CHAPTER 7

Marine birds and climate fluctuation in the North Atlantic

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7.1 Introduction: seabirds and their food web

Very few studies have directly assessed the relationship between climate and population performance in seabirds in general, and North Atlantic seabirds in particular. Nevertheless, there are many data from diverse sources that provide insights into the likely impact of climate variations upon these species. Most of these studies have been conducted over relatively short, recent timescales, being based on direct observations of bird populations over the last century or so. Nevertheless, paleoecological studies of penguin populations have illustrated that longer-term changes in abundance, occurring over a period of 3000 years, may also be related to climate variation (Sun *et al*. 2000). In this chapter we summarize—and synthesize—what currently is known about the ecological effects of climate fluctuation on seabirds in the North Atlantic region.

Any effects of climate on these species are likely to occur through two main processes: either directly through physiological effects or indirectly through an influence on prey availability (see Chapter 1). Direct physiological effects include metabolic processes during key stages of the life cycle such as reproduction and moult. Variations in the physical environment may also affect feeding rate or competition for food resources through changes in either energetic requirements or food availability. Such effects may be seen as a modification by the climate of the threshold level in energy necessary to carry out particular life-history activities (cf. Stearns 1992). For example, there is an important energy trade-off between reproductive investment and maintenance (cf. Williams 1966; Stearns 1992).

The fact that their prey includes a wide variety of organisms, each with populations that may fluctuate in response to climatic change, means that we must also consider indirect effects through changes in food availability. Because seabirds are found at higher trophic levels and may take prey from various levels, their relationship with climate becomes even more complex. For example, an ambient temperature that is favourable for both seabirds and their main prey, might at the same time be unfavourable for the prey's primary food resources. Consequently, such a temperature might be globally unfavourable for the bird because of the reduction in the availability of its own prey. Therefore, the relationship between seabirds and climate will be complicated by the biology of the lower members of the food web. In this context, oceanographic factors (e.g. water temperature and currents) and large-scale climatic and hydrographic processes (e.g. the North Atlantic Oscillation (NAO)) generate variation in the production, distribution and abundance of organisms upon which birds feed (Chapters 4–6).

In the following, we show how climate might influence seabirds directly through variations in temperature and wind. We also provide an overview of the potential indirect impact of climate variability on North Atlantic seabird populations. First, however, we briefly describe key features of seabird biology that are relevant for an improved understanding of the nature of such climatic effects.

## 7.2 Seabird biology: breeding on land, feeding at sea

Several bird species depend upon marine food resources at some point in their annual cycle. These include species from orders such as Gaviiformes, Podicipediformes, and Anseriformes. However, here our main focus will be on birds that are completely dependent on the marine environment; the seabirds. Seabirds are represented by only four orders (as compared to around twentyeight orders for terrestrial birds). In the Northern Hemisphere, only three orders of seabirds are found: the Charadriiformes, Procellariiformes, and Pelecaniformes. Each of these orders has specific adaptations, but all depend upon the sea for their food resources.

Seabirds have in general low fertility. Many species lay only one egg per year (Jouventin and Mougin 1981) and in some species reproduction does not occur every year (Jouventin and Mougin 1981; Weimerskirch 2001). On the other hand, this low birth rate is compensated for by high longevity (review in Weimerskirch 2001). Hence, since most seabirds cannot adjust clutch size in response to food supply, they have less flexibility in their breeding response to environmental fluctuation than terrestrial birds. Long-lived species tend to adjust their expenditure on parental care to balance benefits to the offspring against costs to the parents, thus maximizing individual fitness (Williams 1966; Erikstad et al. 1998; Weimerskirch et al. 2000b). Therefore, even if climatic variation does not have a profound effect on adult survival rate, it might have important effects on fledging success. However, since many of these species typically delay reproduction until they are between 2 and 9 years old (Jouventin and Mougin 1981), and in albatrosses the age of first breeding can even reach extreme values of 13 years (Marchant and Higgins 1990), it may take several years for such effects of climate variation on population size to become apparent (Thompson and Ollason 2001).

Seabirds are typically not constrained to a central place (Lack 1968; Ashmole 1971; Prince et al. 1992; Weimerskirch et al. 1993), and they can therefore often overcome to a large extent the problem of environmental variability. Their great mobility allows them to exploit locally and ephemerally favourable conditions and resources over great distances. However, during the breeding season, seabirds are typical central-place foragers, tied to a breeding site on land and foraging for marine resources. During foraging trips many seabirds regularly traverse hundreds or thousands of kilometres within a period of days (Harrington 1977; Stahl et al. 1985; Jouventin and Weimerskirch 1990; Flint 1991). A major constraint on breeding for seabirds is the distance between the breeding grounds on land and the feeding zones at sea (Weimerskirch and Cherel 1998). The distance of foraging is limited by the need to incubate egg(s) or to rear chick(s), neither of which can usually be left alone for long periods. For many species, suitable breeding sites are limited, and the dependence of birds to foraging areas around these sites increases the effects of temporal variation in environmental conditions within flying distance around the nest-site. During the chick growth period, adults must make frequent visits to the nest in order to feed the young, even if both parents normally share the task of incubation and rearing the young. Making foraging trips at a frequent rhythm to feed their chick adds an additional energy constraint upon the parents through fasting. Some species have even evolved a dual strategy for these feeding trips, within which adults alternate short trips to feed their chick with a long trip during which they increase their body mass (Fig. 7.1; Weimerskirch et al. 1997a,b, 1999; Weimerskirch and Cherel 1998; Catard et al. 2000; Dearborn 2001; Watanuki et al. 2001). On average, birds conduct one long foraging trip followed by two short trips, with the duration of the long trip depending on the need to increase body mass and replenish the body reserves during the chick rearing period (Catard et al. 2000; Dearborn 2001).

In the Northern Hemisphere, foraging distances from breeding colonies are typically smaller than in the Southern Hemisphere (Hunt et al. 1999). Northern seabirds usually forage within 200 km
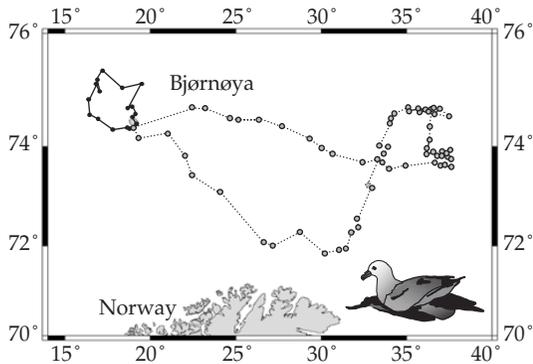
Figure 7.1 Two foraging trips (short and long) during the late brooding period of a female northern fulmar (*F. glacialis*) breeding at Bjørnøya (adapted from Weimerskirch *et al*. 2001).

from their colonies. This is, first, because available breeding sites are spread more evenly through suitable near-shore foraging areas in the north. Second, prey availability differs between the two hemispheres, with more invertebrate prey in the southern oceans. Consequently, the long-distance forager species (mainly Procellariiformes) are more represented in the Southern Hemisphere. For example, the short-tailed shearwater *Puffinus tenuirostris* may feed more than 2000 km away from their breeding colony during the chick-rearing period (Klomp and Schultz 1998; Nicholls *et al*. 1998). Despite its extreme foraging range, this shearwater is still able to provision its chicks at a sufficient rate by using the two-fold strategy that alternates long and short feeding trips.

The long foraging trips of these seabirds appear to result from the need to obtain prey from patchy oceanic resources. Seabirds take a wide variety of prey, but they typically favour small pelagic schooling fishes, moderately sized pelagic crustaceans, and squid from the upper- and mid-water column (Montevecchi and Myers 1996; Garthe 1997). Oceanographic features (such as fronts, pycnoclines) may concentrate these prey species and provide for seabirds a spatially and temporally predictable food supply (Hunt 1990; Schneider 1990; Begg and Reid 1997; Mehlum *et al*. 1998) explaining why they forage preferentially at such physical conditions (Hunt and Schneider 1987; Begg and Reid 1997; Hunt *et al*. 1999; Hoefer 2000; Skov and Durinck 2000).

7.3 Direct influences of climate on seabirds

Reproductive characteristics, such as clutch size or timing of breeding, are typically related to latitude (Olsen and Marples 1993; Sanz 1999)—partly through climatic conditions. In the North Atlantic, few studies have been conducted on the influence of climate on seabird biology (Table 7.1). However, data from more general studies of seabird ecology together with findings from the more detailed studies conducted in the Pacific (Schreiber 2001) provide valuable insight on how climate variability may influence energetic costs, reproductive output, and mortality rates in these species.

7.3.1 Reproduction

Birds require much resources to produce eggs, and the quality of the produced eggs may affect the survival of chicks (Carey 1996). Obtaining resources for egg production may be particularly difficult when other factors constrain the timing of the breeding season (Perrins 1996), implying that birds must obtain the necessary resources by a certain date. Consequently, the timing of breeding itself is often dependent upon food availability, meaning that laying date is (by-and-large) correlated to the natural changes in food resources (Meijer and Drent 1999).

During incubation, the adult uses part of its energy reserves to maintain the egg(s) at the optimal temperature for embryonic development, a temperature usually ranging from 36 °C to 38 °C (see Stoleson and Beissinger 1999); if the egg's temperature drops below 24–27 °C (physiological zero), embryo development is halted. Excessive exposure to temperatures between this physiological zero and normal incubation temperature (i.e. on average 24–36 °C) can lead to abnormal development or the death of the embryo. Consequently, decreases in ambient temperature may lead either to an increase in the transfer of heat between the adult and the egg, resulting in higher energy costs of incubation, and/or a decrease in hatching success (Williams 1996). During incubation, adults must support both the cost of incubation and their own metabolic needs, either by leaving the egg to go foraging, or by drawing upon their body reserves with fasting that could last several months in the extreme cases of the emperor penguin (*Aptenodytes forsteri*:

Table 7.1 Relationships between climate variability and some seabirds species in the North Atlantic

Species	Climate variable(s)	Population parameter(s)	Observed effect	Ref.
Arctic tern (*Sterna paradisaea*)	Salinity	Sea distribution	−	1
Atlantic puffin (*F. arctica*)	SST	Hatch + Fldg + Brd. S.	none	2
		Laying date	+	3
	Sea temperature	Fldg. S.	+	4
Black-baked gull (*L. marinus*)	SST	Hatch + Fldg + Brd. S.	+	2
Black-headed gull (*L. ridibundus*)	Salinity	Sea distribution	−	1
Common guillemot (*U. aalga*)	SST, salinity	Sea distribution	+	1, 5
	Stormy conditions	Foraging cost	+	6
	SST	Hatch + Fldg + Brd. S.	none	2
	SST	Laying date	−	7
	Air temperature	Fledging date	−	8
Common gull (*Larus canus*)	Salinity	Sea distribution	−	1
Common tern (*Sterna hirundo*)	Salinity	Sea distribution	−	1
Herring gull (*L. argentatus*)	Salinity	Sea distribution	−	1
	SST	Hatch + Fldg + Brd. S.	+	2
Black-legged kittiwake	SST, salinity	Sea distribution	+/none	1, 5
(*R. tridactyla*)	SST	Hatch + Fldg + Brd. S.	+	2
Leach's storm petrel	SST	Hatch + Fldg + Brd. S.	none	2
(*O. leucorhoa*)				
Manx shearwater (*P. puffinus*)	SST, salinity	Sea distribution	+	5
Northern fulmar (*F. glacialis*)	SST, salinity	Sea distribution	+	1, 5
	Wind speed	FMR	−	9
	NAO, air temp	Hatch + Fldg. S.	−/+	10
Northern gannet (*Sula bassana*)	SST	Breeding density	+	11
Razorbill (*Alca torda*)	SST	Sea distribution	+	5
	SST	Laying date	−	12
European shag (*P. aristotelis*)	Wind	Laying date	+	13

SST = sea surface temperature; Hatch + Fldg + Brd. S. = hatching success, fledging success and breeding success; FMR = Field metabolic rate; NAO = North Atlantic Oscillation.
+ means that an increase in the value of the climate variable is correlated to an increase of the population parameter.
*References*: 1. Garthe 1997; 2. Regehr and Rodway 1999; 3. Harris *et al*. 1998; 4. Durant *et al*. 2003, 5. Begg and Reid 1997, 6. Finney *et al*. 1999, 7. Harris and Wanless 1988, 8. Hedgren 1979, 9. Furness and Bryant 1996, 10. Thompson and Ollason 2001, 11. Montevecchi and Myers 1997, 12. Harris and Wanless 1989, 13. Aebischer and Wanless 1992.

Le Maho 1977). In either case, reductions in ambient temperature will result in an increased energy cost for re-warming the egg (Williams 1996).

Chick growth rate and fledging mass are sometimes directly correlated with survival up to breeding age (Chastel *et al*. 1993; Croxall *et al*. 1988). Brief periods of low food availability can be overcome by using stored fat (Ricklefs and Schew 1994), but longer periods may result in slower growth. In a long-term study of Atlantic puffin (*Fratercula arctica*), a general sigmoidal avian growth curve (Ricklefs 1968, 1973) differed between years (Anker-Nilssen and Aarvak 2002). Higher asymptote was generally observed in years when food delivery to the chick was greatest, and chicks, in turn, had higher fledging success (Fig. 7.2); the influence of food supply on chick growth rates was later verified experimentally (Øyan and Anker-Nilssen 1996; Cook and Hamer 1997). However, several factors may explain differences in chick provisioning rates. The availability of the birds' primary prey is the more likely factor, but the presence of alternative prey and the distance to foraging areas may also influence parental effort (Erikstad *et al*. 1998).

A central issue in life history is how animals balance their investment in young against their
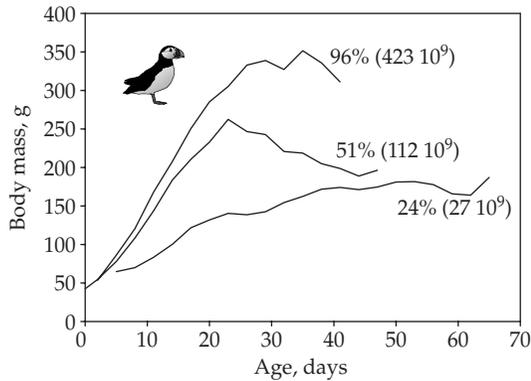
Figure 7.2 Mean body mass in relation to age of Atlantic puffin chicks (*F. arctica*) in Røst, North Norway during three different years. For each year, their fledging success (in percent) and the abundance (numbers in parentheses) of their main prey, the first-year herring, are indicated (adapted from Anker-Nilssen and Aarvak 2002).

own chances to survive and reproduce in the future (Stearns 1992). The long-lived seabirds are presumably less likely to increase their effort when raising young to ensure that they do not jeopardize their own survival. It has even been suggested that these long-lived species have evolved a fixed level of investment in their young in order to maximize their own survival (Sæther *et al*. 1993). Thus, they may be adjusting their feeding effort in relation to both their own body condition and to the short-term needs of the chicks (Erikstad *et al*. 1997). In years of poor feeding conditions, birds can reduce their parental effort so as to sustain themselves, resulting in a lower food supply for the chick, delayed growth (Øyan and Anker-Nilssen 1996) and potentially a lower chick survival. Indeed, the chances of a chick surviving to breed appears to be maximized if the chick reaches a high asymptotic mass during growth (Weimerskirch *et al*. 2000b). This suggests that climatic variation may have a stronger influence on breeding success and recruitment rate than on adult survival, particularly as these climatic effects are likely to be primarily linked to food availability (Cairns 1987, 1992). Thus, only the more drastic climatic events are likely to have clear effects on adults (see below), although the impact of those events influencing adult survival are expected to have the stronger influence on population dynamics.

7.3.2 Mortality

Direct evidence of increased adult mortality caused by environmental conditions is rare for seabirds. This may largely be due to the difficulty in determining the weather conditions that seabirds experience while they are at sea (assessments of the influence of weather on adult mortality are restricted to periods when they are on land). Consequently, in the absence of any obvious pathology, adult mass mortality is typically attributed to starvation. However, the cause of the starvation could be either the absence of prey or the inaccessibility of prey due to bad weather. For example, in 1983, 30,000 auks washed ashore from the North Sea following a series of storms (Harris and Wanless 1984). Conversely, in the Gulf of Alaska large numbers of common guillemots (*Uria aalge*) were found dead in 1993, apparently having died from starvation most probably due to the offshore unavailability of food (Piatt and van Pelt 1997). In the southeast Bering Sea, hundreds of thousands of emaciated short-tailed shearwaters died in 1997—a phenomenon quite likely due to long-term climatic changes (Baduini *et al*. 2001). These climatic effects could either be severe weather that hampered foraging, or anomalous oceanographic conditions that change the distribution and abundance of prey (Harris and Wanless 1996; Piatt and van Pelt 1997). For example, the highest numbers of seabird carcasses found along the central California coast between 1980–86 occurred during years of strong El Niño (Bodkin and Jameson 1991).

For chick mortality the relationship with weather conditions is more easily observed. The tendency for more extreme storms, or variations in prevailing wind conditions, may also have direct effect on the populations by increasing egg loss or chick mortality. For instance, heavy rain during chick period resulted in chicks dying of exposure when birds' feeding is disrupted in European shag (*Phalacrocorax aristotelis*) in the Cies Islands (NW Spain; Velando *et al*. 1999). Similarly, a severe gale at Isle of May, Scotland destroyed 49% of exposed European shag nests. This event forced the adults to rebuild their nest and lay a replacement clutch (Aebischer 1993). Burrow-nesting species, on the other hand, typically suffer nest loss during heavy rain after flooding and subsequent erosion (Warham 1990; Rodway *et al*. 1998). In general, such extreme weather will primarily affect birds nesting in the lower-quality nest-sites, and hence mostly affect the less-experienced birds (Coulson 1968).

7.3.3 Energetics

Birds are endothermic animals that maintain a constant core temperature by utilizing ingested or stored energy reserves. The thermoneutral zone (TNZ) is the range of temperatures between which the metabolism is not affected by temperature changes (Schmidt-Nielssen 1997). Whenever ambient temperature is outside a bird's TNZ, the bird experiences a thermoregulatory response that results in an increase in energy use. Ambient temperatures can vary over a very wide range in the North Atlantic, and seabirds are therefore often faced with environmental temperatures outside their TNZ (Dawson and O'Connor 1996). This is particularly so, for species making deep dives to catch their prey as sea temperature decrease with depth (Fig. 7.3; Koudil *et al*. 2000). However, over a typical annual cycle, sea-surface temperature (SST) generally varies much less than air temperature. Consequently, birds may respond behaviourally to extreme bouts of very hot or very cold air temperatures by remaining in contact with seawater, thus reducing the cost of thermoregulation.

The thermoregulatory response to a decrease in temperature has been demonstrated by measuring an increase in the field metabolic rate (FMR); the organism's daily energy expenditure measured in the field (Schmidt-Nielssen 1997; Ellis and Gabrielsen 2001). The maintenance of core temperatures through thermogenesis requires energy substrate deriving either directly from an increased food intake or from the utilization of body reserves. Opportunities to increase foraging effort may therefore be crucial

during periods of cold or wet weather. Incubation causes additional energetic costs due to the exchange of heat between their brood patch and the egg(s). When ambient temperature falls below the TNZ, incubation behaviour may increase adult metabolic rates by 19–50% compared to nonincubating birds. In seabirds, the metabolic rate during incubation is 1.2 times the basal metabolic rate (BMR) (Williams 1996). Furthermore, if eggs are left unattended, or when parents exchange incubation duties in very cold conditions, the subsequent re-warming of egg has additional energetic costs (Williams 1996; Schmidt-Nielssen 1997). During the chick-rearing period there may also be a marked increase in field metabolic rate, with the FMR/BMR-ratio varying from 1.8 to 4.8 (Ellis and Gabrielsen 2001). All stages of reproduction are certainly energetically stressful for seabirds, and poor weather conditions may further increase these costs. Obviously the availability of suitable prey within range of breeding colonies is very important during these critical periods.

Seabird chicks are highly dependent upon adults for the delivery of food required for their development. Young chicks may also be brooded by their parents to reduce thermoregulatory costs. More typically, however, the long distances between breeding colonies and foraging areas mean that chicks are left alone while adults forage at sea. The length of time that chicks are left alone will differ between species and sites, but may also vary in relation to climate-driven variation in the location of prey or of the cost of travel (see below). Chicks left alone in this way must confront the problem of heat loss which, again, may vary in extent due to
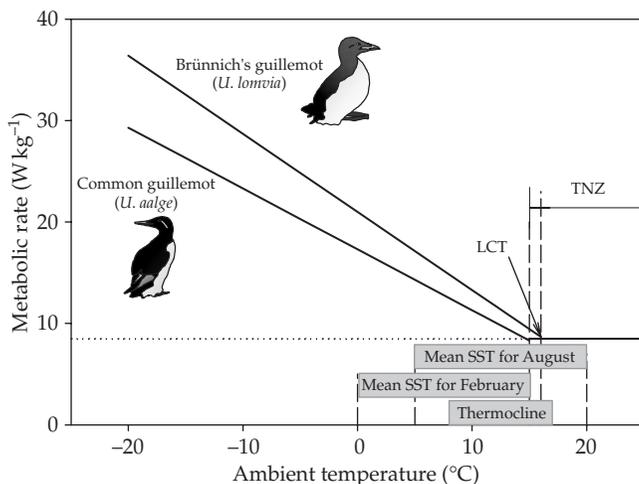

Figure 7.3 The influence of ambient temperature on the metabolic rate (MR) in two seabirds. The lower critical temperature (LCT) is the temperature under which the bird has to increase its metabolism to maintain its body temperature. LCT is the lower limit of the TNZ. Both seabirds are diving in water that changes in function of the season and latitude in North Atlantic (SST = sea surface temperature). Moreover, they are able to dive as deep as 200 m and are confronted to a thermocline; here average range for temperate water (adapted from Croll and McLaren 1993).

Note: TNZ could be very broad for polar species such as the Ivory gull (*Pagophila eburnea*) in which MR does not increase until −30 °C.

variations in ambient temperature, wind speed, and precipitation (Konarzewski and Taylor 1989). Nestlings may maintain high body temperatures in cold environments through plumage insulation, particular behaviours such as huddling, and thermoregulation. However, since the clutch size in seabirds is typically small, benefits from huddling does not occur except for penguins forming crèches. Consequently, chicks often have to rely on their own capacity to thermoregulate, which therefore may drain crucial energy that could otherwise be used for growth. Compared to adults, chicks also have a higher surface-to-volume ratio, which is less favourable for heat conservation (Visser 1998), and their underdeveloped muscles contribute little to heat production by thermogenesis (Hohtola and Visser 1998). Hence, changes of ambient temperature may have a strong impact on chick's energy budget. The type of nest site may moderate this problem, with the protection afforded by cavity-nesting reducing the chick's energetic costs compared to open-nesting (Martin and Li 1992). In addition, the cavity-nesters' chicks tend to grow slower than the open-nesters' and thus require relatively less food per day, which in turn can decrease the daily parental effort in foraging and nest protection (Martin and Li 1992).

Studies on several species (e.g. Manx shearwater, *Puffinus puffinus*: Harris 1966; Atlantic puffins: Anker-Nilssen 1987; Øyan and Anker-Nilssen 1996; and yellow-eyed penguin, *Megadytes antipodes*: van Heezik 1990) suggest that developing chicks faced with food shortages allocate resources preferentially to certain body parts. For instance, the rapid development of thermogenic tissue is especially important for chicks. Periods of bad weather preventing adults from foraging may then have an important effect on the chick's development and survival (Fig. 7.4(a); see also below). In Atlantic puffins, this relationship between the chick's development and climate is illustrated by a threshold value for mean sea temperature (Fig. 7.4(b)), below which there is no fledging. However, this relationship may be explained as a result of an indirect effect on food supply as well as by the expected direct effect of temperature on the chick's metabolism (Williams 1996; Anker-Nilssen and Aarvak 2002).

Climatic fluctuation could also directly influence seabirds by influencing the cost of flight which, in turn, leads to variations in the cost of foraging. There are considerable differences in the style of flight between different groups of seabirds, with
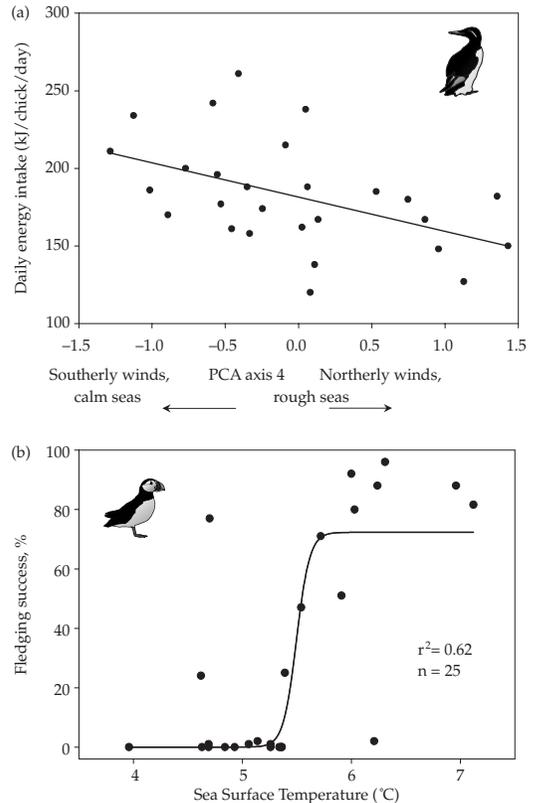
Figure 7.4 Relationship between reproduction and climate: (a) Relationship between mean daily energy intake of young common guillemots (*U. aalge*) on the Isle of May and the most important explanatory weather covariate (data from all-day watches carried out between 1983 and 1997). During stormy weather, the mean energy value of loads and the proportion of chicks attended are reduced indicating a decrease in the foraging efficiency (Finney *et al*. 1999). (b) Relationship between fledging success of Atlantic puffin chicks (*F. arctica*) in Røst in 1975–2001 (Anker-Nilssen and Aarvak 2002) and mean sea temperature at 0–75 m depth from March to July (G. Ottersen, IMR, Bergen, personal communication). A logistic regression curve is fitted to the data set ($F_{2,24} = 21.40$, $P < 0.0001$, Durant *et al*. 2003).

the two extremes being gliding and flapping. Variations in wind speed may profoundly affect the cost of flight (Furness and Bryant 1996) but the extent of this influence depends upon the flight style (Spear and Ainley 1997). For example, birds relying on flapping will be disadvantaged when the wind is strong, whereas the effect will be the opposite for gliding species (Furness and Bryant 1996; Finney *et al*. 1999). For example, the northern fulmar (*Fulmarus glacialis*) has a high at-sea FMR

during low wind speeds because it uses gliding flight extensively during foraging (Furness and Bryant 1996). As a consequence, the lack of wind might limit the breeding range of this and other Procellariiformes species. In contrast, flapping species such as black-legged kittiwake (*Rissa tridactyla*) and the little auk (*Alle alle*) have been shown to have higher FMR during periods of strong wind (Gabrielsen *et al*. 1987). Similarly, Hodum *et al*. (1998) found that high FMR typically is due to the high cost of flight and pursuit diving in the pelagic feeding Cassin's auklet (*Ptychramphus aleuticus*).

As one of the major features of climatic fluctuation is the variation of wind speeds and direction, suggesting an important influence upon foraging energetics. Furthermore, such influences may affect different members of the seabird community in different ways. As such, changes in climatic conditions could affect the strength of both inter- and intraspecific competition. Gliding species with low flight costs can forage at great distances from breeding colonies (Weimerskirch *et al*. 2000a) and in areas of low productivity (Ballance *et al*. 1997). During periods of low productivity, flight proficiency becomes increasingly important because only species with relatively low flight costs may be able to move between prey patches (Ballance *et al*. 1997). Changes of climatic conditions may therefore influence both population distributions and competitive interactions between different seabirds.

7.4 Indirect influences of climate on seabirds

Seabird populations are typically more likely to be affected by climate variation indirectly rather than directly, through changes in the availability of key habitats or prey (cf. Schreiber 2001). For instance, climate change may create new, or redistribute existing, feeding areas for Arctic seabirds by melting the high-Arctic ice pack (Brown 1991). Alternatively, there may be changes in breeding site availability or quality through sea-level change or variations in the frequency of extreme storm events. Variations in temperature may also affect the extent of sea ice, which has been shown to influence the mode and cost of travelling between breeding and foraging areas in incubating emperor penguins (Williams 1995; Barbrand and Weinershirch 2001; Croxall *et al*. 2002).

Changes in prey availability have been shown to influence several key demographic parameters, even

if most studies have focussed upon variations in reproductive success (e.g. Martin 1987; Barrett and Krasnov 1996). For example, successful reproduction in several seabirds in the northwest Atlantic is related to the availability and timing of the inshore movements of the capelin (Montevecchi and Myers 1996). One of the earliest studies to link variations in climate to such a relationship between prey availability and reproductive success in North Atlantic seabirds was carried out by Aebischer *et al*. (1990) and documenting parallel long-term trends in weather conditions, prey abundance, and breeding performance of North Sea kittiwakes. This indirect role of climate variation has later been suggested through several studies. For example, in years when the arrival of capelin (*Mallotus villosus*) in Newfoundland is delayed, hatching, fledging, and breeding success of kittiwake, herring gull (*Larus argenteus*) and great black-baked gull (*Larus marinus*) are reduced (Regehr and Rodway 1999). Such delayed capelin arrival was explained by an anomalously cold SST resulting in a delay of one month of the spawning migration of the capelin (Nakashima 1996). Data on the Atlantic puffins of Røst, North Norway show a threshold relationship between food resources (first-year herring, *Clupea harengus*) and fledging success (Anker-Nilssen 1992; Anker-Nilssen and Aarvak 2002; Durant *et al*. 2003) such that there is complete breeding failure when prey abundance is below a certain level. The Norwegian spring-spawning stock of herring has experimented great fluctuations during the twentieth century (Toresen and Østvedt 2000, Chapter 6); presumably to a large extent as a response to changes in ocean climate.

These examples may be explained by the match/mismatch of food availability and requirement (Cushing 1990; see also Chapter 1). If herring availability does not match the Atlantic puffin's requirements at the time of rearing, it produces a dramatic reduction in chick survival (Anker-Nilssen 1992; Anker-Nilssen and Aarvak 2002; Durant *et al*. 2003). Even during years of high herring productivity, a too early puffin's breeding relative to the growth and migration of its main prey, would render the prey unavailable for the chick rearing. This mismatch can thus be considered both in terms of timing and abundance. Changes in climatic conditions between the period when the birds assess the environmental quality prior to laying and the actual time of chick rearing could modify food availability creating a mismatch.

As discussed above, foraging seabirds select habitats where prey are more predictably concentrated and more easily captured. For seabirds, the choice of such foraging habitats is especially important since prey densities are low in many oceanic areas, and prey may remain at inaccessible depths. In both the horizontal and vertical dimensions, then, seabirds must focus their foraging activities in areas where prey interact with different processes to produce predictably located concentrations in near-surface waters. In some cases, such concentrations may be a result of the interactions with other predators (e.g. where the foraging activities of sub-surface predators enhance the surface availability of prey for shallow diving seabirds; Ballance and Pitman 1999). In other cases, however, prey concentrations occur where physical processes produce either areas of high productivity, or aggregations of prey.

Obviously, changes in ocean climate may thus influence seabird prey availability by affecting timing, location or strength of these oceanographic features. Recent attempts to understand the potential indirect impacts of climate variation on seabirds have therefore explored relationships between these oceanographic features and the birds' distribution and demographic parameters. In the following, we address the potential effects on seabirds by changes in SSTs, frontal systems and larger-scale proxies of ocean climate.

7.4.1 The influence of SST on seabirds

The abundances and assemblages of seabirds are influenced by short- and long-term changes in SST (Veit *et al*. 1996, 1997; Guinet *et al*. 1998). For example, in the Antarctic, the blue-petrel (*Halobaena caerulea*) breeding performance is reduced if their body condition is lowered as a result of a high SST during the preceding winter. Similarly, in the Pacific Ocean there is a coupling between seabird reproduction and ocean temperature (Ainley *et al*. 1994, 1996; Veit *et al*. 1996) leading to poorer reproductive performance during warm-water years for inshore species such as the sooty shearwater (*Puffinus griseus*) and increase for offshore species such as the Leach's storm petrel (*Oceanodroma leucorhoa*; Veit *et al*. 1996). This implies that a long-term increase of the SST certainly could result in a decrease in the abundance of some seabirds (Veit *et al*. 1996). Although such links are now being described for more systems, the causal relationships between SST and reproductive success are less clear in many of the sea-bird

systems. Nevertheless, some work does point to potential links through known effects of temperature on key prey populations. During the early 1990s, cold-water events in the northwest Atlantic appear to have inhibited migratory pelagic species such as mackerel (*Scomber scombrus*) and squid (*Illex illecebrosus*) from moving into the region (Montevecchi and Myers 1997). As the distance to food supply is a main factor influencing seabird reproduction, this in turn created a major shift in the pelagic food webs (Montevecchi and Myers 1997). As a consequence, there were profound negative effects on the reproductive success of surface-feeding birds such as black-legged kittiwakes (Regehr and Montevecchi 1997). This highlights that a slight change in oceanographic conditions, possibly associated with climate change, might have a large-scale and profound effect on seabird population. This indirect effect of SST on seabirds through changes in their prey resources is also seen in the Atlantic puffin. At the puffin colonies in Røst, fledging success is related to both sea temperature and food availability, both factors being correlated (Durant *et al*. 2003). Here, the lower sea temperatures affect the population of the main prey for the seabird, creating a mismatch between the Atlantic puffins' energy requirements and their food availability. However, this influence is quite complex since changes in SST do affect different species in different ways (Fig. 7.5). Warm-sea temperatures tend to decrease the plankton productivity, but low temperatures may also negatively affect fish growth (Chapter 6), potentially having effects thousand of kilometres from the seabirds' breeding colonies (Montevecchi and Myers 1997). Depending upon the birds' feeding biology (planktivorous or piscivorous) changes in the SST may have a variety of effects. For example, the reproductive success of planktivorous auklets in northwest Pacific (*Aethia cristatella* and *Cyclorhinchus psittacula*) is negatively correlated with SST, whereas for piscivorous puffins (*Lunda cirrhata* and *Fratercula corniculata*) it is positively correlated (Kitaysky and Golubova 2000).

7.4.2 Fronts, currents and seabirds

Oceanographic features such as fronts at the boundaries of water masses, ice edges, and currents that interact with bathymetry may all concentrate prey. The mixing of water masses at these features creates conditions that support all the members of the food web. Frontal systems support enhanced stocks of phytoplankton, zooplankton, fish, and seabirds
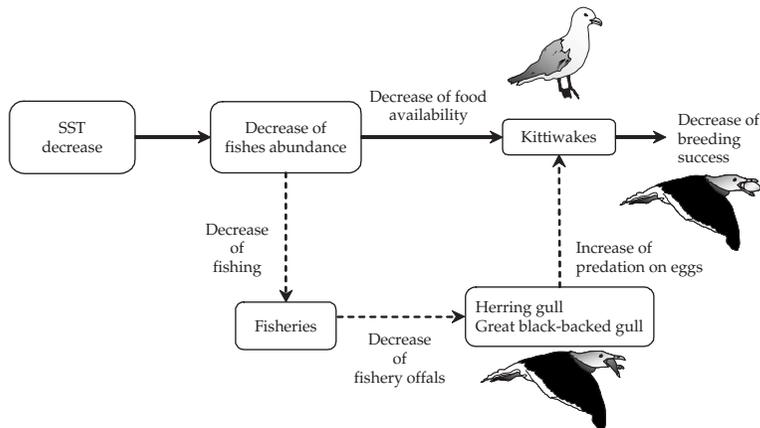
Figure 7.5 Interactive and synergic effect. The decrease of the SST has a double negative effect on kittiwakes (*R. tridactyla*) trough the decrease of the food supply and the increase of nest predation by gulls (*L. argentatus* and *L. marinus*; adapted from Regehr and Montevecchi 1997).

(Kinder *et al*. 1983; Coyle and Cooney 1993; Decker and Hunt 1996). As a consequence, seabird populations are associated with these physical features (Hunt 1990; Schneider 1990); for example, the distribution of Antarctic and sub-Antarctic seabirds is closely linked to the polar front and sub-Antarctic front (Hunt 1991; Guinet *et al*. 1997; Ainley *et al*. 1998; Charrassin and Bost 2001). The abundance and the success of the reproduction of these seabirds are intimately linked to the extent of the sea-ice (Hunt 1991; Barbraud *et al*. 2000; Barbraud and Weimerskirch 2001; Croxall *et al*. 2002) and to the changes of winter temperature that influence ice formation (Barbraud and Weimerskirch 2001). In the North Atlantic we may expect similar phenomena, and several frontal systems within the Irish Sea and North Sea appear to provide predictable resources for seabirds (Begg and Reid 1997; Hunt *et al*. 1999; Skov and Durinck 2000). However, such fronts may only be formed seasonally and can be subject to variations in response to wind-induced mixing (Allen *et al*. 1980). Usually, the influence of hydrography on seabird distribution is through variations in surface salinity, transparency and thermal stratification. For example, fulmar (and to some extent common guillemot) occurrence is correlated with highly saline, thermally stratified water with high-water clarity—all characteristics of their main prey habitat (Garthe 1997). In the northwest Atlantic, seabird populations off Newfoundland are linked to sea currents, and variations in the

strength of the Gulf Stream may influence the migration of the pelagic prey (Montevecchi and Myers 1995).

7.4.3 Large-scale influences on seabirds

In the Southern Hemisphere and the Pacific, changes in seabird populations have been well-studied in relationship to large-scale climatic phenomena (reviewed in Schreiber 2001) where El-Niño-Southern Oscillation (ENSO) influences wind and sea currents which may lead to important changes in temperature, precipitation, and food resources. This phenomenon can affect birds all around the world, as illustrated by the black-throated blue warbler (*Dendroica caerulescens*), a North American migratory passerine whose demographic rates varied in relation to the ENSO (Sillett *et al*. 2000). For seabirds, ENSO may reduce both breeding success and adult survival. During the most severe cases of ENSO, many adult seabirds can die due to the disappearance of their food sources, affecting both population size and population structure (Schreiber and Schreiber 1984; Duffy 1990; Piatt and van Pelt 1997; Bertram *et al*. 2000). ENSO seems to affect conditions during the breeding season in many seabirds species (Croxall 1992; McGowan *et al*. 1998). In the Galapagos penguin (*Spheniscus mendiculus*), it has been reported that body condition is related to the ENSO events, with a deterioration in body condition during ENSO leading to a reduced
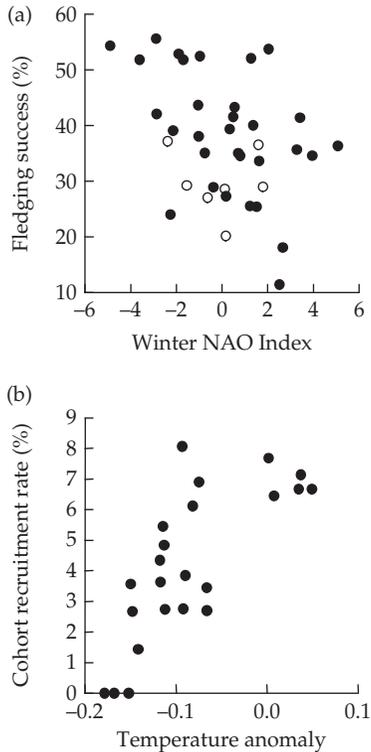
Figure 7.6 Variation in (a) the percentage of northern fulmars (*F. glacialis*) nests producing fledglings in relation to the NAO index for the winter before the breeding season (1952–95) and (b) the effect of the temperature on the percentage of each cohort of chicks (1958–80) that recruits to the colony. The recruitment rate for different cohorts of chicks is significantly related to anomalies in Northern Hemisphere growing season temperatures (Thompson and Ollason 2001).

in the NAO have been related to variability in biological populations (Ottersen *et al.* 2001; Stenseth *et al.* 2002). Reported effects of the NAO on the abundance of zooplankton (Chapters 4 and 5) and key fish prey (Chapter 6) suggest that the NAO may influence the dynamics of seabird populations, but it is only recently that studies have started to explore these relationships. Nevertheless, there is evidence that the winter NAO influences both the probability of breeding and subsequent reproductive success in the northern fulmar (Thompson and Ollason 2001). Furthermore, cohort recruitment rates at this Scottish colony were related to temperature anomalies in the birds' first year (Fig. 7.6), highlighting the potential for further research that explores the relationships between these different large-scale proxies of climate variation and seabird population dynamics.

7.5 Conclusion

Effect of climate change on seabird populations may take many years to become apparent (Thompson and Ollason 2001). Its effect is complex and involves a large number of physical and biological processes. To understand the true mechanisms it is often necessary to conduct a deep, thorough ecological study of the food web and its many different relationships with the environment. However, an overall pattern of the response of seabirds to climate begins to appear and very interesting interdisciplinary studies are becoming more and more common. Seabirds are sensible to climate change either positively as shown by the extension of the fulmar population or negatively as shown by the Atlantic puffins. Thanks to their position as top predators, their response to climate change is a good index of its effect on the whole food web. In order to improve our scientific understanding of what might happen under various scenarios of global change, the study of seabird populations could be of great value.

breeding success (Boersma 1978) and a decline of the population (Boersma 1998).

In the Atlantic Ocean, an equivalent phenomenon to the ENSO is the NAO. The impacts of the NAO appear less extreme (and less clear) than the mass mortalities associated with ENSO, and it is only since the mid-1990s that temporal patterns

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