

Community-wide decline in the occurrence of lesser sandeels *Ammodytes marinus* in seabird chick diets at a North Sea colony

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ABSTRACT: Many pelagic marine ecosystems have a wasp-waist trophic structure characterised by low diversity of mid-trophic species, typically small, shoaling forage fish that are eaten by a wide range of top predators. In the North Sea, this mid-trophic position is occupied by the lesser sandeel *Ammodytes marinus*. Over the last 30–40 yr, the abundance and length-at-age of sandeels have declined, but information on concurrent changes in the diets of seabird communities is scarce. We used data on chick diet composition, sandeel length-at-age and energy density collected at a colony in the western North Sea from 1973–2015, to test for dietary shifts in this seabird community during a period when a local sandeel fishery opened, operated and was closed. We found a long-term decline in the overall importance (measured as the frequency of occurrence and proportion of biomass in diet samples) of sandeels, particularly 1+ group fish. However, there were species-specific differences such that the overall decline in sandeels was strongest in common guillemots *Uria aalge*, while the shift from 1+ group to 0 group sandeels was apparent in all species except European shags *Phalacrocorax aristotelis*. Community-level differences were also apparent in the alternative prey to sandeels, with common guillemot, razorbill *Alca torda*, Atlantic puffin *Fratercula arctica*, and black-legged kittiwake *Rissa tridactyla* chicks being fed clupeids, predominantly sprat *Sprattus sprattus*, while shag chicks received a wide range of benthic fish species. There was also evidence for a decline in the quality of sandeels fed to chicks with significant decreases in length-at-age of 0 group and 1+ group. However, there was no significant annual variation in the energy density of sandeels except for 2004, when values were exceptionally low. Neither the opening nor the closing of the sandeel fishery had any detectable effect on chick diet composition, sandeel length or sandeel energy density. Overall, our results suggest marked community-level changes in seabird diet composition over the last 3 decades that may reflect long-term declines in the abundance and quality of their principal prey.

KEY WORDS: Dietary shifts · Fishery closure · Forage fish · Industrial fisheries · Predator-based diet sampling · Sand lance · Snake pipefish · Trophic interactions

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INTRODUCTION

Many pelagic marine ecosystems are characterised by a 'wasp-waist' trophic structure, with high species diversity at upper and lower trophic levels and low diversity of mid-trophic species (Cury et al. 2000).

Typically, this mid-trophic position is occupied by an abundant forage fish that forms a major prey item for a wide range of higher predators. However, changing conditions, in particular rising sea temperatures, are thought to be causing changes in the distribution, abundance and energetic quality of mid-trophic for-

age fish, and in some regions, the situation has been further exacerbated by pressure from industrial fisheries (Sydeman et al. 2017a). Given the importance of these forage fish species to marine predators, a decline in their availability and/or quality might be reflected in changes in predator diet with potentially important demographic consequences if the alternative prey are less available and/or less energetically profitable. Furthermore, sympatric species are expected to vary in their dietary responses, for example in avian predators because of different foraging strategies such as surface-feeding versus diving species, and during the breeding season, because of different prey delivery methods such as whole fish transported in the bill versus regurgitation of semi-digested prey (Furness & Tasker 2000). However, although dietary shifts in particular species of avian predator have been identified in wasp-waist systems (Miller & Sydeman 2004, Gaston & Elliott 2014), community-level predator responses remain poorly known (Sydeman et al. 2017b).

In the North Sea, the principal pelagic mid-trophic species is the lesser sandeel *Ammodytes marinus* (hereafter sandeel), a small, lipid-rich, shoaling fish with a complex life cycle after metamorphosis that alternates periods buried in sandy substrates with periods of activity in the water column (Winslade 1974, Wright & Bailey 1993). Sandeels make up a major component of the diet of many marine mammals, fish and birds in the North Sea and are also the main target species for a large industrial fishery (Gislason & Kirkegaard 1998, Engelhard et al. 2014). The species is considered to be particularly at risk from rising sea temperatures due to its specialised habitat requirements and limited capacity to shift distribution in response to changing hydrographic conditions and prey distributions (Heath et al. 2012a, Frederiksen et al. 2013). Sandeels have also become smaller over the past 4 decades, with significant declines in mean lengths-at-age being most marked in the northwestern North Sea (Wanless et al. 2004, Frederiksen et al. 2011, Rindorf et al. 2016). Mass/length relationships in sandeels are non-linear and thus mass and energy value have decreased disproportionately, meaning that particularly in the northwestern North Sea, predators now need to catch more individual sandeels to meet their own and their offspring's energetic requirements (Rindorf et al. 2016). Analyses of sandeel body composition have also highlighted that in 2004, the mean energy density of sandeels in the northwestern North Sea was drastically lower than values in the previous 30 yr (Wanless et al. 2005). Concurrent with these changes,

poor breeding success of seabirds at colonies along the west coast of the North Sea has repeatedly been attributed to declines in sandeel availability and quality (Mitchell et al. 2004, Daunt et al. 2017). However, for the most part direct information on chick diets for a range of seabird species has been lacking, precluding a systematic evaluation of the evidence for community-level dietary shifts.

Much of what is known about changes in seabird diets in the North Sea in recent decades has come from long-term studies on the Isle of May, a major seabird colony off the coast of southeast Scotland. Here, standardised monitoring of prey brought in for chicks over the last 30–40 yr has documented marked changes in diet composition, notably a decline in the relative importance of sandeels. However, to date the emphasis has been on single-species assessments, such as for common guillemots *Uria aalge* (Smout et al. 2013, Anderson et al. 2014) and European shags *Phalacrocorax aristotelis* (Howells et al. 2017), rather than comparing responses at a community scale. Here, we used chick diet data from 3 pursuit-divers (Atlantic puffin *Fratercula arctica*, razorbill *Alca torda* and common guillemot) that carry back intact fish held in the beak for the chick, and 1 surface-feeder (black-legged kittiwake *Rissa tridactyla*) and 1 pursuit-diver (European shag) that regurgitate semi-digested food to their offspring, to quantify dietary trends in a seabird community over a 30 yr period. Together these 5 species account for >90% of the biomass of seabirds on the Isle of May that feed on marine prey during the breeding season (Daunt et al. 2008). All 5 have traditionally been viewed as relying on sandeels (both 0 group [fish of the year] and 1+ group [older fish]) as food for their chicks (Pearson 1968, Furness & Tasker 2000). Conditions for sandeels in the waters around the Isle of May have changed substantially over the period during which seabird diet data have been collected. Sea temperatures have risen, and the thermal environment for the copepod *Calanus finmarchicus*, a major prey of sandeels, has deteriorated (Burthe et al. 2012, Frederiksen et al. 2013). In addition, between 1990 and 1999, sandeels were the target of a large industrial fishery that operated within 30–50 km of the Isle of May (Rindorf et al. 2000).

Since 2000, an area down the east coast of Britain, including the areas used for feeding by many Isle of May seabirds, has been closed to commercial sandeel fishing with the aim of conserving prey stocks for predators including seabirds (Daunt et al. 2008). A condition of the closure was that there should be an evaluation of whether the removal of

sandeels by the fishery had a measurable effect on sandeel predators such as seabirds, and whether the establishment of a closed area could ameliorate any deleterious effects. Assessments based on seabird breeding success indicated that there was indeed evidence of a negative effect of the fishery and a positive effect of the closure in black-legged kittiwakes, whereas the other species were unaffected (Daunt et al. 2008, Frederiksen et al. 2008). However, the focus of these analyses was on reproductive output rather than changes in diet composition or sandeel quality per se. Our specific aims were therefore to test (1) for trends in the overall mean annual proportion of sandeel in chick diets of the 5 seabird species; (2) for changes in the relative importance of different age classes of sandeels in chick diets; (3) whether the downward trend in sandeel length has continued; and (4) whether the energy density of sandeels had been exceptionally low in any year since 2004. For each of these measures, we also assessed whether there was evidence for step changes associated with the commencement of the local sandeel fishery in 1990 and/or its closure in 2000.

MATERIALS AND METHODS

Fieldwork was carried out on the Isle of May National Nature Reserve, Firth of Forth, southeast Scotland (56° 11' N, 2° 33' W), with diet samples collected throughout the chick-rearing periods of all species. Full details of the species-specific sampling periods and annual sample sizes are presented in Table S1 in the Supplement at www.int-res.com/articles/suppl/m600p193_supp.pdf.

Diet sampling

Atlantic puffin

Atlantic puffins (hereafter puffins) carrying bill loads of fish destined for chicks were caught in mist-nets each year from 1973–2015. Most loads were obtained in the early morning (04:00–07:00 h, all times given as GMT) or evening (18:00–21:00 h), but some additional loads were collected throughout the day. When caught, puffins dropped their fish and a thorough search was made of the ground around the net to ensure that the complete load was collected. Each fish load (diet sample) was taken back to the laboratory where prey items were identified and the length of each intact fish was measured from the tip

of the snout to the tip of the tail. Sandeels (Ammodytidae) were classified as 0 group or 1+ group. In 2000–2015, ageing was based on otolith macrostructure (ICES 1995). Prior to this, we used year-specific discriminant analysis of fish length distributions (Wanless et al. 2004). Checks of the discriminant method against otolith macrostructure for 4169 otoliths from 3 years showed that classification of 0 group and 1+ group was 99.8% reliable. The occurrence of 0 group and 1+ group sandeels was not recorded at the sample level, so annual measures of frequencies of these groups correspond to the proportions in the pooled sample of fish in a given year.

Razorbill

Visual observations of fish brought back to the colony by adult razorbills were made each year from 1982–2015. Data were collected on many days during the chick-rearing period and covered the period from dawn to dusk (02:30–21:30 h). The species and size of fish in each load were recorded, with the latter assessed qualitatively in relation to the size of the adult's bill and scored as minute, small, medium or large. For sandeels, these size classes were assumed to correspond to body lengths of 40, 50, 70 and 80 mm, respectively, for clupeids to correspond to lengths of 50, 60, 80 and 90 mm, respectively, and for rockling (Lotidae) to correspond to an average fish length of 35 mm (Thaxter et al. 2013). Minute and small sandeels were assumed to be 0 group and longer fish to be 1+ group.

Common guillemot

Diet of common guillemot (hereafter guillemot) chicks was assessed visually from observations of fish brought by adults and subsequently fed to chicks. Data were collected between dawn and dusk (02:30–21:30 h) on most days throughout each chick-rearing period from 1982–2015. The species and size of each fish were recorded, with the latter classed as minute, small, medium or large relative to the size of the adult's bill (Anderson et al. 2014). These size classes were converted to fish length using fish found dropped in the colony each year. Minute sandeels were assumed to be 0 group and all others to be 1+ group. Examination of otoliths of 475 sandeels collected in the colony supported these assumptions of fish age.

European shag and black-legged kittiwake

Diet was sampled using regurgitates from chicks or adults with chicks collected each year from 1985–2015 (European shag, hereafter shag) and 1986–2015 (black-legged kittiwake, hereafter kittiwake). Previous work has shown that food regurgitated by adults at the nest is predominantly destined for the brood (Wanless et al. 1993), so samples from chicks and adults with chicks were pooled for analysis. Regurgitates were taken back to the laboratory and weighed, and the approximate contributions of the main prey groups (see below) present were assessed visually. Each regurgitate was dissolved in a warmed, saturated solution of biological washing powder (Biotex®) until all of the soft tissue had been digested (Lewis et al. 2001, Howells et al. 2017). The hard items, predominantly otoliths and large fish bones, were extracted and identified to the lowest possible taxon using keys in Härkönen (1986) and Watt et al. (1997). Otoliths were counted and measured under a binocular microscope. Sandeels were classed as 0 group or 1+ group using otolith macrostructure (ICES 1995). Where no otoliths or hard items were present following digestion, the initial visual assessments of prey biomass proportions were used since there was very close accordance between these 2 methods in samples where both were available (r^2 of arcsine transformed proportions of sandeels to non-sandeels = 0.96; $n = 185$; Howells et al. 2017).

Diet composition

Irrespective of the method used to sample diet, it was not always possible to identify all items to species level. Since the primary aim of this study was to assess temporal changes in the importance of sandeels during chick-rearing in this seabird community, for analysis prey were grouped as 0 group and 1+ group sandeels (all those identified to species were *Ammodytes marinus*), Clupeidae (sprat *Sprattus sprattus* and herring *Clupea harengus*, separated, where possible, by examination of otoliths or counts of vertebrae) and other species (mainly cod-fishes Gadidae, rockling Lotidae and gunnel or rock butterfly Pholidae, depending on the seabird species). For each seabird species and year, diet was expressed as (1) the frequency of samples (bill loads or regurgitates) containing each of these prey groups except for the puffins, where the relative proportions of 0 group and 1+ group sandeels were based on the total sandeels examined that year, and (2) the proportion by

mass of each prey group in the diet after pooling all the samples for the year, using species-specific otolith length to fish length and fish length to mass relationships (Harris & Hislop 1978, Lewis et al. 2003, Howells et al. 2017). The number and length of fish in a razorbill load typically show an inverse relationship, so where there was uncertainty about the numbers of prey items, we followed Thaxter et al. (2013) and assumed that loads of minute, small, medium and large fish contained 16, 6, 4 and 2 items, respectively. Frequency estimates derived from occurrence and biomass proportions were highly correlated, e.g. for sandeels (puffin $r = 0.741$, $n = 43$, $p < 0.001$; razorbill $r = 0.948$, $n = 34$, $p < 0.001$; guillemot $r = 0.977$, $n = 34$, $p < 0.001$; shag $r = 0.942$, $n = 31$, $p < 0.001$; kittiwake $r = 0.821$, $n = 30$, $p < 0.001$), so unless otherwise stated, results relating to diet composition refer to the annual proportions based on biomass.

Changes in energy value of sandeels

Samples of intact sandeels collected from puffins (0 group, $n = 988$; 1+ group, $n = 123$) and guillemots (1+ group, $n = 10$) in 19 yr were retained for analysis to determine energy content. Those collected between 1973 and 1987 were analysed using freeze-drying techniques and adiabatic bomb-calorimetry (Harris & Hislop 1978, Hislop et al. 1991). Details of methods used to analyse samples collected between 1988 and 2015 are given in Wanless et al. (2005). Each fish was dried to constant weight at 60°C and the fat extracted using diethyl ether in a soxhlet apparatus (Reynolds & Kunz 2001). The remaining material was dried, reweighed and put into a muffle furnace at 600°C for 10 h to incinerate the protein. The resulting ash was then weighed to determine the mineral content. All measurements were made to 0.0001 g accuracy. The energy value of each fish was then obtained from the body composition using energy equivalents of 39.6 kJ g⁻¹ for fat and 23.7 kJ g⁻¹ for protein (Crisp 1971). All energy values were expressed on a dry weight basis.

Statistical analysis

Annual- rather than sample-level biomass proportions were analysed, as this allowed us to include data from puffins where sandeels were not aged within individual samples. Generalised linear models (GLMs) with a logit link function, with year, species and a year × species interaction as fixed effects, were

used to test trends in annual biomass proportions of different prey types. Following Wanless et al. (2004) and Frederiksen et al. (2008), we also fitted presence (1990–1999) or absence (all other years) of the industrial sandeel fishery as a fixed effect, to test for evidence of a step change in diet composition when the fishery was operating. In analyses of biomass proportions, a change in one prey type cannot be distinguished from an opposing change in the other prey types (Howells et al. 2017). To allow for this, we used a hierarchical approach sequentially testing for changes in (1) the proportion of sandeels relative to all prey, (2) the proportion of 1+ group sandeels relative to 0 group sandeels and (3) the proportion of clupeids relative to other non-sandeel prey.

Temporal trends in lengths of 0 group and 1+ group sandeels were analysed by fitting linear mixed models using residual maximum likelihood (REML, Patterson & Thompson 1971). Year, date (1 June = 1) and fishery presence were fitted as covariates, and categorical sampling day, categorical year and date by categorical year as random effects. A full description of the model is given in Wanless et al. (2004). The model was used to obtain annual estimates of the length standardised to 1 July (for 0 group sandeels) and 1 June (for 1+ group sandeels).

Trends in energy density (kJ g^{-1}) were investigated by fitting linear mixed models using REML. Year, age (0 group and 1+ group) and fishery presence were fitted as fixed effects, and a categorical variable for year was fitted as a random effect. However, data were only available for 7 sandeels during the fishery years, limiting the power of the test for fishery presence.

RESULTS

Diet composition

The number of chick diet samples (food loads brought in by puffins, razorbills and guillemots and

regurgitates from shags and kittiwakes) collected during the study are summarized in Table 1 along with the total biomass of these samples. Species-specific estimates of the frequency of occurrence of sandeels, overall and for 0 group and 1+ group separately, and for the proportion of the biomass made up of sandeel both overall and by age group are also shown. These summaries indicate that, with the exception of guillemots, sandeels dominated the diet of chicks of all species both in terms of frequency of samples containing sandeels and as a proportion of the total biomass. Overall, the frequency of occurrence of 0 group sandeels was higher than that of 1+ group sandeels in puffin, razorbill and kittiwake with the reverse being the case in shag and particularly in guillemot, where 0 group sandeels made up a trivial proportion of chick diet.

Puffin

Except for 1974–1978 and 1993, sandeels always made up >50% of the biomass, and only in 1979 and 1982–1987 did 1+ group sandeels comprise more of the biomass than 0 group sandeels (Fig. 1a, Table S1a). The main alternative prey to sandeels was clupeids (Clupeidae). In 33 of the 42 yr of study, the bulk of these were sprat and only in 1980–1982, 1984 and 1988 did herring constitute >10% of the diet. In terms of other prey species, juvenile gadids (Gadidae) were the most important group but only in 1990–1992 and 2004 did the proportion of gadids exceed that of clupeids. In 2008, rockling (Lotidae) were the dominant other prey type.

Razorbill

Sandeel was the most important species in razorbill chick diet, but its contribution varied markedly over short time periods, for example making up 100% of

Table 1. Diet samples obtained from seabirds on the Isle of May showing the overall importance of sandeels to the diets of chicks. For Atlantic puffin, the frequencies refer to the proportions of all fish ($n = 57\,205$) and not samples

Species	Period	Samples		Frequency in sample			Proportion of biomass		
		No. of samples	Total mass (g)	0 group sandeel	1+ group sandeel	Total sandeel	0 group sandeel	1+ group sandeel	Total sandeel
Atlantic puffin	1973–2015	6489	59329	0.692	0.059	0.823	0.504	0.185	0.690
Razorbill	1982–2015	4854	13849	0.694	0.124	0.825	0.514	0.130	0.644
Common guillemot	1982–2015	33456	228680	0.010	0.386	0.396	0.001	0.330	0.331
European shag	1985–2015	935	35289	0.282	0.759	0.880	0.140	0.698	0.844
Black-legged kittiwake	1986–2015	2020	33805	0.835	0.175	0.904	0.662	0.116	0.778

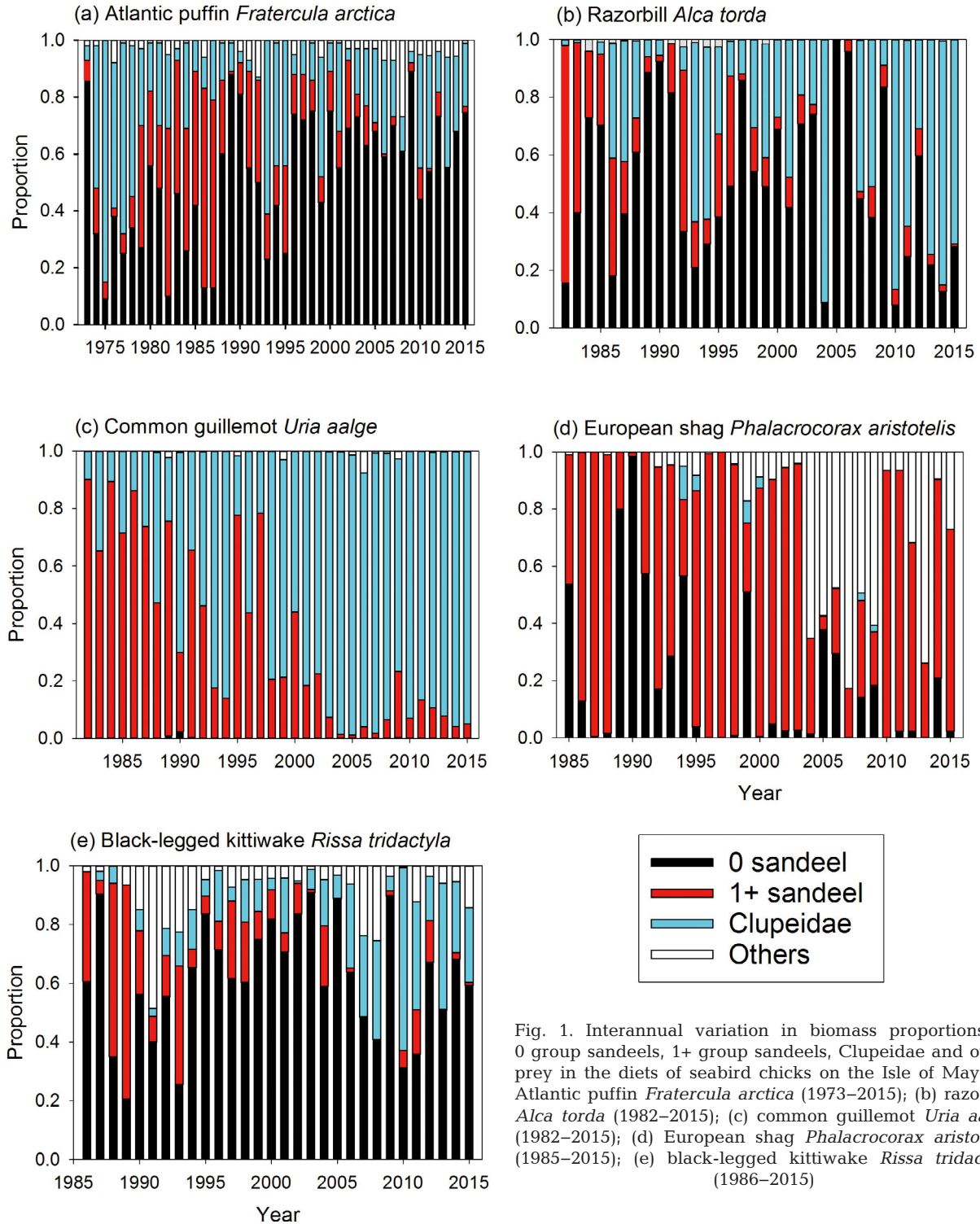


Fig. 1. Interannual variation in biomass proportions of 0 group sandeels, 1+ group sandeels, Clupeidae and other prey in the diets of seabird chicks on the Isle of May. (a) Atlantic puffin *Fratercula arctica* (1973–2015); (b) razorbill *Alca torda* (1982–2015); (c) common guillemot *Uria aalge* (1982–2015); (d) European shag *Phalacrocorax aristotelis* (1985–2015); (e) black-legged kittiwake *Rissa tridactyla* (1986–2015)

the biomass in 2005 and 2006 but only 9% in 2004 (Fig. 1b, Table S1b). Clupeids, probably mainly sprat, were the main alternative prey. Gadids were recorded in very small numbers, and in only 3 years (1999, 2013, 2014) did they contribute >1% of chick diet.

Guillemot

Prior to the late 1990s, sandeels typically accounted for >60% of guillemot chick diet, but after this, 2009 was the only year in which they made up >20% of the biomass (Fig. 1c, Table S1c). Almost all of the

sandeels were 1+ group and only in 1 year (1990) did 0 group constitute >2% of chick diet. The principal alternative prey were clupeids, and based on 167 fish collected from breeding ledges, most (93%) were sprat, with the remainder (7%) being herring. Gadids were recorded in very small numbers and only in 2006 did they account for >5% of the biomass.

Shag

The proportion of sandeel in the diet of shag chicks was >60% except in 2004–2009 and 2013 (Fig. 1d, Table S1d). Except for 1989–1991, 1994, 1999, 2005 and 2006, the predominant age class of sandeel taken was 1+ group. Clupeids were unimportant, only making up >5% of chick diet in 1994, 1995 and 1999. A variety of benthic fish species were the main alternative prey, the commonest being gunnel, which made up >10% of the biomass in 7 years between 2004 and 2014. Sygnathidae (all identified were snake pipefish *Entelurus aequoreus*) occurred in 2006 and 2007 but made up only 0.5 and 0.2% of the biomass, respectively.

Kittiwake

The importance of sandeel in kittiwake chick diet varied markedly, accounting for >90% between 1986 and 1989 but <50% in 1991, 2008 and 2010 (Fig. 1e, Table S1e). In some years in the 1980s and early 1990s, 1+ group sandeels made up >50% of the sandeel biomass in chick diet, but from the mid-1990s onwards, 0 group were the dominant age class. The main alternative prey to sandeels were clupeids, but juvenile gadids were also taken, particularly in years when the sandeel component in the diet was low. In addition, discards from fishing boats were recorded between 1990 and 1994. Sygnathidae (all identified were snake pipefish) occurred between 2005 and 2010, with numbers peaking in 2007 when they made up 10.5% of the biomass.

Temporal trends in diet composition

The proportion of sandeels in the diet of chicks decreased significantly overall during

the study period (Table 2a). There was a significant interaction between species and year in the model, whereby sandeels declined in all species except puffins (as evidenced by the significant interaction with year only apparent in puffins in relation to the reference species, kittiwakes; Table 2a). The proportion of 1+ group relative to 0 group sandeels also decreased over the study period (Table 2b). A species \times year interaction was apparent, such that the decline was apparent in all species except shag (significant interaction with year in shags in relation to the reference species, kittiwakes). The proportion of clupeids relative to other non-sandeel prey increased over the course of the study (Table 2c). Again, there

Table 2. Estimates (\pm SE) and t - and p -values for effects of year and species on biomass proportions in the diet of Isle of May seabirds. The intercept corresponds to the value for the mean study year in black-legged kittiwake when the fishery was not operating. Values are on the logit scale

Parameter	Estimate	SE	t	p
(a) Proportion of sandeel				
Constant	2.026	0.314	6.45	<0.001
Year	-0.0945	0.0302	-3.13	0.002
Fishery	-0.017	0.208	-0.08	0.934
European shag	-0.074	0.423	-0.17	0.862
Razorbill	-1.160	0.354	-3.28	0.001
Common guillemot	-2.819	0.363	-7.76	<0.001
Atlantic puffin	-0.913	0.348	-2.62	0.010
Year.European shag	-0.0285	0.0413	-0.69	0.491
Year.Razorbill	0.0133	0.0352	0.38	0.707
Year.Common guillemot	-0.0482	0.0382	-1.26	0.209
Year.Atlantic puffin	0.1121	0.0329	3.41	<0.001
(b) Proportion of 1+ group relative to 0 group				
Constant	-1.479	0.260	-5.69	<0.001
Year	-0.0963	0.0309	-3.12	0.002
Fishery	-0.041	0.220	-0.19	0.852
European shag	2.533	0.315	8.03	<0.001
Razorbill	0.229	0.321	0.71	0.476
Common guillemot	6.58	1.04	6.35	<0.001
Atlantic puffin	0.099	0.323	0.31	0.759
Year.European shag	0.1441	0.0384	3.75	<0.001
Year.Razorbill	0.0306	0.0376	0.81	0.418
Year.Common guillemot	0.107	0.108	1.00	0.321
Year.Atlantic puffin	0.0382	0.0345	1.11	0.270
(c) Proportion of clupeid relative to other non-sandeel prey				
Constant	0.314	0.225	1.39	0.166
Year	0.0681	0.0242	2.81	0.006
Fishery	-0.278	0.273	-1.02	0.310
European shag	-2.643	0.414	-6.38	<0.001
Razorbill	3.041	0.638	4.77	<0.001
Common guillemot	4.238	0.817	5.19	<0.001
Atlantic Puffin	1.184	0.281	4.21	<0.001
Year.European shag	-0.1286	0.0473	-2.72	0.007
Year.Razorbill	0.1040	0.0628	1.66	0.100
Year.Common guillemot	-0.0729	0.0865	-0.84	0.401
Year.Atlantic puffin	-0.0872	0.0290	-3.01	0.003

was a significant interaction between species and year, such that this increase was not apparent in puffins or shags (significant interaction with year in these 2 species in relation to the reference species, kittiwakes). There was no effect of the presence of the sandeel fishery on any aspect of chick diet composition for any of the species (Table 2a–c).

Temporal trends in sandeel length

Between 1973 and 2015, there were highly significant declines in the mean annual lengths of 0 group and 1+ group sandeels in fish loads brought in by puffins, with no effect of the presence of a fishery (Fig. 2a; REML on 0 group [mm]: year = -0.451 ± 0.081 , $F = 30.77$, $p < 0.001$; date = 0.245 ± 0.050 , $F = 24.28$, $p < 0.001$; fishery = -0.618 ± 2.336 , $F = 0.07$, $p = 0.791$; REML on 1+ group [mm]: year = -0.426 ± 0.137 ,

$F = 9.61$, $p = 0.004$; date = 0.449 ± 0.064 , $F = 48.84$, $p < 0.001$; fishery = 0.314 ± 3.860 , $F = 0.01$, $p = 0.936$; $n = 42$ yr). Thus, in the 1970s, mean annual lengths of 0 group sandeels were typically between 70 and 80 mm, but by the mid-2000s, mean lengths were only between 50 and 60 mm. Similarly, 1+ group sandeel lengths decreased from 110–120 mm to 100–105 mm.

Temporal trends in sandeel energy values

Energy densities of 0 group sandeels were significantly lower than those of 1+ group, but there was no significant time trend over the 19 yr for which data were available, and no effect of the fishery (Fig. 2b, REML: age = 1.654 ± 0.159 , $F = 108.94$, $p < 0.001$; year = 0.051 ± 0.088 , $F = 0.34$, $p = 0.568$; fishery = 2.932 ± 2.747 , $F = 1.14$, $p = 0.300$). The only year characterised by exceptionally low energy densities of both 0 group and 1+ group sandeels was 2004.

DISCUSSION

Our comparison of dietary trends within a North Sea seabird community provides support for (1) a long-term decline in the overall importance of sandeels in chick diet, (2) a decline in the importance of 1+ group sandeels relative to 0 group and (3) an increase in the importance of clupeids, predominantly sprats, as the main non-sandeel prey. Superimposed on these community-level trends were species-specific differences in the strength of all of these dietary shifts. There was also evidence for changes in sandeel quality, with a long-term decline in mean annual lengths of 0 group and 1+ group sandeels, although no marked change in energy density of sandeels, except for the exceptionally low value in 2004. Crucially, we found no evidence that any of these changes were associated with the local sandeel fishery which targeted predominantly 1+ group fish and which operated during the seabird breeding season (May–July) 1990–1999 (Rindorf et al. 2000).

Diet composition and dietary trends

Sandeels have traditionally been viewed as the main prey of most seabirds in the North Sea during the breeding season (Pearson 1968, Furness & Tasker 2000). Sampling of puffin chick diet on the Isle of May started in the early 1970s, 10–15 yr before the

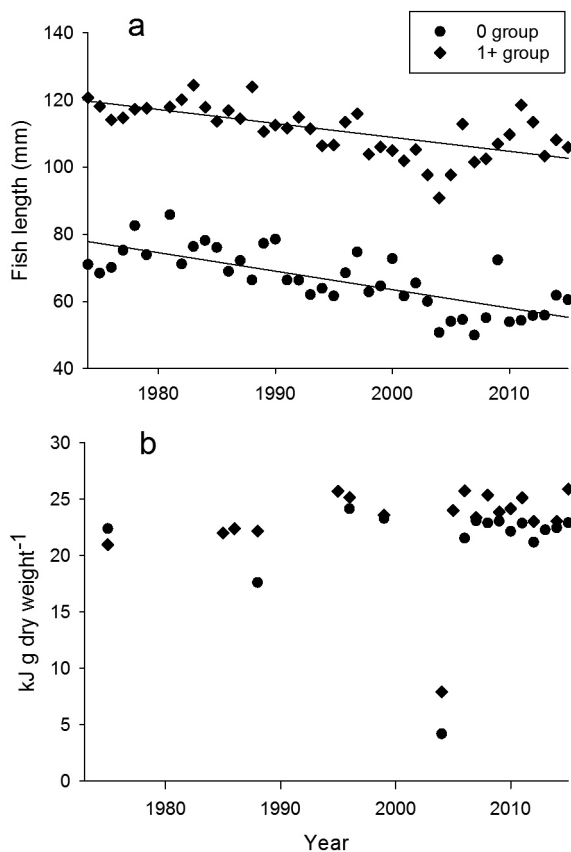


Fig. 2. Long-term changes in (a) annual mean length and (b) energy density of 0 group and 1+ group lesser sandeels *Ammodytes marinus* collected from seabirds on the Isle of May between 1973 and 2015. Lengths of 0 group and 1+ group sandeels are standardized to 1 July and 1 June, respectively. Samples sizes and SEs are given in Tables S2 & S3 in the Supplement at www.int-res.com/articles/suppl/m600p193_supp.pdf

other species, and it is noteworthy that clupeids rather than sandeels were the predominant prey at this time (Fig. 1a). The lack of diet data for the other auks, kittiwake and shag at this time precludes any assessment of whether this was a community-level phenomenon on the Isle of May, while the lack of data from other puffin colonies in the North Sea precludes knowing whether it was a wide-scale effect. However, the importance of sandeels in puffin chick diet subsequently increased, and by the mid-1980s, when diet sampling for the other species started, sandeels were indeed the main prey species across the whole community, albeit with differences in the age class taken, with guillemot and shag chicks being fed predominantly 1+ group, and puffin, razorbill and kittiwake chicks receiving a mixture of 0 group and 1+ group. These initial species differences were apparent in subsequent trends such that the decline in overall importance of sandeels was most pronounced in shags and particularly gullies. In razorbills and kittiwakes, the decline in overall importance was less marked, and in puffins no decline was apparent. Furthermore, for all 3 species, sandeels largely remained the dominant prey but the contribution of 0 group relative to 1+ group increased. Community-level differences were also apparent in the alternative prey to sandeels. Thus in the auks and kittiwake, the shift was relatively simple with clupeids, predominantly sprats, being the main alternative with reliance relative to other non-sandeel species increasing over time in all species except puffin. In contrast, clupeids were of minor importance for shags, with sandeels being replaced by a wide range of benthic fish species resulting in a significant increase in dietary diversity (Howells et al. 2017).

Taken as a whole, the changes in seabird chick diet recorded on the Isle of May are consistent with declines in the local availability of sandeels, particularly 1+ group and/or an increase in availability of clupeids, particularly sprats. Concurrent, independent time series data on prey abundance at a spatial scale relevant to seabird foraging ranges during the breeding season (mainly within 50 km; Thaxter et al. 2012, Wakefield et al. 2017) are lacking. However, the available data for both sandeels and sprats are broadly in line with the observed changes in seabird chick diet. Thus sandeel abundance declined significantly during the 1990s when the commercial sandeel fishery was operating on the Wee Bankie and Marr Bank, 30–50 km from the Isle of May, and apart from a brief recovery immediately after closure of the fishery in 2000, abundance remained low until

the early 2010s (Greenstreet et al. 2006, Frederiksen et al. 2008, Heath et al. 2012b). Furthermore, monitoring of the age structure of the stock after the closure of the fishery highlighted sharply contrasting trends for 0 group and 1+ group, with abundance of the former maintained whilst the latter was greatly reduced (Heath et al. 2012b). In the case of sprats, a fishery prosecuted by small boats based at ports on the Fife coast, started in the late 1960s (Jennings et al. 2012). The stock collapsed in the early 1980s, and fishing ceased in 1985. It is notable that the 1980s was the only period when juvenile herring was the main prey taken by puffins, consistent with sprat stocks being depressed at this time. However, sprat stocks recovered by the late 1990s (Jennings et al. 2012), and sprat has subsequently been the dominant clupeid in chick diets across the Isle of May seabird community.

Declines in sandeel abundance and increases in sprat abundance are both consistent with expected contrasting trends given rising sea surface temperatures (SST) in the North Sea (Heath et al. 2012a). The shift from a boreal to a temperate regime could also enable warm-water forage fish species to colonise and increase in the region. However, as yet there have been no cases of species such as sardine *Sardina pilchardus* or anchovy *Engraulis encrasicolus* that are increasing in the southern North Sea and spreading northwards, being recorded in chick diet samples from the Isle of May (Heessen et al. 2015). The most dramatic example of the appearance of a new prey species during our study was the population explosion in the mid-2000s of snake pipefish that had previously been considered rare in the region (Kirby et al. 2006, Harris et al. 2007, van Damme & Couperus 2008). Snake pipefish were very numerous in the waters around the Isle of May between 2005 and 2007, but the species was only recorded in any numbers in the diet of kittiwake chicks, although there were a few records from shags and opportunistic sightings from puffins (Harris & Wanless 2011). The pipefish explosion coincided with the nadir in sandeel abundance, suggesting that some change in the marine environment had occurred around this time that was beneficial to snake pipefish but detrimental to sandeels (Kirby et al. 2006, van Damme & Couperus 2008, Heath et al. 2012b). However, pipefish numbers subsequently crashed as spectacularly as they increased, and since 2010, the species has again become rare and has not been recorded in chick diets on the Isle of May, nor as far as we are aware, at other colonies in the North Sea (Daan 2015, authors' unpubl. data).

Intriguingly, the temperature responses of sandeels and clupeids in the North Sea seem to be the reverse of those in the northeastern Pacific. Thus while in the former warming conditions have resulted in a shift away from a sandeel-dominated system (Heath et al. 2012b), in the latter the locally prevalent Pacific sandeel species, *Ammodytes personatus*, is dominant during periods of warm ocean conditions but is replaced by alternative forage fish such as clupeids, e.g. the Pacific herring *Clupea pallasii*, and/or osmerids, especially capelin *Mallotus villosus*, during periods of cooling (Sydeman et al. 2017b). Clearly there is considerable potential for future research to exploit predator-based sampling from different ocean basins to compare system-level responses to global climate change and other anthropogenic pressures (Sydeman et al. 2017a).

Changes in sandeel quality

The length and energy density of prey are of key importance for predators when they are provisioning offspring, particularly in species such as common guillemot that only bring back 1 prey item per feeding trip (single prey loaders). Since the relationship between sandeel length and mass is non-linear, the sustained decrease in mean length-at-age of both 0 group and 1+ group sandeels brought in for puffin chicks on the Isle of May indicates a dramatic deterioration in prey quality over the last 40 yr. Combining annual data for sandeel length and energy density suggests overall reductions in average energy values of ca. 70 and 40% for 0 group and 1+ sandeels, respectively, between 1973 and 2015. Puffin was the only species for which sandeel lengths could be measured directly in sufficient numbers for analysis. However, sandeel lengths estimated from otoliths extracted from shag regurgitates also indicate a significant decrease in mean length between 1989 and 2014, with the decline more marked in 0 group compared to 1+ group fish (Howells et al. 2017). Isle of May shags typically forage closer to the shore than puffins (Harris et al. 2012, Bogdanova et al. 2014), suggesting that the decline in sandeel length has occurred in both inshore and offshore habitats and thus that the reduction in prey quality will have affected the whole Isle of May seabird community. Further support for a regional-level reduction in sandeel length comes from data from commercial fishing vessels that also indicate that sandeels in the northwestern North Sea have become significantly shorter and lighter than those in central and northeastern areas (Rindorf et al. 2016).

In this study, we did not specifically investigate the mechanisms underlying the decline in length-at-date of sandeels. However, Frederiksen et al. (2011) previously showed that the situation was complex, with phenological responses predominating in the 1970s to mid-1990s and sandeel hatch dates becoming later. From the mid-1990s onwards, the trend in hatch date was reversed and instead the decline in length-at-date was driven mainly by lower juvenile growth rates (Frederiksen et al. 2011).

Consequences of dietary changes for community-level breeding success

Furness & Tasker (2000) quantified the sensitivity of the North Sea seabird community to reductions in sandeel abundance using an index based on species body size, cost of foraging, potential foraging range, ability to dive, amount of 'spare' time in the daily time budget and ability to switch diet. Applying these criteria to the Isle of May seabird community ranks the species in order of increasing sensitivity as shag, guillemot, razorbill, puffin and kittiwake. In accordance with this, kittiwake, the most sensitive species, was the only one to show reduced breeding success during the period when the sandeel fishery was operating (Daunt et al. 2008, Frederiksen et al. 2008). However, community-level comparisons of breeding success on the Isle of May revealed synchronised declines from the late 1980s to the late 2000s, with the environmental contribution to overall productivity synchrony driven principally by effects operating at the chick stage rather than during incubation (Frederiksen et al. 2007, Lahoz-Monfort et al. 2013). Our analysis demonstrating long-term community level reductions in the importance of sandeels in chick diet therefore suggests that dietary changes may have played a role in the decline in productivity. However, interspecific differences in the change in productivity were also apparent. These suggested that trophic linkages were probably complex and potentially influenced by factors such as interspecific differences in behavioural responses, e.g. time allocation, foraging effort, prey delivery rates and load sizes (Lahoz-Monfort et al. 2013). The community-level analyses of productivity have not been updated, but breeding success of all species has generally increased since the mid-2000s (Newell et al. 2017b). The data on diet composition for the seabird community indicate that these improvements have occurred despite the continuing decline in both the importance of sandeels, particularly 1+ group, in

chick diet and length-at-age of 0 group and 1+ group sandeels used to provision chicks. Species may be able to compensate for changes in sandeel availability by adjusting aspects of their provisioning behaviour to a greater or lesser extent. Recent modelling work has shown that differences in chick provisioning methods and flight costs of guillemots and razorbills could potentially result in differing responses to changes in sandeel length and distribution of prey patches (Thaxter et al. 2013). However, taken at face value, the dietary data suggest that the alternative prey (either clupeids in the case of auks and kittiwakes or benthic species in the case of shags) can currently compensate for decreases in the contribution of sandeels to chick diet. In accordance with this, the dietary quality of the alternative prey are all broadly comparable in energetic value to sandeels, and indeed are generally energetically superior to 0 group sandeels (Hislop et al. 1991, Harris et al. 2008, Howells et al. 2017).

Changes in length-at-age of sandeels might also be expected to affect breeding success because of the non-linear relationship between body length and energy value. Guillemot was the only obligate single prey loader among our study species and thus the one most likely to be sensitive to changes in energy value of single prey items. In accordance with this, guillemots showed the most extreme reduction in sandeels in chick diet such that in 12 of the last 13 yr of the study, sandeels made up <10% of prey biomass. Moreover, the series of years with exceptionally low guillemot breeding success on the Isle of May (2004–2007; Ashbrook et al. 2010) coincided with the period when sandeel lengths were shortest (Fig. 2a) and 2004 when energy density was exceptionally low (Fig. 2b). Sandeels grow during the seabird breeding season and hence the long-term decline in length-at-date has meant that, on average, the date when 0 group (and probably 1+) sandeels reach a given length has become later (Burthe et al. 2012). Predators such as seabirds could therefore reduce the energetic impacts of this delay by breeding later so that the period of peak demand (mid-chick-rearing) tracked the changes in sandeel size. Breeding phenology of all species in our analysis, except shag, became later between 1983 and 2006 (Burthe et al. 2012). However, these changes were insufficient to keep pace with the changes in sandeel length and consequently the length (and energy value) of sandeels during chick rearing showed a net decline over this period (Burthe et al. 2012). Despite this, there was no evidence for an adverse effect on breeding success. Since the mid-2000s, the trend

towards later breeding among Isle of May seabirds has ceased (Newell et al. 2017a), but the decline in sandeel length has continued (Fig. 2a). This suggests that the net decrease in energy value of sandeels during chick rearing will have been exacerbated and thus it is perhaps surprising that breeding success has generally improved (Newell et al. 2017b). These findings highlight the need to consider energy values of alternative prey and whether, like those of sandeels, these have decreased over time due to changes in average length.

The aim of the present paper was to use predator-based sampling to elucidate community-level trends in the importance of sandeels in chick diets at a major North Sea colony. However, as the preceding paragraphs indicate, current evidence for links between breeding success and chick diets in the Isle of May seabird community is equivocal, and productivity has improved since some of the key analyses were carried out. Updating these analyses and ideally also considering temporal changes in length and thus energetic quality of the alternative prey is therefore a research imperative.

CONCLUSIONS

Overall, our results add to the growing body of information highlighting the effects of changing conditions for forage fish stocks on marine predators, particularly seabirds (Cury et al. 2011, Sydeman et al. 2017a). Such information is vital for ecosystem-scale assessments such as updating food web linkages, as input data for bioenergetics models and providing advice on potentially important feeding areas as part of marine spatial planning processes. The species making up the Isle of May seabird community are typical of many other colonies in the North Sea (Mitchell et al. 2004). However, generalising from our findings to other colonies needs to be made with caution, as studies of individual species within the region indicate that chick diet can differ markedly both locally, e.g. among kittiwake colonies in the Firth of Forth (Bull et al. 2004), and regionally, e.g. among guillemot colonies up the east coast of Britain (Anderson et al. 2014). Thus while it seems likely that the decline in importance of sandeels in chick diet will be reflected in other colonies in the North Sea, more community-level assessments are needed to substantiate this and to identify what the alternative prey are.

For much of the past 30–40 yr, the seabird community on the Isle of May has been experiencing a dete-

rioration in the quality and quantity of sandeel prey available during the chick-rearing period. Closure in 2000 of the commercial sandeel fishery off the coast of eastern Britain adjacent to many seabird colonies, including the Isle of May, resulted in improved breeding success of kittiwakes, although not the other species (Daunt et al. 2008, Frederiksen et al. 2008). However, the fishery ban appears not to have reversed the decline in importance of sandeels in chick diet nor the shift from 1+ group to 0 group. In the case of shags, a detailed analysis demonstrated that the shift from a sandeel-dominated diet to a more species diverse one was associated with rising SST (Howells et al. 2017). Given the climate projections for further increases in SST in the North Sea (IPCC 2014), it seems likely that the diet trajectories for shags and other seabirds will continue and further diminish the importance of sandeels in chick diet. Such changes could have consequences for future population and community dynamics, but the magnitude and even the direction of responses are currently difficult to predict and will depend on the ability of species to exploit alternative prey and the energy value of these prey compared to sandeels.

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