Climate-Driven Trophic Cascades Affecting Seabirds around the British Isles

Article *in* Oceanography and Marine Biology · August 2015

DOI: 10.1201/b18733-3

14 authors, including:

Alan MacDonald
Scottish Association for Marine Science
5 PUBLICATIONS **46** CITATIONS
SEE PROFILE

Michael Heath
University of Strathclyde
230 PUBLICATIONS **7,270** CITATIONS
SEE PROFILE

Martin Edwards
Plymouth Marine Laboratory
190 PUBLICATIONS **17,443** CITATIONS
SEE PROFILE

Robert W Furness
University of Glasgow
532 PUBLICATIONS **29,004** CITATIONS
SEE PROFILE

Oceanography and Marine Biology: An Annual Review, 2015, **53**, 55-80
© R. N. Hughes. D. J. Hughes, I. P. Smith, and A. C. Dale, Editors
Taylor & Francis

CLIMATE-DRIVEN TROPHIC CASCADES AFFECTING SEABIRDS AROUND THE BRITISH ISLES

ALAN MACDONALD[1], MICHAEL R. HEATH[1], MARTIN EDWARDS[2],
ROBERT W. FURNESS[3], JOHN K. PINNEGAR[4], SARAH WANLESS[5],
DOUGLAS C. SPEIRS[1], & SIMON P.R. GREENSTREET[6]

[1]University of Strathclyde, Department of Mathematics and Statistics,
Livingstone Tower, 26 Richmond Street, Glasgow, G1 1XH, United Kingdom
E-mail: alan.macdonald@strath.ac.uk (corresponding author)
[2]Sir Alister Hardy Foundation for Ocean Science,
The Laboratory, Citadel Hill, Plymouth, PL1 2PB
[3]Graham Kerr Building, University of Glasgow, Glasgow, G12 8QQ, United Kingdom
[4]Centre for Environment, Fisheries and Aquaculture Science (Cefas),
Pakfield Road, Lowestoft, Suffolk, NR33 0HT, United Kingdom
[5]Centre for Ecology and Hydrology, Bush Estate, Penicuik, EH26 0QB, United Kingdom
[6]Marine Scotland Science, Marine Laboratory, Aberdeen, AB11 9DB, United Kingdom

After flourishing during the second half of the twentieth century, many North Sea seabird populations are now in decline. Much evidence is accumulating that climate change is driving these negative trends in growth rate. Climate-driven changes in the physical environment may affect seabirds both directly and indirectly. Direct impacts such as increasingly common extreme weather events will result in negative physiological responses. However, climate effects on seabirds are more likely to be indirect and mediated by prey quality and availability. Mounting evidence suggests that climate impacts on lower trophic levels are altering the pathway of energy to seabirds. While the basis for changes in primary production are complex and uncertain, climate-driven changes in the availability of sandeels (primarily *Ammodytes marinus*) and the copepod *Calanus finmarchicus*, key prey species in adjacent trophic levels, appear to be causing a reduction in breeding success and growth rate in several British seabird species.

Keywords: pelagic food web, North Sea, trophic interactions, *Ammodytes marinus*, *Calanus finmarchicus*, seabird community, regime shift

Introduction

Numbers of many species of seabirds around the United Kingdom increased between 1970 and 2000 (Figure 1). However, since the Seabird 2000 census (Mitchell et al. 2004), populations of some of the species have started to decline, such as the Atlantic puffin *Fratercula arctica* (Harris & Wanless 2011), northern fulmar *Fulmarus glacialis*, and great cormorant *Phalacrocorax carbo*. Others have continued to increase, for example, the common guillemot *Uria aalge*, razorbill *Alca torda*, and especially the northern gannet *Morus bassanus*. In Scotland, northern gannets are possibly the only species to increase in abundance in the past decade (Wanless & Harris 2012) and are continuing to form new colonies (Wanless et al. 2005b).

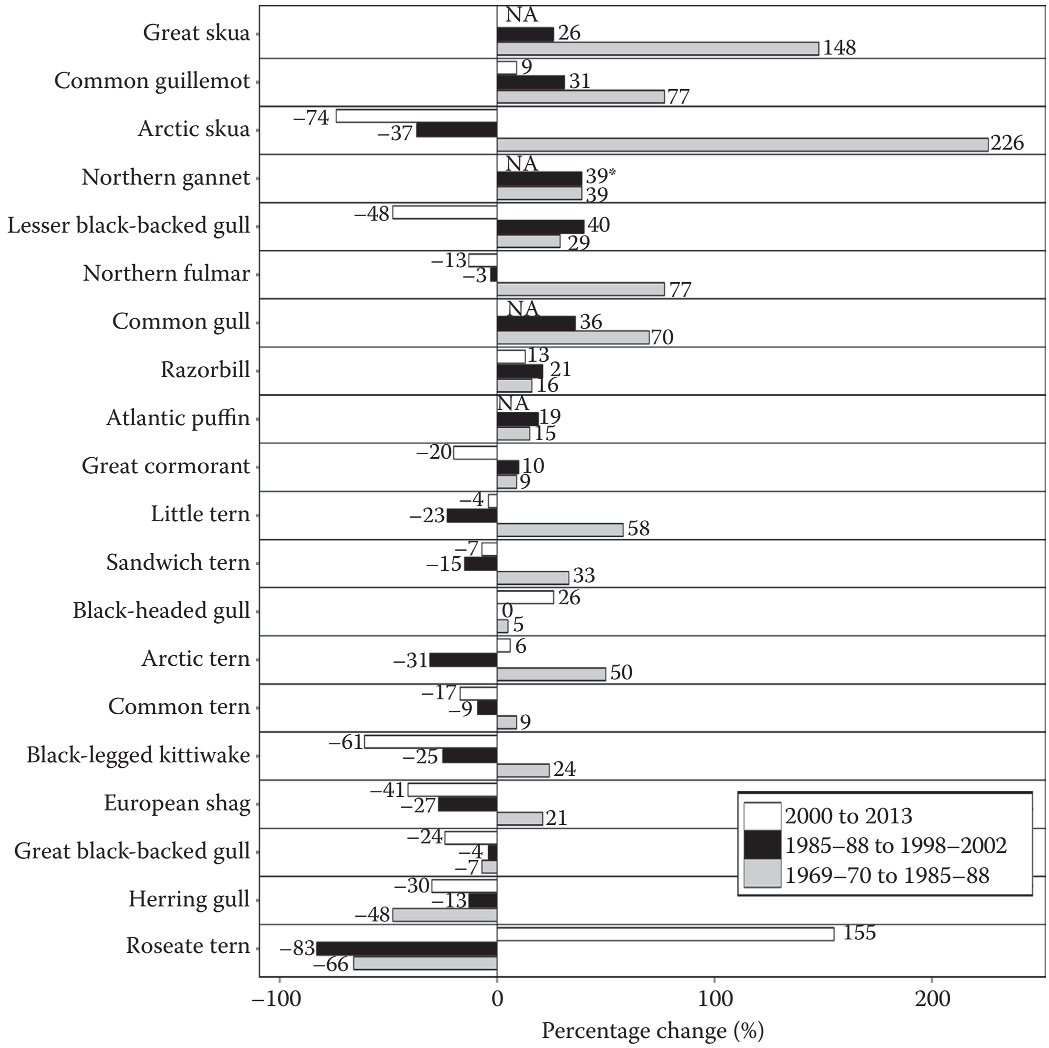

Figure 1 Changes in the numbers of breeding seabirds in the United Kingdom 1969–2002 (JNCC 2014c). Percentage changes refer to coastal-nesting seabirds only; inland colonies were not surveyed during the Operation Seafarer (1969–1970) (Cramp et al. 1974) and the Seabird Colony Register (SCR) censuses (1985–1988) (Lloyd et al. 1991). Manx shearwater, Leach's storm petrel, and European storm petrel are omitted as they were not surveyed during the Operation Seafarer (1969–1970) and the SCR censuses (1985–1988). Survey methods for black guillemots during Operation Seafarer (1969–1970) were not comparable with Seabird 2000 (1998–2002). Change from 2000 to 2012 (i.e., over the period since the last national census) was estimated from trends derived from the Seabirds Monitoring Programme sample of colonies; this analysis is only available for species with sufficient data to estimate trends accurately. *Change between censuses in 1984–1985 and 2004–2005.

Most surface-feeding seabird species in the northern North Sea have suffered breeding failure since 2003. In Shetland, similar declines in breeding success happened earlier, during the 1980s. Large pursuit-diving species have not been so affected (Heubeck 1989, Okill 1989). Consequences of such declines in breeding success only become apparent in the population numbers after a considerable time lag, as these year-classes of birds mature and join the breeding population (Frederiksen et al. 2004, Mavor et al. 2005, 2006, 2008, Reed et al. 2006).

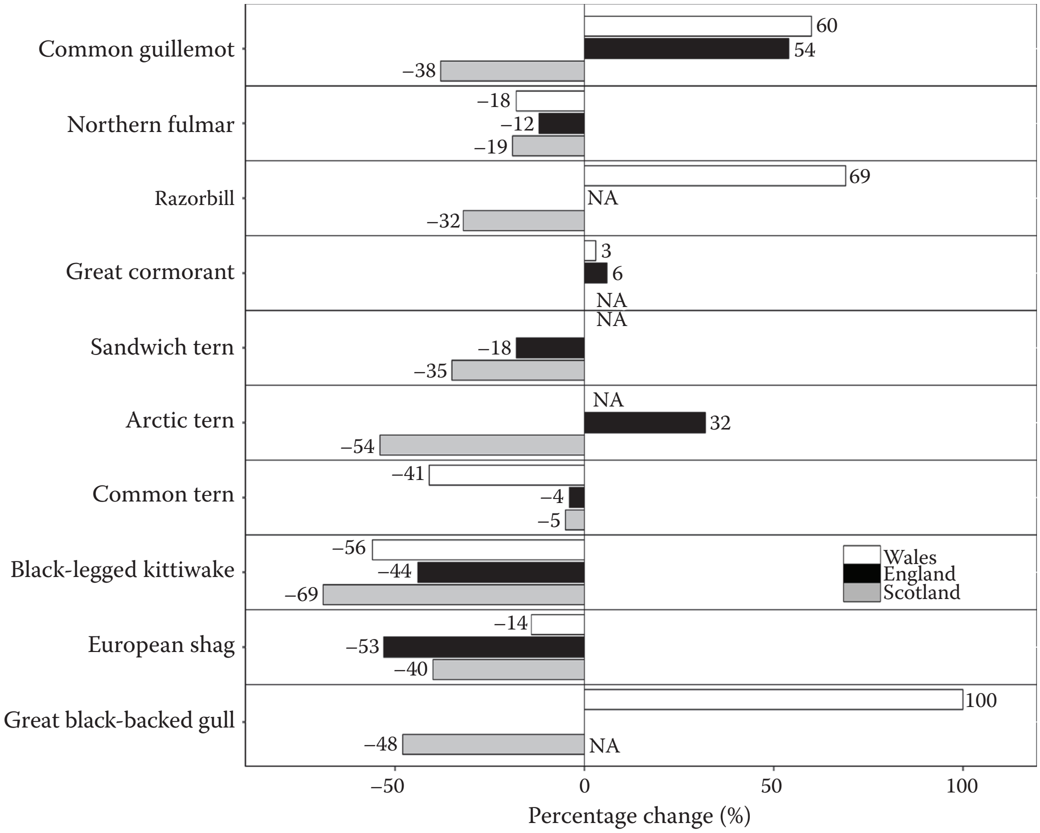

Figure 2 Changes in the numbers of breeding seabirds in Scotland, England, and Wales during the period 2000–2013 (JNCC 2014c). Change from 2000 to 2013 (i.e., over the period since the last national census) was estimated from trends derived from the Seabirds Monitoring Programme sample of colonies; this analysis is only available for species with sufficient data to estimate trends accurately (JNCC 2014c).

The overall trends in numbers of breeding seabirds over recent decades mask some marked regional variations (Figure 2). Significant increases were observed in the breeding numbers of, for example, guillemots in England and Wales; however, the trend was the opposite for those breeding in Scotland. Within any one year, some species have bred successfully, and others have not. For a given species, some regions have produced successful breeding and others not. In some cases, a lack of consistency has even been found among species inhabiting the same region (Wanless & Harris 2012).

Climate change is considered to be playing a significant role in the declines in seabird breeding numbers (Russell et al. 2014). In particular, sea-surface temperatures (SSTs) in UK coastal waters, which have been rising between 0.1°C and 0.5°C per decade for the past 30 years (Dye et al. 2013), have shown a strong negative relationship with the demographic rates of several seabird species. For example, the productivity of northern fulmar and black-legged kittiwake *Rissa tridactyla* on the Scottish eastern coast shows a negative relationship with SST (Burthe et al. 2014). Furthermore, survival rates of kittiwakes, European shags *Phalacrocorax aristotelis* (Burthe et al. 2014), Atlantic puffins, guillemots, and razorbills (Lahoz-Monfort et al. 2011) are also strongly negatively correlated with SST.

The physical environmental changes that accompany climate change may affect seabirds in a variety of direct and indirect ways. Direct effects include incidences of extreme weather events causing mass mortalities and damage to nests in breeding colonies (Frederiksen et al. 2008a, Wanless

& Harris 2012). Physiological responses to higher temperatures can be expected to cause changes in vital rates for population dynamics (Oswald et al. 2008, 2011). Population dynamics of long-lived seabird species are especially sensitive to adult survival (Lebreton & Clobert 1991, Sæther & Bakke 2000, Ratcliffe et al. 2002, Furness 2003). Indeed, reduced overwinter survival rates for breeding Atlantic puffins on the Isle of May in 2006–2007 and 2007–2008, combined with an increase in immature mortality (Harris et al. 2013), were sufficient to explain a 30% reduction in breeding population between 2003 and 2008 (Harris & Wanless 2011). Synchrony in guillemot survival rates from different colonies around Britain that share overwintering areas provides further evidence that climate could be the key determinant of mortality (Reynolds et al. 2011).

In contrast, indirect effects may be mediated through prey quality and availability (Wanless et al. 2005a, Burthe et al. 2012), affecting growth rates and breeding success. These are referred to as bottom-up cascading trophic effects (Carpenter et al. 1985, Pace et al. 1999, Polis et al. 2000, Heath et al. 2014). The aim of this work is to review and synthesize the evidence for these climate-driven trophic cascade effects on seabirds in waters around the British Isles. In particular, evidence relating to the hypothesis that increasing climate-driven changes in phytoplankton and zooplankton have led to a decline since 2000 in the abundance of small planktivorous fish, especially sandeels (*Ammodytes marinus*), and hence to the observed changes in seabird breeding success, frequency of breeding, and survival is assessed (Figure 3). The matter is approached by addressing the coupling between successive trophic levels in the food web, beginning with the connection between seabirds and fish and working towards lower levels.

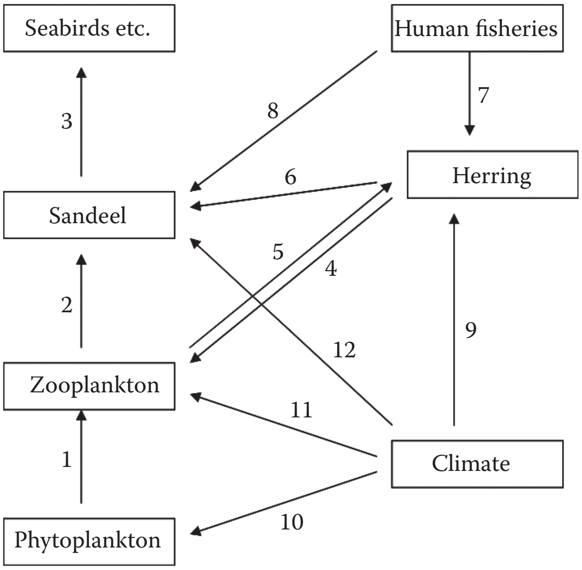

Figure 3 Simplified diagram of some documented and probable trophic and climatic controls in the North Sea pelagic ecosystem (after Frederiksen et al. 2007). 1, Bottom-up control of zooplankton by phytoplankton (Richardson & Schoeman 2004); 2, bottom-up control of sandeel larvae by zooplankton (Frederiksen et al. 2006); 3, bottom-up control of seabird breeding success by sandeels (Hamer et al. 1993, Frederiksen et al. 2006); 4, top-down control of zooplankton by herring predation (Arrhenius 1997); 5, bottom-up control of herring by zooplankton (Corten 2001, Beaugrand 2004); 6, top-down control of sandeels by herring predation (Frederiksen et al. 2007); 7, top-down control of herring by fisheries (Jennings et al. 2001); 8, local top-down control of sandeels by human fisheries (Rindorf et al. 2000); 9, climatic control of herring recruitment (Sætre et al. 2002); 10 and 11, climatic control of phytoplankton and zooplankton (Edwards & Richardson 2004, Hays et al. 2005); 12, climatic control of sandeel recruitment (not known if direct) (Arnott & Ruxton 2002).

Connections between seabirds and fish

The majority of open-sea bird species around Britain are essentially piscivorous. The prey items brought back to breeding sites by the 26 major seabird species were analysed during the Seabird 2000 survey (1998–2002) (Table 1) and found to consist mostly of sandeels (mainly *Ammodytes marinus*), small clupeoid fish, and zooplankton. Prey were either self-caught (i.e., taken alive from the sea) or stolen from other birds (Furness 1987, Davis et al. 2005). Exceptions were scavenging species such as northern fulmars and gulls, which feed opportunistically and rely partly on discarded fish and offal from commercial fishing vessels (Camphuysen & Garthe 1997, Furness 2003), and some of the diving species, whose diet includes a proportion of benthic organisms (Furness et al. 2012).

There is abundant evidence that fish communities are being affected by climate change. Geographical shifts in the distribution of many shelf-sea fish communities around the British Isles have been well documented. Broadly speaking, these changes can be viewed as a response to warming sea temperatures to maintain individuals in a preferred temperature range (Hedger et al. 2004, Perry et al. 2005, Poulard & Blanchard 2005, Desaunay et al. 2006, Heath 2007, Dulvy et al. 2008). In some areas, this is manifested as a polewards shift in distribution or a move into deeper water. However, local topography and hydrography may limit the extent of such shifts.

Polewards shifts in distribution lead to decreases in abundance at the southern edge of the geographic range of a species and increases at the northern edge (in the Northern Hemisphere). Temperature-associated species-level changes in abundance that may be accounted for in this way have been identified in 39 of 50 of the most common fish species in the North Sea (Simpson et al. 2011). Catches of warm-water species (e.g., European anchovy *Engraulis encrasicolus*, sardine *Sardina pilchardus*, and striped red mullet *Mullus surmuletus*) all increased in the North Sea, coinciding with increased temperatures after 1995 (International Council for the Exploration of the Sea [ICES] 2007). Moreover, statistical modelling shows northwards movements for Atlantic horse mackerel *Trachurus trachurus*, European anchovy, European sprat *Sprattus sprattus*, pollack *Pollachius pollachius*, common sole *Solea solea*, saithe *Pollachius virens*, and turbot *Scophthalmus maximus* between the 1960s and the period 2000–2005 (Lenoir et al. 2011). Northwards movements in the geographical range of these species, with the exception of pollack, are predicted to increase substantially under projected Intergovernmental Panel on Climate Change (IPCC) changes in SST (IPCC 2007). Some fish species now inhabit areas where they were absent prior to the 1980s. Examples include anchovy and sardine (Beare et al. 2004a), striped red mullet (Beare et al. 2004b), and bluemouth *Helicolenus dactylopterus* (Mamie et al. 2007).

Although many of the fish species mentioned are not directly preyed on by seabirds, their responses to climate change may be significant for understanding the impacts on birds because they are potential competitors for the main food of piscivorous birds: the common sandeel *Ammodytes marinus*. This species is currently at the southern edge of its latitudinal range around the British Isles (Fishbase 2014), but unlike most other fish species, sandeels are not free to move into deeper waters in response to warming sea temperatures because they are tightly associated with sandy sediments with a rather narrow range of grain size composition (Wright et al. 2000, Holland et al. 2005, Greenstreet et al. 2010b). In addition, sandeel stocks display a complex spatial population structure, which may further limit their capacity to adjust their distribution in response to warming. For example, the North Sea stock is composed of seven distinct populations, each exhibiting different population dynamics (Boulcott et al. 2007, ICES 2010, 2013, Boulcott & Wright 2011). Since 2000, some sandeel populations have decreased in abundance in parts of the northern North Sea, primarily Shetland and the north-western North Sea (Figure 4), but not in the southern North Sea. The drivers behind patterns of decline in sandeels are complex and may include a combination of climate and fishing impacts.

Table 1 Names and life history characteristics of seabird species regularly breeding in the British Isles included in the JNCC's Seabird Monitoring Programme and the Seabird Colony Register

Common name	Scientific name	General diet	Clutch size (no. eggs)	Age at first breeding (yr)	Adult survival rate (yr^{-1})	Lifespan (yr)
Red-throated diver	*Gavia stellata*	Primarily fish, captured by seizing in bill,;also frogs, large invertebrates	2	3 (Okill 1994)	0.840 (Hemmingsson & Eriksson 2002)	9
Northern fulmar	*Fulmarus glacialis*	Crustaceans, squid, fish, offal, carrion mostly from surface	1	9 (Dunnet & Ollason 1978a)	0.972 (Dunnet & Ollason 1978b)	44
Manx shearwater	*Puffinus puffinus*	Mostly small fish and squid, also small crustaceans and offal from surface or diving	1	5 (Thompson 1987)	0.905 (Brooke 1990)	15
European storm petrel	*Hydrobates pelagicus*	Mainly surface plankton, small fish; feeds from water surface without alighting	1	4–5 (Scott 1970)	0.870 (Cramp et al. 1977–1994)	11–12
Leach's storm petrel	*Oceanodroma leucorhoa*	Mainly surface plankton, small fish; feeds from water surface without alighting	1	4–5 (Huntington & Burtt 1972)	0.880 (Furness 1984)	12–13
Northern gannet	*Morus bassanus*	Fish (up to 30 cm), usually plunging from heights of 10–40 m	1	5 (Alerstam 1990)	0.919 (Wanless et al. 2006)	17
Great cormorant	*Phalacrocorax carbo*	Fish, mostly by diving from surface	3–4	2–4 (Cramp 1977)	0.880 (Frederiksen & Bregnballe 2000)	10–12
European shag	*Phalacrocorax aristotelis*	Fish, mostly by diving from surface	3	3 (Potts et al. 1980)	0.878 (Harris et al. 1994)	11
Arctic skua	*Stercorarius parasiticus*	Summer: mostly birds, small mammals, insects Winter: fish, mostly by piracy from other birds	2 (Furness 1987)	4 (Lloyd et al. 1991)	0.886 (O'Donald 1983)	12
Great skua	*Catharacta skua*	Mostly fish, obtained from sea, scavenging or by piracy	2 (Furness 1987)	7 (Klomp & Furness 1991)	0.888 (Ratcliffe et al. 2002)	15

(Continued)

Table 1 (Continued Names and life history characteristics of seabird species regularly breeding in the British Isles included in the JNCC's Seabird Monitoring Programme and the Seabird Colony Register

Common name	Scientific name	General diet	Clutch size (no. eggs)	Age at first breeding (yr)	Adult survival rate (yr^{-1})	Lifespan (yr)
Mediterranean gull	*Larus melanocephalus*	Summer: insects Winter: marine fish and molluscs	3	NA	NA	NA
Black-headed gull	*Larus ridibundus*	Opportunist, insects, earthworms, also plant material and scraps	2–3	2–5 (Clobert et al. 1994)	0.900 (Prévot-Julliard et al. 1998)	11–14
Mew gull	*Larus canus*	Invertebrates, some fish; preference for foraging on ground	3	3–4 (Cramp & Simmons 1983)	0.860 (Bukacinski & Bukacinska 2003)	10–11
Lesser black-backed gull	*Larus fuscus*	Omnivorous; often feeds at rubbish dumps or on shoals of fish	3	4–5 (Harris 1970)	0.913 (Wanless et al. 1996)	15–16
Herring gull	*Larus argentatus*	Omnivorous, but mostly animal material; also scavenges and kleptoparasitizes	3	4–5 (Chabrzyk & Coulson 1976)	0.880 (Wanless et al. 1996)	12–13
Great black-backed gull	*Larus marinus*	Omnivorous, but mostly animals, including other seabirds; also scavenges and kleptoparasitizes	2–3	4–5 (Cramp & Simmons 1983)	NA	NA
Black-legged kittiwake	*Rissa tridactyla*	Mainly marine invertebrates and fish	2	3–4 (Coulson & White 1959)	0.882 (Harris et al. 2000a)	11–12
Sandwich tern	*Sterna sandvicensis*	Fish; mostly plunge-diving	1–2	3 (Snow & Perrins 1998)	0.898 (Robinson 2010)	12
Roseate tern	*Sterna dougallii*	Fish; mostly plunge-diving	1–2	3–4 (Spendelow 1991)	0.855 (Ratcliffe et al. 2008)	9–10
Common tern	*Sterna hirundo*	Mostly fish, also crustaceans in some areas, mostly by plunge-diving	2–3	3–4 (Nisbet et al. 1984)	0.900 (Becker & Ludwigs 2004)	12–13
Arctic tern	*Sterna paradisaea*	Fish, crustaceans, and insects	1–2	4 (Coulson & Horobin 1976)	0.900 (Balmer & Peach 1997)	13

(Continued)

Table 1 (Continued Names and life history characteristics of seabird species regularly breeding in the British Isles included in the JNCC's Seabird Monitoring Programme and the Seabird Colony Register

Common name	Scientific name	General diet	Clutch size (no. eggs)	Age at first breeding (yr)	Adult survival rate (yr^{-1})	Lifespan (yr)
Little tern	*Sterna albifrons*	Small fish and invertebrates; often hovers before plunge-diving	2–3	3 (Massey et al. 1992)	0.899 (Tavecchia et al. 2006)	12
Common guillemot	*Uria aalge*	Mostly fish, usually taken from depths up to 60 m	1	5 (Olsson et al. 2000)	0.946 (Harris et al. 2000b)	23
Razorbill	*Alca torda*	Fish, some invertebrates	1	4–5 (Lloyd 1976)	0.900 (Chapdelaine 1997)	13–14
Black guillemot	*Cepphus grille*	Mostly fish, also crustaceans, especially in the Arctic	1–2	3–4 (Ewins 1988)	0.870 (Frederiksen & Petersen 1999)	10–11
Atlantic puffin	*Fratercula arctica*	Mostly fish, also crustaceans, especially in the Arctic	1	4–6 (Harris 1983, Johnsgard 1987)	0.924 (Harris et al. 1997)	17–19

Source: Joint Nature Conservation Committee (JNCC). 2014c. Seabird population trends and causes of change: 1986–2013 report. Peterborough, UK: Joint Nature Conservation Committee. Online. http://www.jncc.defra.gov.uk/page-3201 (accessed 17 October 2014).General diet description taken from Robinson (2005). Data on seabird clutch size is taken from Snow & Perrins (1998) and Harrison (1975) unless stated otherwise. Lifespan is calculated as $\lambda = \mu - 1/\ln(\varphi)$, where λ = lifespan, μ = age at first breeding, φ = adult survival rate (Robinson 2005).

Note: All except the red-throated diver were included in the Seabird 2000 Census or Seabird Colony Register.

The decrease in stocks of sandeels in the north-western North Sea since the late 1990s has occurred despite a substantial reduction in fishing activity, suggesting a strong environmental effect. Although larval abundance, and by inference spawning stock biomass, decreased after 2001, recruitment was maintained due to an increasing larval survival rate (Heath et al. 2012). The number of sandeels less than age 1 (year) around the time of seabird breeding therefore would not have changed dramatically over time, yet the number of older sandeels continued to decline.

Two main factors have been proposed as responsible for the decline in sandeel abundance. Data from chick-feeding Atlantic puffins and Continuous Plankton Recorder samples indicate that the size-at-date of sandeels less than age 1, hereafter referred to as ‘0 group’, has declined substantially since 1973. However, it is unclear what the exact cause of this decline might be (Wanless et al. 2004). A decline in 0-group size-at-date is presumably due to changes in hatch or spawning dates or changes in growth rate (Frederiksen et al. 2011). However, there is no evidence of trends in hatch dates on the Scottish eastern coast (Heath et al. 2012), so the proximate cause for the decline in 0-group size-at-date must be a reduction in growth rates.

Alternatively, it is noted that sandeels undergo an overwinter fasting period between late summer and the spawning period in January, during which they remain buried in the seabed to evade predation. Individuals show significant weight loss during this period (Boulcott et al. 2007, Boulcott

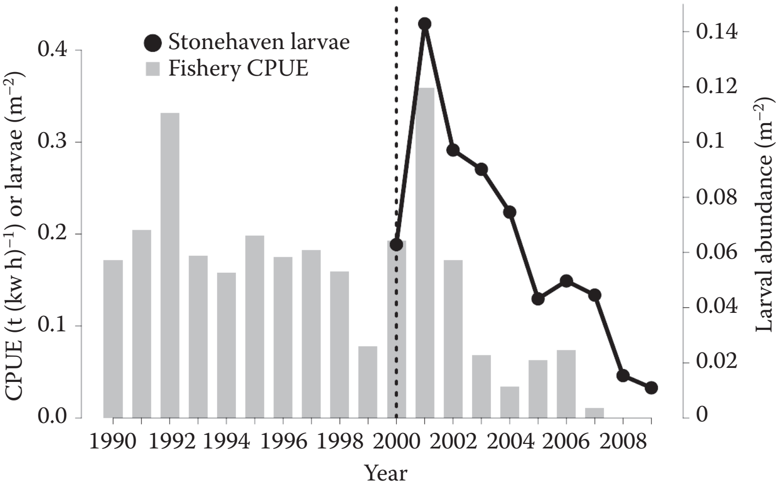

Figure 4 Catch per unit effort (CPUE) of sandeel larvae off the Firth of Forth (bars) and abundance of early larvae (3–7 days old) at Stonehaven (symbols and lines). CPUE data from 1990 to 2000 were derived from analysis of vessel logbooks from the Danish sandeel fishery. CPUE data from 2000 onwards were taken from a supervised monitoring fishery. CPUE data for 2006 and 2007 were taken from H. Jensen, Danish Institute for Fisheries Research. Larval abundance was measured at Stonehaven (56°57.83'N 2°6.74'W) and is taken from Heath et al. (2012). The dotted line delineates the fishery closure.

& Wright 2008), and it is speculated that increased temperature will increase this rate of loss due to elevated metabolism. The energy reserves required to sustain the animals through the winter fast must be accumulated the previous summer, so unless warming is accompanied by increased scope for summer feeding, which does not appear to be the case (Wanless et al. 2004, Boulcott et al. 2007), then the net effect is likely to be reduced overwinter survival (van Deurs et al. 2011). The recruiting age class in the population, entering its first winter, may be particularly vulnerable to overwintering mortality. Fish older than age 1 usually enter the overwintering period in August and remain buried in the sediment until April the following year, emerging only to spawn in January (Winslade 1974). However, many young-of-the-year sandeels may not begin to overwinter until December (Macer 1966, Reeves 1994, Kvist et al. 2001), suggesting that they require extra time to accumulate the necessary energy reserves.

Overwintering mortality may also have played a role in declining sandeel abundances around the Shetland Isles because sandeel growth rates are much lower at Shetland than elsewhere around Britain (Wright & Bailey 1993, Bergstad et al. 2002). However, recruitment failure appears to be the more likely cause, and increased predation by fish that consume sandeel larvae could explain the decline in this region (Frederiksen et al. 2007). Herring *Clupea harengus* are known to feed on larval sandeels (Hardy 1924, Last 1989), and stocks of herring have increased from 100,000 tonnes in the late 1970s to 2 million tonnes in 2004 (ICES 2004), in approximately inverse relationship with sandeel abundance around Shetland. Such a mirror-image pattern may indicate a top-down effect of herring predation on sandeel in the northern North Sea. There are precedents for such a phenomenon elsewhere; for example, herring predation has been implicated in the recruitment variability of Barents Sea capelin *Mallotus villosus* (Gjøsæter & Bogstad 1998). However, counterevidence is that although adult herring biomass has been high since 2000, the survival and growth rate of herring larvae have declined (Payne et al. 2009, 2013), which might suggest a common environmental factor affecting both sandeels and herring. Other possible reasons for recruitment failures of the northern sandeel populations are changes in the dispersal patterns of larvae from spawning to settlement sites (Proctor et al. 1998, Christensen et al. 2009) or changes in the phenology of the spring plankton bloom in relation to burial and spawning times of the sandeels (Greenstreet et al. 2006, Scott et al. 2006).

Data from other regions support the idea that a variety of factors may be causing the climate-related changes in sandeel abundances. Recruitment is strongly inversely related to winter temperatures for the sandeel stocks in the central North Sea, especially around Dogger Bank (Arnott & Ruxton 2002), although the causal mechanism is not known (ICES 2013). In contrast, there is little evidence of direct climate impacts on southern stocks, although changes in growth rates in the southern North Sea have been linked to fluctuations in zooplankton abundance (van Deurs et al. 2014).

Turning to the effects of changes in fish abundance and community composition on seabird populations, the evidence is strikingly clear. Sandeels constitute a significant proportion of the diet for many North Sea seabirds during the breeding season (Wanless et al. 1998, Furness & Tasker 2000, Furness 2002, Frederiksen et al. 2004, Sandvik et al. 2005, Lahoz-Monfort et al. 2011). Between 1991 and 2011 on the Isle of May, sandeels comprised approximately 75% of the diet of European shag, kittiwake, and Atlantic puffins (Newell et al. 2013). Some seabirds, such as kittiwakes and Arctic skuas *Stercorarius parasiticus*, are highly sensitive to fluctuations in sandeel abundance; others, such as the northern gannet, appear less affected (Furness & Tasker 2000). The most sensitive seabirds are those with high foraging costs, little ability to dive below the sea surface, little 'spare' time in their daily activity budget, short foraging range from the breeding site, and little ability to switch diet (Furness & Tasker 2000). The well-documented declines in breeding productivity of kittiwakes, shags, and Atlantic puffins (Lahoz-Monfort et al. 2013) are highly correlated with the availability of sandeels, especially the older age classes of sandeel (Pinaud & Weimerskirch 2002, Frederiksen et al. 2006, 2013).

In addition to interspecific variation in the importance of sandeel in the seabird diet, there are strong regional variations. In northern UK waters, sandeels are the only significant prey for seabirds. For example, sandeels have been the only common high-lipid schooling fish around Shetland in recent decades. Breeding success of most seabirds is therefore strongly related to sandeel abundance in that region (Hamer et al. 1993, Davis et al. 2005). Seabirds off south-eastern Scotland have access to other fish prey (e.g., young herring and sprat; Bull et al. 2004, Harris et al. 2004, Wilson et al. 2004), but sandeels are still the main prey (Wanless et al. 1998). However, in south-western British waters there are higher abundances of alternative prey such as sprat and juvenile herring, so the linkage to sandeel availability is correspondingly weaker. However, it cannot be ruled out that climate change could result in the growth of sprat or juvenile herring populations in northern waters. In fact, a pronounced increase in abundance of European sprat in the North Sea between 2000 and 2005 can be explained by increases in temperature (Lenoir et al. 2011). During this time, guillemots at Fair Isle, between Orkney and Shetland, underwent a dietary shift (Heubeck 2009), consuming more gadoids and sprat and fewer sandeels, than previously. Moreover, records on guillemot chick diet composition from the Isle of May in the Firth of Forth indicate that sprat have accounted for the majority of chick diet since 2000 (Anderson et al. 2014). While this is probably a response to lack of sandeels, it is possible that guillemot diet partially reflects their preference for sprat. Indeed, sprat might actually represent a higher-quality prey resource than sandeels (Smout et al. 2013). For example, in 2000 the guillemots in the Firth of Forth switched to sprat even though they were two orders of magnitude less abundant than sandeels (Greenstreet et al. 2010a).

In the north-western North Sea, other potential effects on seabirds arise from the apparent changes in growth rates of sandeels since the 1970s. The decline in size-at-date of the recruiting 0-group stages leads to a mismatch between the timing of seabird breeding and availability of adequate prey. The weight-specific energy content of sandeel is related to their body size, so slower growth rates mean declining calorific content of prey fed to chicks on a given day of the year (Wanless et al. 2004, Burthe et al. 2012). Interestingly, there has been a trend towards later breeding in several species (Burthe et al. 2012), partially mitigating the decline in prey length. Nevertheless, chicks of guillemot, shag, kittiwake, Atlantic puffin, and razorbill have all suffered net reductions in energy value because of this decline in sandeel length (Burthe et al. 2012).

In addition to effects on seabird chicks, a lack of 0-group sandeel availability and quality can affect adult seabird mortality, which is particularly influenced by prey availability during the breeding season. This is because seabirds must attain a sufficient level of body energy to meet breeding costs (Oro & Furness 2002, Ratcliffe et al. 2002). In Shetland, sandeel abundance is related to adult survival of various species, in particular kittiwake and great skua *Catharacta skua* (Oro & Furness 2002, Ratcliffe et al. 2002).

Other fish species responding to climate change may have indirect effects on birds by interfering with the relationship between sandeels and seabirds. This interference may take the form of competition for sandeels as prey (Greenstreet et al. 2010a) or being present as an abundant but less-nutritious alternative prey. The much-reported influx of snake pipefish *Entelurus aequoreus* into European waters in 2003 (Lindley et al. 2006, Kloppmann & Ulleweit 2007, Harris et al. 2008, van Damme & Couperus 2008) represents an example of the latter. Trawl survey records show that catches of snake pipefish began to increase off north-western Scotland in 2003 and over the entire North Sea by 2007 (Figure 5). Catches declined sharply in 2009. A simultaneous population explosion and subsequent contraction happened in the Barents Sea (Høines et al. 2009). It is unclear why snake pipefish numbers increased. However, Continuous Plankton Recorder samples show that high numbers of larval and juvenile stages extended as far west as the Mid-Atlantic Ridge and may have coincided with a rise in sea temperatures between January and September, when the eggs are developing and the larvae are growing in the plankton (Kirby et al. 2006). Alternatively, a shift in zooplankton species composition may have helped facilitate the explosion of pipefish numbers (van Damme & Couperus 2008).

In 2003, snake pipefish began to appear in the diet of several seabird species (Harris et al. 2007, Anderson et al. 2014). It is unknown whether seabirds mistook pipefish for their usual prey or whether they were capturing them because sandeels and clupeoid fish were in short supply. In either case, the pipefish represented a poor-quality resource: low in lipid, bony, and difficult to digest (Harris et al.

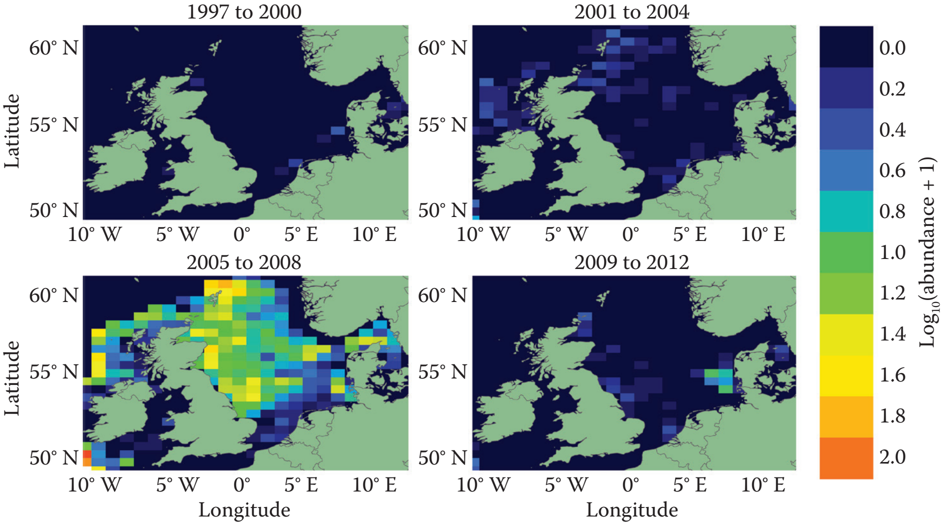

Figure 5 Four-year aggregated mean ($\log_{10}$) abundance of snake pipefish caught by commercial trawlers for the periods 1997–2000 (top left), 2001–2004 (top right), 2005–2008 (bottom-left), and 2009–2012 (bottom right). Trawl survey data extracted from ICES DATRAS (Database of Trawl Surveys). The domain of interest lies between 49°45’N and 61°45’N and between 10°30’W and 12°30’E. World borders are from Sandvik (2009).

2008). Previous work has shown that most seabird colonies have less-successful breeding years when chicks are fed on prey with lower-than-average energy content (Wanless et al. 2005a).

Connections between fish and zooplankton

The principal role of zooplankton in the food web is as a vector for transferring primary production to fish. Sandeels are likely to be bottom-up limited by zooplankton abundance (Frederiksen et al. 2006). In particular, the crucial larval stage is more likely to be affected by bottom-up effects through the plankton (Pitois et al. 2012).

During the 1980s, the North Sea ecosystem underwent a regime shift that resulted in pronounced changes to the composition of the fish and plankton community (Beaugrand 2004). These changes have been ascribed to increased sea temperature (Beaugrand et al. 2002, Perry et al. 2005). Moreover, recent decades have seen pronounced northwards shifts in the range of calanoid copepods (Reid et al. 1998, 2001, Beaugrand et al. 2002, Drinkwater et al. 2003, Reygondeau & Beaugrand 2011). The mean rate of northwards movement for some north-eastern North Atlantic species assemblages between 1958 and 2005 has been estimated at roughly 23 km yr^{-1} (Beaugrand et al. 2009). During this time, the critical threshold separating boreal and temperate zooplankton systems has moved northwards by 22 km yr^{-1} (Beaugrand et al. 2008).

The calanoid copepod *Calanus finmarchicus* is currently vital in the diet of sandeel larvae, as larval survival depends specifically on the abundance of *C. finmarchicus*, not overall abundance of *Calanus* spp., or *C. helgolandicus* (van Deurs et al. 2009). However, despite being previously dominant in the North Sea, *C. finmarchicus*, has declined in biomass by 70% since the 1960s. Species with warmer-water affinities (e.g., *C. helgolandicus*) are moving northwards to replace *C. finmarchicus*, but these species are not as numerically abundant or nutritionally beneficial (lower lipid contents) to higher trophic levels. Moreover, recent temperature increases have reduced the size of zooplankton. Declines in sandeel length have been linked with these changes (van Deurs et al. 2014). A time series of sandeel length at age in the southern North Sea shows a decrease in the late 1980s, around the time when the mean size of calanoid copepods decreased by a factor of two (Beaugrand et al. 2003). This decrease in copepod size was an effect of the regime shift that took place in the North Sea in the late 1980s, associated with a switch in the NAO (North Atlantic Oscillation) index from a negative to a positive phase (Reid et al. 2001, Beaugrand et al. 2002, 2003, Beaugrand & Reid 2003, Beaugrand 2004).

Despite the documentation of changes in species distribution, there is little clear evidence of changes in overall zooplankton production in the North Sea. Trends in zooplankton production off the Scottish eastern coast do not reflect the pattern of decline in sandeels (Heath et al. 2012, O’Brien et al. 2013). Apart from changes in zooplankton abundance, changes in seasonality (van Deurs et al. 2009), size (Beaugrand et al. 2003), and lipid content of zooplankton (Wanless et al. 2005a, Beaugrand et al. 2009) could all affect sandeel populations. Zooplankton community production is exceptionally difficult to estimate, even by direct experimental measurements and certainly from just data on species abundances.

Northwards shifts of plankton species are expected to continue with increasing sea temperatures (Reygondeau & Beaugrand 2011). How these changes will affect higher trophic levels remains unclear. However, it is thought that the retreat of *Calanus finmarchicus* will be damaging to sandeel populations (van Deurs et al. 2009) and, ultimately, seabirds (Frederiksen et al. 2013). A recent niche model study (Frederiksen et al. 2013) showed that the breeding success of kittiwakes and Atlantic puffins on the Isle of May is significantly related to environmental suitability for *C. finmarchicus* (van Deurs et al. 2009). Therefore, it may become increasingly difficult for several boreal seabird species to maintain adequate breeding success as this *Calanus* species continues its retreat.

The future of sandeels in the North Sea will rest on whether a suitable replacement prey can be found, with the most viable candidate being *Calanus helgolandicus*. However, *C. finmarchicus* abundance peaks in spring (Bonnet et al. 2005) concurrently with mean larval hatch date (Heath et al. 2012), whereas *C. helgolandicus* abundance peaks in autumn (Bonnet et al. 2005). Therefore, a mismatch between larval emergence and prey availability may occur if *C. helgolandicus* becomes the dominate prey species for sandeels.

Geographical shifts in plankton species can be related to environmental changes (Beaugrand & Helaouët 2008). There can be reasonable confidence in predictions of shifts in geographical distributions for different climate change scenarios, subject to the assumption that the underlying processes governing species' environmental preferences and tolerances (their 'environmental envelope') will remain constant in the future (Davis et al. 1998, Pearson & Dawson 2003). In addition, it seems reasonably certain that the zooplankton diversity in waters around the British Isles will increase with continued warming (Beaugrand et al. 2008), with a progressive shift towards smaller-size plankton. A shift towards smaller zooplankton may lead to reductions in trophic transfer efficiency due to increased food-chain length.

Ocean modelling predicts a reduction in zooplankton biomass in the North Sea over the next century (Chust et al. 2014). These changes are thought to arise via bottom-up amplification of negative climate-driven impacts on phytoplankton (Chust et al. 2014). Therefore, it is important to understand how climate change may affect zooplankton indirectly through changes in primary production.

Connections between zooplankton and phytoplankton

The production of zooplankton, fish, and higher trophic levels in the marine ecosystem must ultimately be related to primary production and the efficiency of transfer between trophic levels (Aebischer et al. 1990, Schwartzlose et al. 1999, Chavez et al. 2003). Hence, comparing across ecosystems in the north-western Atlantic, there is a positive correlation between long-term average chlorophyll concentration and fishery yield (Frank et al. 2005). In the case of sandeels, it is clear that primary production drives stock biomass in some ecosystems (Eliasen et al. 2011). However, within individual ecosystems, the relationship between primary production and fisheries yield varies over time depending on a range of factors affecting the transfer of energy up the food web and the intensity of exploitation of the fish stocks.

Over several decades, changes in phytoplankton species and communities in the North Atlantic have been associated with temperature trends and variations in the NAO index (Beaugrand & Reid 2003). These changes have included the occurrence of subtropical species in temperate waters, changes in overall phytoplankton biomass and seasonality, and changes in the ecosystem functioning and productivity of the North Atlantic (Edwards et al. 2001, Beaugrand 2004). In the North Sea, overall phytoplankton biomass has increased in recent decades (Edwards et al. 2001), and there has been a concurrent increase in smaller flagellates, which are promoted by warmer and more stratified conditions (Edwards & Richardson 2004). Over the whole north-eastern Atlantic, there has been an increase in phytoplankton biomass with increasing temperatures in cooler regions, but a decrease in phytoplankton biomass in warmer regions (Barton et al. 2003). However, nutrient concentrations are likely to limit any sustained positive response to warming (O'Brien et al. 2012).

Unfortunately, it is only possible to speculate on how climate change may indirectly impact zooplankton through changes in phytoplankton. For example, it is possible that climate-driven changes in phytoplankton and zooplankton phenology (Edwards & Richardson 2004) may reduce prey availability for zooplankton. The key point is clear evidence that changes in climate have already impacted phytoplankton, resulting in zooplankton changes, remains thin.

Discussion

There is much evidence to suggest that climate-driven trophic cascades have already affected seabirds in the waters around the British Isles. Whilst the basis for changes being driven by primary production are complex and uncertain, there is growing evidence of direct climate impacts on zooplankton and the immediate prey of seabirds. The key route of energy transfer to many of the main seabird species is through *Calanus finmarchicus* and *Ammodytes marinus*. Climate change is disrupting this pathway of energy transfer and appears to be causing a decline in breeding success and survival of several important seabirds around the British Isles, primarily those in northern areas (e.g., the eastern coast of Scotland).

In the short term, it can be predicted with reasonable confidence that the recent succession of poor breeding years will propagate through seabird populations to cause a decline in breeding numbers. Beyond this, changes will depend on the balance between breeding success and adult survival. The future patterns of seabird breeding success and survival may depend critically on the scope for feeding on alternative prey if sandeel stocks do not recover over time with continued warming. However, the strength of resilience to food shortages may vary among species. For example, kittiwakes are sensitive to reductions in sandeel availability (Furness & Tasker 2000), while adult guillemots seem able to maintain provisioning of their chicks despite fluctuating abundances of key prey (Smout et al. 2013). Interspecific variation in sensitivity to reductions in sandeel abundance may explain why climate effects appear to be species specific (Lahoz-Monfort et al. 2011), assuming that sandeel abundance is negatively correlated with climate indices. Winter NAO and SST are contributing to synchrony, as well as desynchrony, in survival rates of auks (Alcidae) off the Scottish eastern coast (Lahoz-Monfort et al. 2011).

Continued decline in sandeel quality and abundance may cause the North Sea seabird community to become increasingly dominated by species least reliant on sandeels (Furness & Tasker 2000). The increase in populations of the northern gannet in recent decades may be an example of this (Wanless et al. 2005b, Murray et al. in press). These birds are insensitive to reductions in sandeel availability, owing in part to their high ability to switch diet (Furness & Tasker 2000). Northern gannets are also the largest seabirds in the North Atlantic. Therefore, a trend towards a seabird community dominated by larger seabirds contrasts strongly with observed trends in prey length in lower trophic levels.

The regional pattern of decline in seabird numbers is strikingly similar to the decline in sandeel populations. Regional differences in the strength of bottom-up regulation may provide an explanation. In the Irish Sea, Celtic Sea, and the English Channel, there appears to be little evidence of bottom-up regulation (Lauria et al. 2013). However, evidence for bottom-up effects has been found in the north-western North Sea (Frederiksen et al. 2006), which could be indicative of different oceanographic conditions (Lauria et al. 2013). Climate change impacts on lower trophic levels may therefore affect seabird numbers in the northern North Sea but have little effect on seabirds in southern areas.

While the predicted short-term increase in sprat abundance around Britain in response to warming (Lenoir et al. 2011) may mitigate a shortage of sandeels, it probably does not represent a long-term solution for seabirds. Sprat are predicted to disappear from these waters by the end of the twenty-first century, with their distribution shifting to the Barents Sea (Lenoir et al. 2011). In fact, warm-water midtrophic fishes such as anchovies (Lenoir et al. 2011) will likely be performing the ecosystem role vacated by sandeels and sprat. Although these fishes could potentially fill the void left by sprat and sandeels in seabird diets, whether or not there will be a smooth transition in prey is unknown. Consistent recruitment failure of herring (Payne et al. 2009, 2013) places in doubt the viability of this species as alternative prey for seabirds. Many seabirds are able to prey on piscivorous demersal fish like whiting (*Merlangius merlangus*), but these have a low energy density, and the body condition of chicks is much poorer in years when whiting are the main prey (Harris 1980).

In the case of seabirds that feed opportunistically by scavenging at fishing vessels (especially great skuas, northern fulmars, great black-backed gulls *Larus marinus*), part of the impact on their breeding success may be due to reduced amounts of fishery discards and offal in recent years (Votier et al. 2004, 2007, Käkelä et al. 2005, 2007, Furness 2006, 2007). Although these seabirds prefer to feed on sandeels, they turn to fishery offal and discards as an alternative food, and in the last few years, there have been large reductions in amounts of discards and offal provided to seabirds around the British Isles at a time when sandeels have also declined. Great skuas appear to have responded to this situation by increasingly killing other seabirds but have also suffered breeding failures due to food shortage, part of which results from the fact that great skuas will kill chicks of neighbouring conspecific pairs. The depredations on other seabirds will also reduce their breeding success, as chicks have a much lower chance of surviving if a parent has been killed during the breeding season. Although gannets mainly feed on pelagic fish in summer, discards of unwanted catches from fishing vessels make up a significant component of the diet in winter. A trend for gannets to range further south in winter than they did previously may be related to reductions in discarding (Kubetzki et al. 2009).

In 2014, the Common Fisheries Policy (CFP) of the European Union was re-formed to include a complete ban on fishing 'discards' (i.e., an obligation was imposed to record and land all catches of species subject to catch limits). This applied to pelagic species from January 2015, will apply to most valuable demersal species (e.g., cod *Gadus morhua*, hake *Merluccius merluccius*, and sole) from January 2016, and to all other species from January 2019 (European Commission 2013). This will almost certainly have a major impact on many seabird populations throughout Europe that are, at the moment, reliant on discards. Species native to the north-eastern Atlantic that currently exploit fishery discards extensively are kittiwakes, herring gulls *Larus argentatus*, the lesser black-backed gull *Larus fuscus*, the great black-backed gull, the great skua, the northern fulmar, and the northern gannet (Bicknell et al. 2013). It seems likely that the cessation in discards could slow the sustained growth in gannet populations.

In the second sentence of the paragraph "In 2014, the Common," do you mean "demersal species that are most valuable" or "most demersal species that are valuable"?

Evidence suggests that anthropogenic and climate impacts on seabirds could be additive (Frederiksen et al. 2004, Votier et al. 2005). On the Scottish eastern coast, the species most vulnerable to these combined threats are northern fulmars, kittiwakes, and shags (Burthe et al. 2014). The vital rates (e.g., growth and survival rates) of these species have been decreasing with rising temperature, most likely through changes in prey such as sandeels. To ameliorate any declines in these demographic parameters, efforts to safeguard vital seabird prey around important colonies, such as the Isle of May, could be put in place.

The most notable example of such a measure is the sandeel fishery closure off the eastern coast of Scotland in 2000. Established with the aim of avoiding depletion of the sandeel stock, a substantial area covering approximately 21,000 km^2 was closed to sandeel fisheries (Frederiksen et al. 2008b, Greenstreet et al. 2010a). However, closing the area to fishing has not been sufficient to ensure high sandeel abundance (Figure 4).

Recent measures have been implemented to protect marine habitats adjacent to seabird colonies. In 2009, the boundaries of 31 of the Special Protection Areas (SPAs) designated for seabird breeding colonies in Scotland were extended seawards (Scottish Natural Heritage 2009); however, these expanded areas are extremely small (extending to < 5 km off shore) and therefore may not effectively safeguard seabird prey. This is especially true for sandeel-feeding seabirds because of the patchiness of sandeel habitat. Moreover, many seabirds have foraging ranges that span many tens of kilometres (Thaxter et al. 2012).

In addition to protecting sandeels in the vicinity of seabird colonies, measures to protect sources of sandeel larvae that are exported to these areas can be put in place. Recently, two marine protected areas (MPAs), to the north-west of the Orkney Islands (59°31′N 3°14′W) and around Turbot Bank (off the north-eastern coast of Scotland, 57°23′N 0°56′W), have been established with the aim of protecting the supply of sandeel larvae (Joint Nature Conservation Committee [JNCC]

2014a,b). These locations were chosen as they are thought to be important sources of newly hatched sandeel larvae (Wright & Bailey 1996), which, through dispersal, support sandeel stocks afar. It is possible that MPAs may lead to increased abundance outwith the MPA through larval 'spillover' (Christensen et al. 2009); however, the extent of effective spillover will obviously depend on availability of suitable habitat elsewhere.

Conclusions

The key findings from this review may be summarized as follows:

- Climate-driven trophic cascades are already affecting seabirds in waters around the British Isles.
- There appears to be marked interspecies variation in sensitivity to climate change.
- Strong regional differences exist in climate effects on seabirds, possibly due to spatial variation in prey affecting the strength of bottom-up effects.
- Higher winter temperature appears to be having a negative impact on sandeel populations in the north-western North Sea. These populations are characterized by low growth rates, so metabolic costs of overwintering should increase with rising temperatures.
- A reduction in mean copepod size may explain a long term decline in sandeel size-at-date. This ongoing reduction in sandeel size-at-date is causing a mismatch between seabird peak energy requirements and adequate sandeel prey.
- The copepod *Calanus finmarchicus* is a key prey species of sandeel, so further deleterious impacts on sandeels should be expected in the future in response to the ongoing northwards shift of this *Calanus* species. This will have the effect of a reduction in seabird breeding success.
- There is no evidence of indirect climate impacts on zooplankton through changes in phytoplankton. Therefore, any indirect climate impacts on seabirds may be restricted to changes in fish prey or zooplankton.
- Future patterns of sandeel-dependent seabird breeding success and survival will depend critically on the scope for feeding on alternative prey.
- An increase in sprat abundance should temporarily mitigate the impact of a shortage of sandeels for some seabirds. However, modelling indicates that they may not represent a long-term solution.
- Declines in sandeel quality and abundance could cause the North Sea seabird community to become increasingly dominated by larger species.

References

Aebischer, N.J., Coulson, J.C. & Colebrook, J.M. 1990. Parallel long-term trends across four marine trophic levels and weather. *Nature* **347**, 753–755.

Alerstam, T. 1990. *Bird Migration*. Cambridge, UK: Cambridge University Press.

Anderson, H.B., Evans, P.G.H., Potts, J.M., Harris, M.P. & Wanless, S. 2014. The diet of common guillemot (*Uria aalge*) chicks at colonies in the UK, 2006–2011: evidence for changing prey communities in the North Sea. *Ibis* **156**, 23–34.

Arnott, S.A. & Ruxton, G.D. 2002. Sandeel recruitment in the North Sea: demographic, climatic and trophic effects. *Marine Ecology Progress Series* **238**, 199–210.

Arrhenius, F. 1997. Top-down controls by young-of-the-year herring (*Clupea harengus*) in the northern Baltic proper. In *Forage Fishes in Marine Ecosystems*, B.R. Baxter (ed.). Fairbanks, Alaska: University of Alaska Sea Grant College Program AK-SG-97-01, 77–86.

Balmer, D.E. & Peach, W.J. 1997. Review of natural avian mortality rates. BTO Research Report No. 175. Thetford, Norfolk, UK: British Trust for Ornithology. Online. http://www.bto.org/sites/default/files/u196/downloads/rr175.pdf (accessed 19 November 2014).

Barton, A.D., Greene, C.H., Monger, B.C. & Pershing, A.J. 2003. The Continuous Plankton Recorder survey and the North Atlantic Oscillation: interannual- to multidecadal-scale patterns of phytoplankton variability in the North Atlantic Ocean. *Progress in Oceanography* **58**, 337–358.

Beare, D.J., Burns, F., Peach, K., Portilla, E., Greig, A., McKenzie, E. & Reid, D.G. 2004a. An increase in the abundance of anchovies and sardines in the north-western North Sea since 1995. *Global Change Biology* **10**, 1209–1213.

Beare, D.J., Burns, F., Peach, K. & Reid, D.G. 2004b. Red mullet migration into the northern North Sea during late winter. *Journal of Sea Research* **53**, 205–212.

Beaugrand, G. 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography* **60**, 245–262.

Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S. & Reid, P.C. 2003. Plankton effect on cod recruitment in the North Sea. *Nature* **426**, 661–664.

Beaugrand, G., Edwards, M., Brander, K., Luczak, C. & Ibanez, F. 2008. Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecology Letters* **11**, 1157–1168.

Beaugrand, G. & Helaouët, P. 2008. Simple procedures to assess and compare the ecological niche of species. *Marine Ecology Progress Series* **363**, 29–37.

Beaugrand, G., Luczak, C. & Edwards, M. 2009. Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Global Change Biology* **15**, 1790–1803.

Beaugrand, G. & Reid, P.C. 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology* **9**, 801–817.

Beaugrand, G., Reid, P.C., Ibañez, F., Lindley, J.A. & Edwards, M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* **296**, 1692–1694.

Becker, P.H. & Ludwigs, J.-D. 2004. *Sterna hirundo* common tern. *BWP Update: The Journal of Birds of the Western Palearctic* **6**, 93–139.

Bergstad, O.A., Høines, Å.S. & Jørgensen, T. 2002. Growth of sandeel, *Ammodytes marinus*, in the northern North Sea and Norwegian coastal waters. *Fisheries Research* **56**, 9–23.

Bicknell, A.W.J., Oro, D., Camphuysen, C.J. & Votier, S.C. 2013. Potential consequences of discard reform for seabird communities. *Journal of Applied Ecology* **50**, 649–658.

Bonnet, D., Richardson, A.J., Harris, R., Hirst, A., Beaugrand, G., Edwards, M., Ceballos, S., Diekman, R., López-Urrutia, A., Valdes, L., Carlotti, F., Molinero, J.C., Weikert, H., Greve, W., Lucic, D., Albaina, A., Yahia, N.D., Umani, S.F., Miranda, A., Santos, A., Cook, K., Robinson, S. & Fernandez de Puelles, M.L. 2005. An overview of *Calanus helgolandicus* ecology in European waters. *Progress in Oceanography* **65**, 1–53.

Boulcott, P. & Wright, P.J. 2008. Critical timing for reproductive allocation in a capital breeder: evidence from sandeels. *Aquatic Biology* **3**, 31–40.

Boulcott, P. & Wright, P.J. 2011. Variation in fecundity in the lesser sandeel: implications for regional management. *Journal of the Marine Biological Association of the United Kingdom* **91**, 1273–1280.

Boulcott, P., Wright, P.J., Gibb, F.M., Jensen, H. & Gibb, I.M. 2007. Regional variation in maturation of sandeels in the North Sea. *ICES Journal of Marine Science* **64**, 369–376.

Brooke, M. 1990. *The Manx Shearwater*. London: Poyser.

Bukacinski, D.B. & Bukacinska, M.B. 2003. *Larus canus* common gull. *BWP Update: The Journal of Birds of the Western Palearctic* **5**, 13–39.

Bull, J., Wanless, S., Elston, D.A., Daunt, F., Lewis, S. & Harris, M.P. 2004. Local-scale variability in the diet of black-legged kittiwakes *Rissa tridactyla*. *Ardea* **92**, 43–52.

Burthe, S., Daunt, F., Butler, A., Elston, D.A., Frederiksen, M., Johns, D., Newell, M., Thackeray, S.J. & Wanless, S. 2012. Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web. *Marine Ecology Progress Series* **454**, 119–133.

Burthe, S.J., Wanless, S., Newell, M.A., Butler, A. & Daunt, F. 2014. Assessing the vulnerability of the marine bird community in the western North Sea to climate change and other anthropogenic impacts. *Marine Ecology Progress Series* **507**, 277–295.

Camphuysen, C.J. & Garthe, S. 1997. An evaluation of the distribution and scavenging habits of northern fulmars (*Fulmarus glacialis*) in the North Sea. *ICES Journal of Marine Science* **54**, 654–683.

Carpenter, S.R., Kitchell, J.F. & Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. *Biosciences* **35**, 634–639.

Chabrzyk, G. & Coulson, J.C. 1976. Survival and recruitment in the herring gull *Larus argentatus*. *Journal of Animal Ecology* **45**, 187–203.

Chapdelaine, G. 1997. Pattern of recoveries of banded razorbills (*Alca torda*) in the western Atlantic and survival rates of adults and immatures. *Colonial Waterbirds* **20**, 47–54.

Chavez, F.P., Ryan, J., Lluch-Cota, S.E. & Niqeun, M.C. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* **299**, 217–221.

Christensen, A., Mosegaard, H. & Jensen, H. 2009. Spatially resolved fish population analysis for designing MPAs: influence on inside and neighbouring habitats. *ICES Journal of Marine Science* **66**, 56–63.

Chust, G., Allen, J.I., Bopp, L., Schrum, C., Holt, J., Tsiaras, K., Zavatarelli, M., Chifflet, M., Cannaby, H., Dadou, I., Daewel, U., Wakelin, S.L., Machu, E., Pushpadas, D., Butenschon, M., Artioli, Y., Petihakis, G., Smith, C., Garçon, V., Goubanova, K., Le Vu, B., Fach, B.A., Salihoglu, B., Clementi, E. & Irigoien, X. 2014. Biomass changes and trophic amplification of plankton in a warmer ocean. *Global Change Biology* **20**, 2124–2139.

Clobert, J., Lebreton, J.-D., Allainé, D. & Gaillard, J.M. 1994. The estimation of age-specific breeding probabilities from capture or resightings in vertebrate populations. II. Longitudinal models. *Biometrics* **50**, 375–387.

Corten, A. 2001. Northern distribution of North Sea herring as a response to high water temperatures and/or low food abundance. *Fisheries Research* **50**, 189–204.

Coulson, J.C. & Horobin, J. 1976. The influence of age on the breeding biology of the Arctic tern *Sterna paradisaea*. *Journal of Zoology* **178**, 247–260.

Coulson, J.C. & White, E. 1959. The post-fledging mortality of the kittiwake. *Bird Study* **6**, 97–102.

Cramp, S. (ed.). 1977. Family Phalacrocoracidae cormorants, shags. In *Handbook of the Birds of Europe the Middle East and North Africa,* Vol. 1, S. Cramp & K.E.L. Kinnon (eds). Oxford, UK: Oxford University Press, 199–222.

Provide all editors' names for Cramp et al. 1977–1994.

Cramp, S., et al. (eds). 1977–1994. *Birds of the Western Palearctic*. Oxford: Oxford University Press.

Cramp, S., Bourne, W.R.P. & Sanders, D. 1974. *The Seabirds of Britain and Ireland*. London: Collins.

Cramp, S. & Simmons, K.E.L. (eds). 1983. *The Birds of the Western Palearctic*. Vol. 3. Oxford, UK: Oxford University Press.

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**, 783–786.

Davis, S.E., Nager, R.G. & Furness, R.W. 2005. Food availability affects adult survival as well as breeding success of parasitic jaegers. *Ecology* **86**, 1047–1056.

Desaunay, Y., Guerault, D., Le Pape, O. & Poulard, J.-C. 2006. Changes in occurrence and abundance of northern/southern flatfishes over a 20-year period in a coastal nursery area (Bay of Vilaine) and on the eastern continental shelf of the Bay of Biscay. *Scientia Marina* **70**, 193–200.

Drinkwater, K.F., Belgrano, A., Borja, A., Conversi, A., Edwards, M., Greene, C.H., Ottersen, G., Pershing, A.J. & Walker, H. 2003. The response of marine ecosystems to climate variability associated with the North Atlantic Oscillation in the North Atlantic Oscillation: climatic significance and environmental impact. *Geophysical Monograph* **134**, 211–234.

Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmüller, V., Dye, S.R. & Skjoldal, H.R. 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology* **45**, 1029–1039.

Dunnet, G.M. & Ollason, J.C. 1978a. Survival and longevity in the fulmar. *Ibis* **120**, 124–125.

Dunnet, G.M. & Ollason, J.C. 1978b. The estimation of survival rate in the fulmar, *Fulmarus glacialis*. *Journal of Animal Ecology* **47**, 507–520.

Dye, S.R., Hughes, S.L., Tinker, J., Berry, D.I., Holliday, N.P., Kent, E.C., Kennington, K., Inall, M., Smyth, T., Nolan, G., Lyons, K., Andres, O. & Beszczynska-Möller, A. 2013. Impacts of climate change on temperature (air and sea). *MCCIP Science Review* 2013, 1–12, doi:10.14465/2013.arc01.001-012

Edwards, M., Reid, P. & Planque, B. 2001. Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960–1995). *ICES Journal of Marine Science* **58**, 39–49.

Edwards, M. & Richardson, A.J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**, 881–884.

Eliasen, K., Reinert, J., Gaard, E., Hansen, B., Jacobsen, J.A., Grønkjær, P. & Christensen, J.T. 2011. Sandeel as a link between primary production and higher trophic levels on the Faroe shelf. *Marine Ecology Progress Series* **438**, 185–194.

European Commission. 2013. Proposal for a new regulation on the common fisheries policy. Brussels: European Commission. Online. http://ec.europa.eu/fisheries/reform/proposals/index_en.htm (accessed 15 October 2014).

Ewins, P.J. 1988. An analysis of ringing recoveries of black guillemots *Cepphus grylle* in Britain and Ireland. *Ringing & Migration* **9**, 95–102.

Fishbase. 2014. *Ammodytes marinus* Raitt, 1934. Lesser sand-eel. Online. http://www.fishbase.org/summary/37 (accessed 30 June 2014).

Frank, K.T., Petrie, B., Choi, J.S. & Leggett, W.C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* **308**, 1621–1623.

Frederiksen, M., Anker-Nilssen, T., Beaugrand, G. & Wanless, S. 2013. Climate, copepods and seabirds in the boreal Northeast Atlantic—current state and future outlook. *Global Change Biology* **19**, 364–372.

Frederiksen, M. & Bregnballe, T. 2000. Evidence for density-dependent survival in adult cormorants from a combined analysis of recoveries and resightings. *Journal of Animal Ecology* **69**, 737–752.

Frederiksen, M., Daunt, F., Harris, M.P. & Wanless, S. 2008a. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. *Journal of Animal Ecology* **77**, 1020–1029.

Frederiksen, M., Edwards, M., Richardson, A.J., Halliday, N.C. & Wanless, S. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology* **75**, 1259–1268.

Frederiksen, M., Elston, D.A., Edwards, M., Mann, A.D. & Wanless, S. 2011. Mechanisms of long-term decline in size of lesser sandeels in the North Sea explored using a growth and phenology model. *Marine Ecology Progress Series* **432**, 137–147.

Frederiksen, M., Furness, R.W. & Wanless, S. 2007. Regional variation in the role of bottom-up and top-down processes in controlling sandeel abundance in the North Sea. *Marine Ecology Progress Series* **337**, 279–286.

Frederiksen, M., Jensen, H., Duant, F., Mavor, R.A. & Wanless, S. 2008b. Differential effects of a local industrial sand lance fishery on seabird breeding performance. *Ecological Applications* **18**, 701–710.

Frederiksen, M. & Petersen, A. 1999. Adult survival of the black guillemot in Iceland. *Condor* **101**, 589–597.

Frederiksen, M., Wanless, S., Harris, M.P., Rothery, P. & Wilson, L.J. 2004. The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *Journal of Applied Ecology* **41**, 1129–1139.

Furness, R.W. 1984. Leach's petrel populations on St Kilda. *British Ecological Society Bulletin* **15**, 84–87.

Furness, R.W. 1987. *The Skuas*. London: Poyser.

Furness, R.W. 2002. Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. *ICES Journal of Marine Science* **59**, 261–269.

Furness, R.W. 2003. Impacts of fisheries on seabird communities. *Scientia Marina* **67**, 33–45.

Furness, R.W. 2006. How many fish should we leave in the sea for seabirds and marine mammals? In *Top Predators in Marine Ecosystems: Their Role in Monitoring and Management*, I. Boyd et al. (eds). Cambridge, UK: Cambridge University Press, 211–222.

Furness, R.W. 2007. Responses of seabirds to depletion of food fish stocks. *Journal of Ornithology* **148**, 247–252.

Furness, R.W. & Tasker, M.L. 2000. Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series* **202**, 253–264.

Furness, R.W., Wade, H.M., Robbins, A.M.C. & Masden, E.A. 2012. Assessing the sensitivity of seabird populations to adverse effects from tidal stream turbines and wave energy devices, supplementary material. *ICES Journal of Marine Science* **69**, 1466–1479.

Gjøsæter, H. & Bogstad, B. 1998. Effects of the presence of herring (*Clupea harengus*) on the stock-recruitment relationship of Barents Sea capelin (*Mallotus villosus*). *Fisheries Research* **38**, 57–71.

Greenstreet, S., Fraser, H., Armstrong, E. & Gibb, I. 2010a. Monitoring the consequences of the northwestern North Sea sandeel fishery closure. *Scottish Marine and Freshwater Science* **1**, 1–31.

Greenstreet, S.P.R., Holland, G.J., Guirey, E.J., Armstrong, E., Fraser, H.M. & Gibb, I.M. 2010b. Combining hydroacoustic seabed survey and grab sampling techniques to assess "local" sandeel population abundance. *ICES Journal of Marine Science* **67**, 971–984.

Greenstreet, S.P.R., Robertson, M., Fraser, H., Holland, G., Doyle, K. & Li, R. 2006. Variation in the abundance, distribution, diet and food consumption rates of gadoid predators in the Wee Bankie/Marr Bank region of the northwestern North Sea, and consequences for predator population dynamics. EU-IMPRESS Final Report Appendix 8.

Provide publisher's name, city, country for Greenstreet et al. 2006.

Hamer, K.C., Monaghan, P., Uttley, J.D., Walton, P. & Burns, M.D. 1993. The influence of food supply on the breeding ecology of kittiwakes *Rissa tridactyla* in Shetland. *Ibis* **135**, 255–263.

Hardy, A.C. 1924. The herring in relation to its animate environment. Part 1. The food and feeding habits of the herring with special reference to the east coast of England. *Fishery Investigations, London, Series II* **7**, 1–53.

Harris, M.P. 1970. Rates and causes of increase of some British gull populations. *Bird Study* **17**, 325–335.

Harris, M.P. 1980. Breeding performance of puffins *Fratercula artica* in relation to nest density, laying date and year. *Ibis* **122**, 193–209.

Harris, M.P. 1983. Biology and survival of the immature puffin *Fratercula arctica*. *Ibis* **125**, 56–73.

Harris, M.P., Buckland, S.T., Russell, S.M. & Wanless, S. 1994. Year- and age-related variation in the survival of adult European shags over a 24-year period. *The Condor* **96**, 600–605.

Harris, M.P., Daunt, F., Bogdanova, M.I., Lahoz-Monfort, J.J., Newell, M.A., Phillips, R.A. & Wanless, S. 2013. Inter-year differences in survival of Atlantic puffins *Fratercula arctica* are not associated with winter distribution. *Marine Biology* **160**, 2877–2889.

Harris, M.P., Frederiksen, M. & Wanless, S. 2007. Within and between-year variation in the juvenile survival of common guillemots *Uria aalge*. *Ibis* **149**, 472–481.

Harris, M.P., Freeman, S.N., Wanless, S., Morgan, B.J.T. & Wernham, C.V. 1997. Factors influencing the survival of puffins *Fratercula arctica* at a North Sea colony over a 20-year period. *Journal of Avian Biology* **28**, 287–295.

Harris, M.P., Newell, M., Daunt, F., Speakman, J.R. & Wanless, S. 2008. Snake pipefish *Entelurus aequoreus* are poor food for seabirds. *Ibis* **150**, 413–415.

Harris, M.P. & Wanless, S. 2011. *The Puffin*. London: Poyser.

Harris, M.P., Wanless, S., Murray, S. & Mackley, E. 2004. Isle of May seabird studies in 2004. JNCC Report No. 375. Peterborough, UK: Joint Nature Conservation Committee.

Harris, M.P., Wanless, S. & Rothery, P. 2000a. Adult survival rates of shag *Phalacrocorax aristotelis*, common guillemot *Uria aalge*, razorbill *Alca torda*, puffin *Fratercula arctica* and kittiwake *Rissa tridactyla* on the Isle of May 1986–96. *Atlantic Seabirds* **2**, 133–150.

Harris, M.P., Wanless, S., Rothery, P., Swann, R.L. & Jardine, D. 2000b. Survival of adult common guillemots *Uria aalge* at three Scottish colonies. *Bird Study* **47**, 1–7.

Harrison, C. 1975. *Nests, Eggs and Nestlings of British and European Birds*. London: Collins.

Hays, G.C., Richardson, A.J. & Robinson, C. 2005. Climate change and marine plankton. *Trends in Ecology & Evolution* **20**, 337–344.

Heath, M.R. 2007. Responses of fish to climate fluctuations in the Northeast Atlantic. In *Practicalities of Climate Change: Adaptation and Mitigation. Proceedings of the 24th Conference of the Institute of Ecology and Environmental Management*, *Cardiff, 14–16 November 2006*, L. Emery (ed.). Winchester, UK: Institute of Ecology and Environmental Management, 102–116.

Heath, M.R., Rasmussen, J., Bailey, M.C., Dunn, J., Fraser, J., Gallego, A., Hay, S.J., Inglis, M. & Robinson, S. 2012. Larval mortality rates and population dynamics of lesser sandeel (*Ammodytes marinus*) in the northwestern North Sea. *Journal of Marine Systems* **93**, 47–57.

Heath, M.R., Speirs, D.C. & Steele, J.H. 2014. Understanding patterns and processes in models of trophic cascades. *Ecology Letters* **17**, 101–114.

Hedger, R., McKenzie, E., Heath, M., Wright, P., Scott, B., Gallego, A. & Andrews, J. 2004. Analysis of the spatial distributions of mature cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) abundance in the North Sea (1980–1999) using generalised additive models. *Fisheries Research* **70**, 17–25.

Hemmingsson, E. & Eriksson, M.O.G. 2002. Ringing of red-throated diver *Gavia stellata* and black-throated diver *Gavia arctica* in Sweden. *Wetlands International Diver/Loon Specialist Group Newsletter* **4**, 8–13.

Heubeck, M. 1989. Breeding success of Shetland's seabirds: Arctic skua, kittiwake, guillemot, razorbill and puffin. In *Seabirds and Sandeels: Proceedings of a seminar held in Lerwick, Shetland, 15–16 October 1988*, M. Heubeck (ed.). Shetland Bird Club, 11–18.

Provide city and country of publisher for Heubeck 1989.

Heubeck, M. 2009. Common guillemot *Uria aalge* chick diet and breeding performance at Sumburgh Head, Shetland in 2007–09, compared to 1990–91. *Seabird* **22**, 9–18.

Høines, Å., Johannesen, E. & Bergstad, O.A. 2009. Ikke-kommersielle fiskearter—non-commercial fish. In *Fisken og Havet, Særnummer 1–2009: Havets Ressurser og Miljø 2009*, H. Gjøsæter et al. (eds). Bergen, Norway: Havforskningsinstituttet, 60–61.

Holland, G.J., Greenstreet, S.P.R., Gibb, I.M., Fraser, H.M. & Robertson, M.R. 2005. Identifying sandeel *Ammodytes marinus* sediment habitat preferences in the marine environment. *Marine Ecology Progress Series* **303**, 269–282.

Huntington, C.E. & Burtt, E.H. 1972. Breeding age and longevity in Leach's petrel (*Oceanodroma leucorhoa*). *Proceedings of the International Ornithological Congress* **15**, 653.

Intergovernmental Panel on Climate Change (IPCC). 2007. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, S. Solomon et al. (eds). Cambridge, UK: Cambridge University Press.

International Council for the Exploration of the Sea (ICES). 2004. Report of the ICES Advisory Committee on Fishery Management and Advisory Committee on Ecosystems, 2004. ICES Advice, Volume 1, Number 2. Copenhagen: International Council for the Exploration of the Sea.

International Council for the Exploration of the Sea (ICES). 2007. *Climate Change: Changing Oceans*. Copenhagen: International Council for the Exploration of the Sea. Online. http://www.ices.dk/news-and-events/Documents/Press%20Room/ICES%20CLIM.pdf (accessed 30 June 2014).

International Council for the Exploration of the Sea (ICES). 2010. Report of the Benchmark Workshop on Sandeel (WKSAN), 6–10 September 2010, Copenhagen, Denmark. ICES CM 2010/ACOM:57. Copenhagen: International Council for the Exploration of the Sea.

International Council for the Exploration of the Sea (ICES). 2013. Report of the Herring Assessment Working Group for the area south of 62°N (HAWG), 12–21 March 2013, ICES Headquarters, Copenhagen. ICES CM 2013/ACOM:06. Copenhagen: International Council for the Exploration of the Sea.

Jennings, S., Kaiser, M.J. & Reynolds, J.D. 2001. *Marine Fisheries Ecology*. Oxford, UK: Blackwell.

Johnsgard, P.A. 1987. *Diving Birds of North America*. Lincoln, Nebraska: University of Nebraska Press.

Joint Nature Conservation Committee (JNCC). 2014a. North-west Orkney MPA. Peterborough, UK: Joint Nature Conservation Committee. Online. http://jncc.defra.gov.uk/page-6484 (accessed 7 November 2014).

Joint Nature Conservation Committee (JNCC). 2014b. Turbot Bank MPA. Peterborough, UK: Joint Nature Conservation Committee. Online. http://jncc.defra.gov.uk/page-6490 (accessed 18 November 2014).

Joint Nature Conservation Committee (JNCC). 2014c. Seabird population trends and causes of change: 1986–2013 report. Peterborough, UK: Joint Nature Conservation Committee. Online. http://www.jncc.defra.gov.uk/page-3201 (accessed 17 October 2014).

Käkelä, A., Furness, R.W., Kelly, A., Strandberg, U., Waldron, S. & Käkelä, R. 2007. Fatty acid signatures and stable isotopes as dietary indicators in North Sea seabirds. *Marine Ecology Progress Series* **342**, 291–301.

Käkelä, R., Käkelä, A., Kahle, S., Becker, P.H., Kelly, A. & Furness, R.W. 2005. Fatty acid signatures in plasma of captive herring gulls as indicators of demersal or pelagic fish diet. *Marine Ecology Progress Series* **293**, 191–200.

Kirby, R.K., Johns, D.G. & Lindley, J.A. 2006. Fathers in hot water: rising sea temperatures and a northeastern Atlantic pipefish baby boom. *Biology Letters* **2**, 597–600.

Klomp, N.I. & Furness, R.W. 1991. Recruitment in long-lived birds: studies of nonbreeding great skuas. *Proceedings of the International Ornithological Congress* **20**, 1678–1688.

Kloppmann, M.H.F. & Ulleweit, J. 2007. Off-shelf distribution of pelagic snake pipefish, *Entelurus aequoreus* (Linnaeus, 1758), west of the British Isles. *Marine Biology* **151**, 271–275.

Kubetzki, U., Garthe, S., Fifield, D., Mendel, B. & Furness, R.W. 2009. Individual migratory schedules and wintering areas of northern gannets. *Marine Ecology Progress Series* **391**, 257–265.

Kvist, T., Gislason, H. & Thyregod, P. 2001. Sources of variation in the age composition of sandeel landings. *ICES Journal of Marine Science* **58**, 842–851.

Lahoz-Monfort, J.J., Morgan, B.J.T., Harris, M.P., Daunt, F., Wanless, S. & Freeman, S.N. 2013. Breeding together: modeling synchrony in productivity in a seabird community. *Ecology* **94**, 3–10.

Lahoz-Monfort, J.J., Morgan, B.J.T., Harris, M.P., Wanless, S. & Freeman, S.N. 2011. A capture-recapture model for exploring multi-species synchrony in survival. *Methods in Ecology and Evolution* **2**, 116–124.

Last, J.M. 1989. The food of herring, *Clupea harengus*, in the North Sea, 1983–1986. *Journal of Fish Biology* **34**, 489–501.

Lauria, V., Attrill, M.J., Brown, A., Edwards, M. & Votier, S.C. 2013. Regional variation in the impact of climate change: evidence that bottom-up regulation from plankton to seabirds is weak in parts of the Northeast Atlantic. *Marine Ecology Progress Series* **488**, 11–22.

Lebreton, J.-D. & Clobert, J. 1991. Bird population dynamics, management, and conservation: the role of mathematical modelling. In *Bird Population Studies: Relevance to Conservation and Management*, C.M. Perrins et al. (eds). Oxford, UK: Oxford University Press, 105–125.

Lenoir, S., Beaugrand, G. & Lecuyer, E. 2011. Modelled spatial distribution of marine fish and projected modifications in the North Atlantic Ocean. *Global Change Biology* **17**, 115–129.

Lindley, J.A., Kirby, R.R., Johns, D.G. & Reid, P.C. 2006. Exceptional abundance of the snake pipefish (*Entelurus aequoreus*) in the north-eastern Atlantic Ocean. ICES CM 2006/C:06. Copenhagen: International Council for the Exploration of the Sea.

Lloyd, C., Tasker, M.L. & Partridge, K. 1991. *The Status of Seabirds in Britain and Ireland*. London: Poyser.

Lloyd, C.S. 1976. *The breeding biology and survival of the razorbill* Alca torda. PhD thesis. University of Oxford, UK.

Macer, C.T. 1966. Sandeels (Ammodytidae) in the south-western North Sea: their biology and fishery. *Fishery Investigations, London, Series II* **24**, 1–55.

Mamie, J.C.J., Beare, D.J., Jones, E.G., Kienzle, M., Dobby, H., Heath, M.R. & Reid, D.G. 2007. Aspects of the distribution and growth of bluemouth (*Helicolenus dactylopterus*, Delaroche 1809) since its invasion of the northern North Sea in 1991. *Fisheries Oceanography* **16**, 85–94.

Massey, B.W., Bradley, D.W. & Atwood, J.L. 1992. Demography of a California least tern colony including effects of the 1982–1983 El Niño. *Condor* **94**, 976–983.

Mavor, R.A., Parsons, M., Heubeck, M. & Schmitt, S. 2005. Seabird numbers and breeding success in Britain and Ireland, 2004. UK Nature Conservation No. 29. Peterborough, UK: Joint Nature Conservation Committee. Online. http://jncc.defra.gov.uk/PDF/pub05_seabirdnos_2004.pdf (accessed 19 November 2014).

Mavor, R.A., Parsons, M., Heubeck, M. & Schmitt, S. 2006. Seabird numbers and breeding success in Britain and Ireland, 2005. UK Nature Conservation No. 30. Peterborough, UK: Joint Nature Conservation Committee. Online. http://jncc.defra.gov.uk/pdf/pub06_Seabird_numbers2005.pdf (accessed 19 November 2014).

Mavor, R.A., Parsons, M., Heubeck, M. & Schmitt, S. 2008. Seabird numbers and breeding success in Britain and Ireland, 2006. UK Nature Conservation No. 31. Peterborough, UK: Joint Nature Conservation Committee. Online. http://jncc.defra.gov.uk/PDF/pub08_seabirdnos_2006.pdf (accessed 19 November 2014).

Mitchell, P.I., Newton, S.F., Ratcliffe, N. & Dunn, T.E. 2004. *Seabird Populations of Britain and Ireland*. London: Poyser.

Murray, S., Harris, M.P. & Wanless, S. in press. The Bass Rock—now the world's largest northern gannet colony. *British Birds*.

Please update publication information for Murray et al. in press.

Newell, M., Harris, M.P., Burthe, S., Wanless, S. & Daunt, F. 2013. Isle of May seabird studies in 2011. JNCC Report, No. 475g. Peterborough, UK: Joint Nature Conservation Committee.

Nisbet, I.C.T., Winchell, J.M. & Heise, A.E. 1984. Influence of age on the breeding biology of Common Terns. *Colonial Waterbirds* **7**, 117–126.

O'Brien, T.D., Li, W.K.W. & Morán, X.A.G. (eds). 2012. ICES Phytoplankton and microbial plankton status report 2009/2010. ICES Cooperative Research Report No. 313. Copenhagen: International Council for the Exploration of the Seas.

O'Brien, T.D., Wiebe, P.H. & Falkenhaug, T. (eds). 2013. ICES zooplankton status report 2010/2011. ICES Cooperative Research Report No. 318. Copenhagen: International Council for the Exploration of the Seas.

O'Donald, P. 1983. *The Arctic Skua: A Study of the Ecology and Evolution of a Seabird*. Cambridge, UK: Cambridge University Press.

Okill, D. 1989. Breeding success of Shetland's seabirds: red-throated diver, fulmar, gannet, cormorant and shag. In *Seabirds and Sandeels: Proceedings of a Seminar Held in Lerwick, Shetland, 15–16 October 1988*, M. Heubeck (ed.). Shetland Bird Club, 6–11.

Provide publisher's city and country for Okill 1989.

Okill, J.D. 1994. Ringing recoveries of red-throated divers *Gavia stellata* in Britain and Ireland. *Ringing & Migration* **15**, 107–118.

Olsson, O., Nilsson, T. & Fransson, T. 2000. Long-term study of mortality in the common guillemot in the Baltic Sea: analysis of 80 years of ringing data. Rapport Naturvårdsverket, 5057. Stockholm: Swedish Environmental Protection Agency.

Oro, D. & Furness, R.W. 2002. Influences of food availability and predation on survival of kittiwakes. *Ecology* **83**, 2516–2528.

Oswald, S.A., Bearhop, S., Furness, R.W., Huntley, B. & Hamer, K.C. 2008. Heat stress in a high-latitude seabird: effects of temperature and food supply on bathing and nest attendance of great skuas. *Journal of Avian Biology* **39**, 163–169.

Oswald, S.A., Huntley, B., Collingham, Y.C., Russell, D.J.F., Anderson, B.J., Arnold, J.M., Furness, R.W. & Hamer, K.C. 2011. Physiological effects of climate on distributions of endothermic species. *Journal of Biogeography* **38**, 430–438.

Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* **14**, 483–488.

Payne, M.R., Hatfield, E.M.C., Dickey-Collas, M., Falkenhaug, T., Gallego, A., Gröger, J., Licandro, P., Llope, M., Munk, P., Röckmann, C., Schmidt, J.O. & Nash, R.D.M. 2009. Recruitment in a changing environment: the 2000s North Sea herring recruitment failure. *ICES Journal of Marine Science* **66**, 272–277.

Payne, M.R., Ross, S.D., Clausen, L.W., Munk, P., Mosegaard, H. & Nash, R.D.M. 2013. Recruitment decline in North Sea herring is accompanied by reduced larval growth rates. *Marine Ecology Progress Series* **489**, 197–211.

Pearson, R.G. & Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* **12**, 361–371.

Perry, A.L., Low, P.J., Ellis, J.R. & Reynolds, J.D. 2005. Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–1915.

Pinaud, D. & Weimerskirch, H. 2002. Ultimate and proximate factors affecting the breeding performance of a marine top-predator. *Oikos* **99**, 141–150.

Pitois, S.G., Lynam, C.P., Jansen, T., Halliday, N. & Edwards, M. 2012. Bottom-up effects of climate on fish populations: data from the Continuous Plankton Recorder. *Marine Ecology Progress Series* **456**, 169–186.

Polis, G.A., Sears, A.L.W., Huxel, G.R., Strong, D.R. & Maron, J. 2000. When is a trophic cascade a trophic cascade? *Trends in Ecology & Evolution* **15**, 473–475.

Potts, G.R., Coulson, J.C. & Deans, I.R. 1980. Population dynamics and breeding success of the shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. *Journal of Animal Ecology* **49**, 465–484.

Poulard, J.-C. & Blanchard, F. 2005. The impact of climate change on the fish community structure of the eastern continental shelf of the Bay of Biscay. *ICES Journal of Marine Science* **62**, 1463–1443.

Prévot-Julliard, A.-C., Lebreton, J.-D. & Pradel, R. 1998. Re-evaluation of adult survival of black-headed gulls (*Larus ridibundus*) in presence of recapture heterogeneity. *The Auk* **115**, 85–95.

Proctor, R., Wright, P.J. & Everitt, A. 1998. Modelling the transport of larval sandeels on the north west European shelf. *Fisheries Oceanography* **7**, 347–354.

Ratcliffe, N., Catry, P., Hamer, K.C., Klomp, N.I. & Furness, R.W. 2002. The effect of age and year on the survival of breeding adult great skuas *Catharacta skua* in Shetland. *Ibis* **144**, 384–392.

Ratcliffe, N., Newton, S., Morrison, P., Merne, O., Cadwallender, T. & Frederiksen, M. 2008. Adult survival and breeding dispersal of roseate terns within the northwest European metapopulation. *Waterbirds* **31**, 320–329.

Reed, T.E., Wanless, S., Harris, M.P., Frederiksen, M., Kruuk, L.E.B. & Cunningham, E.J.A. 2006. Responding to environmental change: plastic responses vary little in a synchronous breeder. *Proceedings of the Royal Society of London B* **273**, 2713–2719.

Reeves, S.A. 1994. Seasonal and annual variation in catchability of sandeels at Shetland. ICES CM D:19. Copenhagen: International Council for the Exploration of the Sea.

Reid, P.C., de Fatima Borges, M. & Svendsen, E. 2001. A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. *Fisheries Research* **50**, 163–171.

Reid, P.C., Edwards, M., Hunt, H.G. & Warner, A.J. 1998. Phytoplankton change in the North Atlantic. *Nature* **391**, 546.

Reygondeau, G. & Beaugrand, G. 2011. Future climate-driven shifts in distribution of *Calanus finmarchicus*. *Global Change Biology* **17**, 756–766.

Reynolds, T.J., Harris, M.P., King, R., Swann, R.L., Jardine, D.C., Frederiksen, M. & Wanless, S. 2011. Among-colony synchrony in the survival of common guillemots *Uria aalge* reflects shared wintering areas. *Ibis* **153**, 818–831.

Richardson, A.J. & Schoeman, D.S. 2004. Climate impacts on plankton ecosystems in the northeast Atlantic. *Science* **305**, 1609–1612.

Rindorf, A., Wanless, S. & Harris, M.P. 2000. Effects of sandeel availability on the reproductive output of seabirds. *Marine Ecology Progress Series* **202**, 241–252.

Robinson, R.A. 2005. BirdFacts: profiles of birds occurring in Britain & Ireland. BTO Research Report No. 407. Thetford, Norfolk, UK: British Trust for Ornithology. Online. http://www.bto.org/birdfacts (accessed 28 October 2014).

Robinson, R.A. 2010. Estimating age-specific survival rates from historical ringing data. *Ibis* **152**, 651–653.

Russell, D.J.F., Wanless, S., Collingham, Y.C., Anderson, B.J., Beale, C., Reid, J.B., Huntley, B. & Hamer, K.C. 2014. Beyond climate envelopes: bio-climate modelling accords with observed 25-year changes in seabird populations of the British Isles. *Diversity and Distributions*, doi: 10.1111/ddi.12272

Sæther, B.-E. & Bakke, Ø. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**, 642–653.

Sætre, R., Toresen, R., Søiland, H. & Fossum, P. 2002. The Norwegian spring-spawning herring—spawning, larval drift and larval retention. *Sarsia* **87**, 167–178.

Sandvik, B. 2009. World borders dataset. Online. http://thematicmapping.org/downloads/world_borders.php (accessed 7 November 2014).

Sandvik, H., Erikstad, K.E., Barrett, R.T. & Yoccoz, N.G. 2005. The effect of climate on adult survival in five species of North Atlantic seabirds. *Journal of Animal Ecology* **74**, 817–831.

Schwartzlose, R.A., Alheit, J., Bakun, A., Baumgartner, T.R., Cloete, R., Crawford, R.J.M., Fletcher, W.J., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, S.E., MacCall, A.D., Matsuura, Y., Nevárez-Martínez, M.O., Parrish, R.H., Roy, C., Serra, R., Shust, K.V., Ward, M.N. & Zuzunaga, J.Z. 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. *South African Journal of Marine Science* **21**, 289–347.

Scott, B.E., Sharples, J., Wanless, S., Ross, O., 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 *Top Predators in Marine Ecosystems: Their Role in Monitoring and Management*, I. Boyd et al. (eds). Cambridge, UK: Cambridge University Press, 46–62.

Scott, D.A. 1970. *The breeding biology of the storm petrel*. DPhil thesis, University of Oxford, UK.

Scottish Natural Heritage 2009. Classification of marine extensions to 31 existing seabird Special Protection Areas (SPAs). Inverness, UK: Scottish Natural Heritage. Online. http://www.snh.org.uk/about/directives/ab-dir15j.asp (accessed 18 November 2014).

Simpson, S.D., Jennings, S., Johnson, M.P., Blanchard, J., Schön, P.-J., Sims, D.W. & Genner, M.J. 2011. Continental shelf-wide response of a fish assemblage to rapid warming of the sea. *Current Biology* **21**, 1565–1570.

Smout, S., Rindorf, A., Wanless, S., Daunt, F., Harris, M.P. & Matthiopoulos, J. 2013. Seabirds maintain offspring provisioning rate despite fluctuations in prey abundance: a multi-species functional response for guillemots in the North Sea. *Journal of Applied Ecology* **50**, 1071–1079.

Snow, D.W. & Perrins, C.M. 1998. *The Birds of the Western Palearctic. Concise Edition*. Oxford, UK: Oxford University Press.

Spendelow, J.A. 1991. Postfledging survival and recruitment of known-origin roseate terns (*Sterna dougallii*) at Falkner Island, Connecticut. *Colonial Waterbirds* **14**, 108–115.

Tavecchia, G., Baccetti, N. & Serra, L. 2006. Modelling survival and movement probability of little tern *Sterna albifrons* at a post-breeding moulting site: the effect of the colony of origin. In *Waterbirds Around the World*, G.C. Boere et al. (eds). Edinburgh: Stationery Office, 560–561.

Thaxter, C., Lascelles, B., Sugar, K., Cook, A.S., Roos, S., Bolton, M., Langston, R. & Burton, N.H. 2012. Seabird foraging ranges as a preliminary tool for identifying candidate marine protected areas. *Biological Conservation* **156**, 53–61.

Thompson, K.R. 1987. *The ecology of the Manx shearwater* Puffinus puffinus *on Rhum, West Scotland*. PhD thesis, University of Glasgow, UK.

van Damme, C.J.G. & Couperus, A.S. 2008. Mass occurrence of snake pipefish: result of a change in climate? *Journal of Sea Research* **60**, 117–125.

van Deurs, M., Hal, R.V., Tomczak, M.T., Jónasdóttir, S.H. & Dolmer, P. 2009. Recruitment of lesser sandeel *Ammodytes marinus* in relation to density dependence and zooplankton composition. *Marine Ecology Progress Series* **381**, 249–258.

van Deurs, M., Hartvig, M. & Steffensen, J.F. 2011. Critical threshold size for overwintering sandeels (*Ammodytes marinus*). *Marine Biology* **158**, 2755–2764.

van Deurs, M., Koski, M. & Rindorf, A. 2014. Does copepod size determine food consumption of particulate feeding fish? *ICES Journal of Marine Science* **71**, 35–43.

Votier, S.C., Bearhop, S., Crane, J.E., Arcos, J.M. & Furness, R.W. 2007. Seabird predation by great skuas *Stercorarius skua*—intra-specific competition for food? *Journal of Avian Biology* **38**, 234–246.

Votier, S.C., Furness, R.W., Bearhop, S., Crane, J.E., Caldow, R.W.G., Catry, P., Ensor, K., Hamer, K.C., Hudson, A.V., Kalmbach, E., Klomp, N.I., Pfeiffer, S., Phillips, R.A., Prieto, I. & Thompson, D.R. 2004. Changes in fisheries discard rates and seabird communities. *Nature* **427**, 727–730.

Votier, S.C., Hatchwell, B.J., Beckerman, A., McCleery, R.H., Hunter, F.M., Trinder, M. & Birkhead, T.R. 2005. Oil pollution and climate have wide-scale impacts on seabird demographics. *Ecology Letters* **8**, 1157–1164.

Wanless, S., Frederiksen, M., Harris, M.P. & Freeman, S.N. 2006. Survival of gannets *Morus bassanus* in Britain and Ireland, 1959–2002. *Bird Study* **53**, 79–85.

Wanless, S. & Harris, M.P. 2012. Scottish seabirds—past, present & future. *Scottish Birds* **32**, 38–45.

Wanless, S., Harris, M.P., Calladine, J. & Rothery, P. 1996. Modelling responses of herring gull and lesser black backed gull populations to reduction of reproductive output: implications for control measures. *Journal of Applied Ecology* **33**, 1420–1432.

Wanless, S., Harris, M.P. & Greenstreet, S.P.R. 1998. Summer sandeel consumption by seabirds breeding in the Firth of Forth, south-east Scotland. *ICES Journal of Marine Science* **55**, 1141–1151.

Wanless, S., Harris, M.P., Redman, P. & Speakman, J. 2005a. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series* **294**, 1–8.

Wanless, S., Murray, S. & Harris, M.P. 2005b. The status of northern gannet in Britain & Ireland in 2003/04. *British Birds* **98**, 280–294.

Wanless, S., Wright, P.J., Harris, M.P. & Elston, D.A. 2004. Evidence for decrease in size of lesser sandeels *Ammodytes marinus* in a North Sea aggregation over a 30-yr period. *Marine Ecology Progress Series* **279**, 237–246.

Wilson, L.J., Daunt, F. & Wanless, S. 2004. Self-feeding and chick-provisioning diet differ in the common guillemot *Uria aalge*. *Ardea* **92**, 197–208.

Winslade, P. 1974. Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt) III. The effect of temperature on activity and the environmental control of the annual cycle of activity. *Journal of Fish Biology* **6**, 587–599.

Wright, P. & Bailey, M.C. 1993. Biology of sandeels in the vicinity of seabird colonies at Shetland. Fisheries Research Services Report, 15/93. Aberdeen, UK: Scottish Office Agriculture and Fisheries Department Marine Laboratory. Online. http://www.scotland.gov.uk/uploads/documents/15-93.pdf (accessed 19 November 2014).

Wright, P.J. & Bailey, M.C. 1996. Timing of hatching in *Ammodytes marinus* from Shetland waters and its significance to early growth and survivorship. *Marine Biology* **126**, 143–152.

Wright, P.J., Jensen, H. & Tuck, I. 2000. The influence of sediment type on the distribution of the lesser sandeel, *Ammodytes marinus*. *Journal of Sea Research* **44**, 243–256.