41$, $P < 0.001$) and the divisions based on the Regional Seas Monitoring Regions ($F_{5,15} = 4.05$, $P = 0.015$), there was no significant additional effect of latitude on the proportion of sandeel in chick diet ($F_{1,12} = 1.53$, $P = 0.238$). This model had a variance component of 0.965 for colony, compared with 1.535 for a possible alternative model that included both OSPAR region ($F_{1,17} = 4.86$, $P = 0.041$) and latitude ($F_{1,17} = 7.64$, $P = 0.013$). The proportion of sandeels in chick diet showed a positive relationship with latitude (slope on the logit transformed scale = 0.408 ± 0.148). The relationship differed significantly between regions, with the proportion being higher for a given latitude on the west coast compared with that on the east (difference in intercepts on the logit transformed scale = 1.715 ± 0.778). In contrast, when latitude was included in the model for non-sandeel prey, there was no significant improvement in the fit by adding either Regional Seas Monitoring Region ($F_{5,25} = 0.52$, $P = 0.757$) or OSPAR region ($F_{1,17} = 1.47$, $P = 0.242$). Thus, while the proportion of sandeels in chick diet varied not simply latitudinally but also among regions (Fig. 2a), the non-sandeel component showed only a latitudinal change, with clupeids being the main alternative at colonies south of *c.* 56°N, whereas to the north of this, small gadids and other prey became progressively more important (slope on the logit transformed scale = −1.300 ± 0.206, $F_{1,15} = 39.7$, $P < 0.001$) (Fig. 2b).

Examination of within-season changes in prey type indicated that a greater part of chick diet comprised sandeels early in the season (linear date effect on the logit transformed scale = −0.0260 ± 0.0051) and consequently the proportion of non-sandeel prey increased as the season progressed. Within these non-sandeel prey, the proportion of clupeids showed a linear increase with date, indicating that their overall contribution became more important (slope on the logit transformed scale = 0.0416 ± 0.0105, $F_{1,393} = 9.73$, $P = 0.002$).

Pair-wise comparisons of colonies for which we had contemporary and historical data on chick diet indicated that there was a significant decline over time in the proportion of sandeels in Guillemot chick diet at the East Coast colonies on the Isle of May ($Z = 49.1$, $P < 0.001$), Fair Isle ($Z = 35.8$, $P < 0.001$) and Sumburgh Head ($Z = 15.4$, $P < 0.001$), but no significant change at the West Coast colony on Canna ($Z = -0.88$, $P = 0.377$; Fig. 3). The decline in importance of sandeels in chick diet was clearly shown in the long-term data for the Isle of May, with the proportion decreasing from >0.80 in the 1980s to <0.20 from the mid 2000s (Fig. 4a). The slope of the regression line on the logit transformed scale was -0.149 ± 0.023 ($t_{28} = -6.47$, $P < 0.001$). Sprats were the main alternative prey to sandeels throughout the study period, with the proportion of gadids in the non-sandeel component of chick diet only exceeding 0.10 in one of the 30 breeding seasons recorded (Fig. 4b). As sandeels declined in importance as a component of chick diet at Sumburgh Head and Fair Isle, gadids became increasingly important, with their proportions rising from 0.20 to 0.35 at Sumburgh Head and from 0 to 0.43 at Fair Isle, while the proportions of clupeids increased only marginally at both Sumburgh Head (from 0 to 0.07) and Fair Isle (from 0.01 to 0.02).

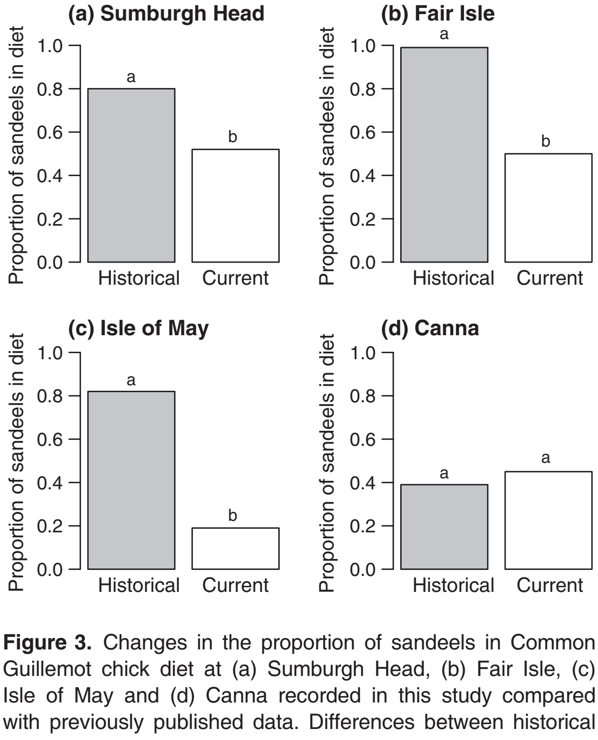

Figure 3. Changes in the proportion of sandeels in Common Guillemot chick diet at (a) Sumburgh Head, (b) Fair Isle, (c) Isle of May and (d) Canna recorded in this study compared with previously published data. Differences between historical and current sandeel proportions at each colony are indicated by different letters above the respective columns; significant differences are at the $P < 0.001$ level.

DISCUSSION

Marked differences in seabird breeding success and population trends have recently been recorded at UK colonies and in many cases have been attributed to variation in local food supply (Frederiksen *et al.* 2005, Mavor *et al.* 2006, Mitchell & Daunt 2010, Cook *et al.* 2011). Obtaining comprehensive data on seabird diet to investigate demographic links directly is often problematic. Guillemots bring in single, relatively conspicuous prey items for their chicks and thus obtaining information on diet during the chick-rearing period is easier than for species that bring back several prey items or feed their chicks by regurgitation. However, although information on Guillemot chick diet is available for a few well-studied colonies such as the Isle of May, Sumburgh Head and Canna (Daunt *et al.* 2008, Swann *et al.* 2008, Heubeck 2009), a multi-colony comparison of chick diet has not been attempted previously. Our study is thus the first integrated analysis of Guillemot chick diet at a UK scale and provides baseline information between 2006 and 2011. Many observations were made opportunistically and so the amount of data varied among colonies with respect to the number of years covered, days sampled within a year and total prey items recorded. Our statistical analyses took account of this heterogeneity in sample sizes by giving more weight to colonies with large sample sizes than to those where sample size was smaller. Furthermore, results from colonies where sampling effort was greater indicated that variation in diet across years within a colony was significantly less than variation among colonies. Although, ideally, Guillemot diet data should be collected over a range of days, we were nevertheless confident that information gathered from colonies where effort was limited would accurately reflect diet over the study period.

Prior to our study, available information on Guillemot chick diet in the UK indicated regional differences with sandeels thought to be more important at northern colonies and clupeids, principally Sprats, being more common in the south (Blake *et al.* 1985, Harris & Wanless 1985, Hatchwell 1991, Uttley *et al.* 1994, Furness & Tasker 2000). Our results for 2006–2011 indicate that, in broad terms, these patterns still hold. However, our detailed analysis indicates differences in the type of spatial variation between the prey categories. Thus, sandeels not only vary

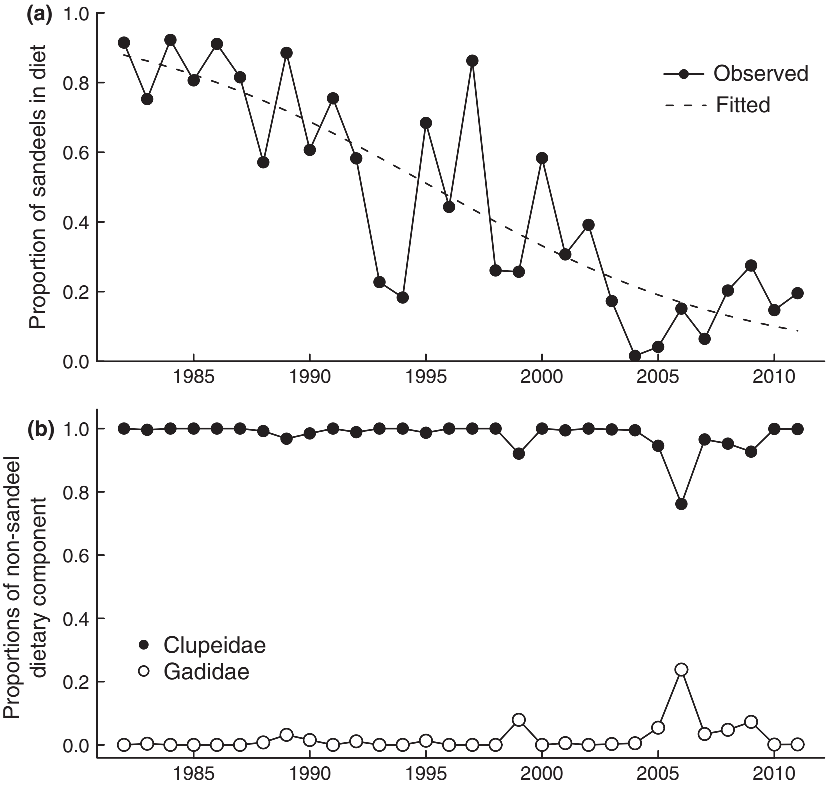

Figure 4. Changes in (a) the proportion of sandeels in the diet of Common Guillemot chicks at the isle of May 1982–2011 (dashed line indicates fitted values from a logistic regression against year) and (b) proportions of the non-sandeel component of the diet made up of Clupeidae and Gadidae.

latitudinally as expected but also show regional clustering, whereas other prey types are mainly associated with latitude, with clupeids predominant in the south and gadids more frequent in the north. Assuming that the majority of sandeels brought in by Guillemots were Lesser Sandeels, the regional groupings apparent in chick diet are broadly congruent with known sandeel populations identified from fish and fishery surveys (Frederiksen *et al.* 2005). Clusters of colonies of Black-legged Kittiwakes showing synchronized variation in breeding success have also been shown to coincide with these sandeel populations although it was not possible to investigate whether these were associated with regional differences in diet (Frederiksen *et al.* 2005).

In terms of non-sandeel prey, the best model was with latitude such that clupeids predominated at southern colonies and gadids at northern ones. Interpreting these relationships is hindered because species-specific identification of fish in both groups is impossible in the field. In the case of clupeids it seems likely that most of the items brought in were Sprat, although this could only be verified on the Isle of May. Field identification of juvenile gadids is even more problematic since a whole range of species could all potentially be brought in by Guillemots for their chicks. These unavoidable uncertainties in the actual prey species involved hinder interpreting results in terms of climatic links because the species differ in their thermal requirements. However, from a Guillemot chick's perspective, while Sprats represent a nutritionally equivalent alternative to sandeels, juvenile gadids have a much lower lipid content and thus a markedly lower energy value (Hislop *et al.* 1991). In accordance with this, Guillemot breeding failures have been more frequent and severe in Shetland where the proportion of gadids in chick diet is higher, compared with elsewhere in the UK (Mavor *et al.* 2008, Mitchell & Daunt 2010).

Although an acute shortage of time series data limited our understanding of long-term trends in Guillemot diet, pair-wise comparisons of our data with previously published information indicate that the proportion of sandeels has decreased at East Coast colonies over the last 15–30 years. The annual data for the Isle of May show this shift in more detail, with diet initially being predominantly sandeel, almost certainly Lesser Sandeel, but with the proportion of Sprat increasing during the 1990s such that this species has accounted for the majority of chick diet since 2000. Very limited data from West Coast colonies hindered firm conclusions, but changes in chick diet appear to have been less marked than on the East Coast. On Skomer Island (SW Wales), for example, Birkhead (1977) recorded 96% of fish brought to Guillemot chicks between 1972 and 1975 as clupeids (thought to be mainly Sprat), and this has remained the main prey (generally >90%; JNCC 2012b). Further north, on the Isle of Canna, Swann *et al.* (2008) noted that Sprat made up on average 47% of the diet between 1982 and 2007, although there were large variations between years, with Sprat generally being less important in the 1980s and 2000s than in the 1990s, and sandeel making up an increasing proportion between 2003 and 2007.

It is likely that both current spatial variation and temporal changes in Guillemot chick diet at UK colonies reflect a combination of climate and fisheries effects. However, despite strong evidence that climate is influencing fish distribution and abundance over and above that due to fishing, changes are only partially explained by simple climate envelope models, indicating that the mechanisms involved are complex (Heath *et al.* 2012). The patterns in Guillemot chick diet accord broadly with those expected if conditions for cold water species such as Lesser Sandeels have become less favourable as sea temperature has risen, whereas those for warmer water species such as Sprat have improved (Heath *et al.* 2012). The increase in Sprats in Guillemot chick diet on the Isle of May in the 1990s followed a shift in the North Sea from a cold water to a warm water regime around 1989, and Sprat stocks in the North Sea have increased over the last 15–20 years (ICES 2010, Alvarez-Fernandez *et al.* 2012). During our study there were no major commercial fisheries for forage fish operating close to UK seabird colonies. However, sandeel fisheries in the North Sea, particularly on the Wee Bankie and Marr Bank, may have reduced stocks in the 1990s (Rindorf *et al.* 2000), exacerbating subsequent poor recruitment due to climatic changes (van Deurs *et al.* 2009). In contrast, Sprat stocks off eastern Scotland collapsed in the early 1980s after targeted fishing but have since recovered as climatic conditions have become more favourable and stocks have been unfished (Jennings *et al.* 2012).

In general, fish brought in for Guillemot chicks in our study accorded with those previously recorded at UK colonies (Mitchell *et al.* 2004). The exception was Snake Pipefish, which, prior to 2004, had not been recorded despite the species being very distinctive and thus easy to identify. The early years of our study coincided with a population explosion of Snake Pipefish in the Northeast Atlantic and the species started to be taken by a wide range of seabirds including Guillemots (Harris *et al.* 2007). The reason for this population explosion remains unclear but may have been part of a general increase in the occurrence of warm water/subtropical species that occurred in the region around this time (Kirby *et al.* 2006). Colonies where Snake Pipefish was recorded were all in northern Britain (Duncansby Head, Fair Isle, Sumburgh Head, Marwick Head, St Kilda), and St Kilda in the Outer Hebrides was the only place where Snake Pipefish made up more than 30% of Guillemot chick diet. From 2009 onwards, Snake Pipefish were almost entirely absent from Guillemot chick diet, a finding that agrees with records for other seabirds, predatory fish and marine mammals, suggesting that Pipefish numbers crashed and/or that stocks of the normal prey species increased (Heath *et al.* 2012, M.P. Harris pers. obs.).

We also found evidence of seasonal changes in prey. Seasonal shifts in diet have previously been recorded in Guillemots (Birkhead 1977, Wilson *et al.* 2004), and other UK seabirds, e.g. Black-legged Kittiwake (Lewis *et al.* 2001), Northern Fulmar *Fulmarus glacialis* (Phillips *et al.* 1999) and Northern Gannet *Morus bassanus* (Lewis *et al.* 2003). Our results indicate a significant decrease in the proportion of sandeel in Guillemot chick diet as the season progresses. We know little about the mechanisms underlying this trend but the pattern is broadly consistent with seasonal changes in Lesser Sandeel activity, with adult fish (the age group fed to Guillemot chicks) retreating back into sandy substrates during June or July (Winslade 1974), making them less available to species such as Guillemots, which feed in mid-water (Daunt *et al.* 2006).

Prey size as well as prey species is important for seabirds such as Guillemots that bring back single items for the chick, with larger items typically representing higher quality food (Hislop *et al.* 1991). Size distributions of Lesser Sandeels in different North Sea stocks vary markedly (Boulcott *et al.* 2007) and thus lengths of sandeels brought in for Guillemot chicks could potentially have differed among colonies. However, standardizing prey lengths visually estimated among observers is known to be subject to bias (Carss & Godfrey 1996, Elliott *et al.* 2008). Coupled with the rapid transfer of food from the parent to the chick (Tschanz 1968), which limits the time available for the observer to assess the prey, we decided to focus data collection on identifying species rather than attempting to include size as well. However, work in Norway has recently highlighted the usefulness of digital photography to assist in the identification and estimation of size of prey items fed to auks (Anker-Nilssen 2010). Using this technique at UK colonies could increase the level of detail recorded and provide a useful addition to the current observer-based approach.

In conclusion, our study has provided baseline data highlighting marked differences in Guillemot chick diet at UK colonies. Hydro-biological conditions in coastal waters, particularly sea temperature in the North Sea, are changing rapidly (Edwards *et al.* 2007, 2010, Hughes *et al.* 2010) and are predicted to become less favourable for Lesser Sandeels, which have traditionally been regarded as the key forage fish for many top predators (Heath *et al.* 2012). Moreover, many of the forage fish taken by seabirds are also the target of important human fisheries. Multi-colony information on seabird diet can be important to indicate changes in forage fish distribution and predator/prey dynamics.

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