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Climatic variation: effects on global seabird populations

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Introduction

The general scientific consensus is that the Earth's climate is warming and since the 1970s has been warming at a greater rate than at any time in the last thousand years (IPCC I and II 2001). This has generated concern about the resultant biological and ecological changes affecting the range and distribution of species, their phenology and physiology, the cycles, composition, and interactions of communities and the structure and dynamics of ecosystems (Walther *et al.* 2002). Apex marine predators such as seabirds can provide an effective insight on the consequences of environmental and climatic variability on ecosystems (Jenouvrier *et al.* 2003) and as such, allow for effective monitoring, management and conservation of both individual populations and entire ecosystems.

Seabirds have distinctive life history characteristics which make them dramatically different from most land birds e.g. Passerines (Schreiber and Burger 2002). Low birth rates combined with high longevity leads to less flexibility in population level responses to environmental fluctuations (Durant *et al.* 2004). Nevertheless, despite the fact that seabird populations tend to vary little over time, there is evidence that they are affected by changes in the marine environment. Stenseth *et al.* 2002, Drinkwater *et al.* 2003 and Ottersen *et al.* 2001 have previously described the effects of large scale climatic variability on marine ecosystems including extensive studies on the effects of El Niño on ecosystems (Glynn 1988, Oedekoven 2001, Schreiber 2002, Stenseth *et al.* 2003) and, in the Northern Hemisphere, it has been shown that climatic fluctuations associated with the North Atlantic Oscillation (NAO) index have important consequences on seabird populations (Hurrell and Van Loon 1997, Drinkwater 2003, Durant *et al.* 2004). These systems are associated with periodic shifts in wind patterns, which in turn affect ocean mixing and sea surface temperature (SST) trends (Irons *et al.* 2008).

This review will identify and outline four dominant climatic systems and describe associated environmental factors including discussion of subsequent effects that they have on global seabird populations. Finally, the review will highlight studies which have investigated how environmental variations affect key behavioural adaptations of seabirds and the consequent effects on their life history traits.

Direct Effects of Climatic Variation

Effects of weather can be long term (over hundreds of years) or short term (a passing storm) (Schreiber 2002). Direct effects are generally physiological and cause direct mortality e.g. increased wind/precipitation and thermal stress. For instance, Durant *et al.* (2004) noted that excessive exposure to temperature during incubation can lead to abnormal development or even death. Additionally, decreases in ambient temperature may lead to an increase in heat transfer between the adult and egg requiring higher energy costs for hatching success (Schreiber 2002). Increases in wind and precipitation can affect feeding rates through changes in energetic requirements for food availability. Furthermore, increased wind/precipitation can cause flooding of nests which can alter or completely demolish nesting habitats, particularly those belonging to burrowing species (petrels, shearwaters) which are commonly lost to flooding or collapse from subsequent erosion (Schreiber 2002). Leach's Petrels (*Oceanodroma leucorhoa*) excavate cavities to nest and in order to avoid large predatory birds e.g. gulls. This makes them highly susceptible to collapse and land slide activity in the event of particularly heavy precipitation (Ainley *et al.* 1990).

Indirect Effects of Climatic Variation

Indirect effects generally influence prey availability (Schreiber 2002). The relationship between seabird populations and climate is often mediated via bottom-up effects with changes to the prey base cascading up to higher trophic level predators (Frederiksen *et al.* 2006). Nevertheless, these multiple trophic linkages mean that it may be problematic to study the effects of global change. Important changes include not only the availability of prey, but also factors that influence the ability to locate prey as well as the costs of catching and transporting food (due to changes in fish or krill distribution and decreased visibility of prey). For instance, Elkins (1995) suggested that terns may have a higher catch rate per day with a moderate level of wind but when wind levels get too high, it often becomes difficult to dive as accurately. Consequently, elevated wind levels instigate deeper swimming by fish, making them both less visible and accessible. Other effects include timing of the breeding season, clutch size, reproductive success, chick growth and adult and chick survival (Schreiber 2002). Durant *et al.* (2004) said 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)". Subsequently, Sandvik *et al.* (2005) found that environmental variables accounted for a substantial proportion of the variation in adult survival in four alcid species.

Key Climate Systems

El Niño Southern Oscillation (ENSO)

El Niño Southern Oscillation (ENSO) refers to the interaction between local oceanographic and atmospheric conditions that intermittently modify large-scale atmospheric pressure systems, wind systems, rainfall, ocean currents and sea level (Glynn 1988). Fluctuations in tropical Pacific sea surface temperature (SST) are related to the occurrence of El Niño, during which the equatorial surface waters warm considerably sometimes to an extent that disappearances in fish and even the collapse of the food chain can occur (Stenseth *et al.* 2003). These events occur every two to seven years and the intensity of the consequences and duration can vary (Schreiber 2002). Although the effects are most pronounced in the south-east Pacific Ocean, they are often experienced in other parts of the Pacific, Southern Ocean, Indian Ocean and southern Atlantic (Sandvik *et al.* 2005). During El Niño years, the productivity of the euphotic zone rapidly declines with subsequent negative effects on the survival and reproduction of populations at higher trophic levels (Glynn 1988). The effects can be catastrophic and during the most severe cases many seabirds die due to disappearance of their food sources (Durant *et al.* 2004).

During an El Niño event, the north-west Atlantic experiences colder than normal sea surface temperatures which influence the timing, movement and availability of pelagic fish and squid to seabirds. Herring, associated with colder temperatures, become an important prey item for Northern Gannets (*Morus bassanus*) as the availability of mackerel decreases during some ENSOs (Montevecchi and Myers 1997). Additionally, in the Bering Sea, unusually high SSTs were thought to have caused a shift in the vertical distribution of euphausiids in the water column, affecting the time of spawning and ultimately decreasing the abundance of this key prey species making them less available for colonies of Short-tailed Shearwaters (*Puffinus tenuirostris*). As a consequence, the mass mortality of thousands of migratory birds was observed (Baduini *et al.* 2001). Mass seabird mortalities along the coast of South Africa have also been shown to coincide with ENSO events (Duffy 1990).

Raymond *et al.* (2010) noted that oceanic winds were broad determinants of foraging distribution and that productive upwellings associated with oceanic processes were highly important. Following an ENSO event which strongly affected Christmas Island in 1982, numbers of various species of petrel, shearwater, terns, boobies, tropic and frigate birds were observed to decline. These seabirds characteristically feed on small fish and squid and the diminished primary and secondary productivity around the island caused reproductive failures and the mortality of many juvenile birds. Furthermore, many birds actually abandoned their breeding ground (Glynn 1988).

Pacific Decadal Oscillation (PDO)

The Pacific Decadal Oscillation is a dominant element of the north Pacific sea surface temperature variability distinguishable from ENSO events by its length (typically twenty to thirty years) and the regions affected (predominantly the North Pacific and the tropics) (Mantua and Hare 2002). This system is poorly investigated, lacking long term study and has only recently been defined (within the past few decades). However, it is still obvious that systems which show long term climate anomalies and can last for one to several decades demonstrate considerable impacts on marine ecosystems (Mantua and Hare 2002). In the north Pacific, for instance, it was found that survival rate of Least Auklets (*Aethia pusilla*) responded continuously with variation in climate and oceanography (Jones *et al.* 2002).

Arctic and Antarctic Oscillations

The Arctic and Antarctic Oscillations are the leading modes of climate variability in the highest latitudes (Fyfe *et al.* 1999). Some of the strongest and most compelling indications of global climate warming have come from Polar Regions (Croxall *et al.* 2002), especially the Antarctic, where significant increases in air temperature and widespread melting of ice shelves have been observed (Vaughan *et al.* 2001). It could be assumed then that biological responses here would be amplified in the highest levels of the food chain. Croxall *et al.* (2002) found that adult survival in Emperor Penguins showed a strong positive correlation with year of extensive sea ice and a strong negative correlation during years with warmer sea surface temperatures.

The North Atlantic Oscillation Index (NAO)

The North Atlantic Oscillation (NAO) index is a north–south alternation in atmospheric mass between the subtropical Atlantic and the Arctic (Stenseth *et al.* 2003). From the 1940s until the early 1970s, the NAO index displayed a downward trend. This period was marked by European wintertime temperatures that were recurrently lower than normal. A sudden reversal has occurred over the past 25 years and, since 1980, the NAO has remained in a highly-positive phase (Hurrell and Van Loon 1997), during which prevailing westerly winds strengthened, moving northwards to bring increased temperatures and precipitation over northern Europe and south-eastern USA, (*figure 1*) (Stenseth *et al.* 2003).

The variability of the NAO is shown to influence abundance, biomass, distribution, species assemblages, growth rates, and survival rates (Drinkwater *et al.* 2003). The effects of the NAO are generally arbitrated through local changes in the physical environment (i.e. wind speed and direction, ocean and air temperatures, precipitation and circulation patterns). Significant changes in SST and heat content, ocean currents and related heat transport, and sea-ice cover in the Arctic and sub-Arctic regions are also generated by changes in the NAO (Stenseth *et al.* 2003). However, Sandvik *et al.* (2005) looked at the NAO index and SST as opposing variables, and found that SST tended to account for more

variation (54%) in adult survival of the Common Guillemot (*Uria aalge*) than the NAO.

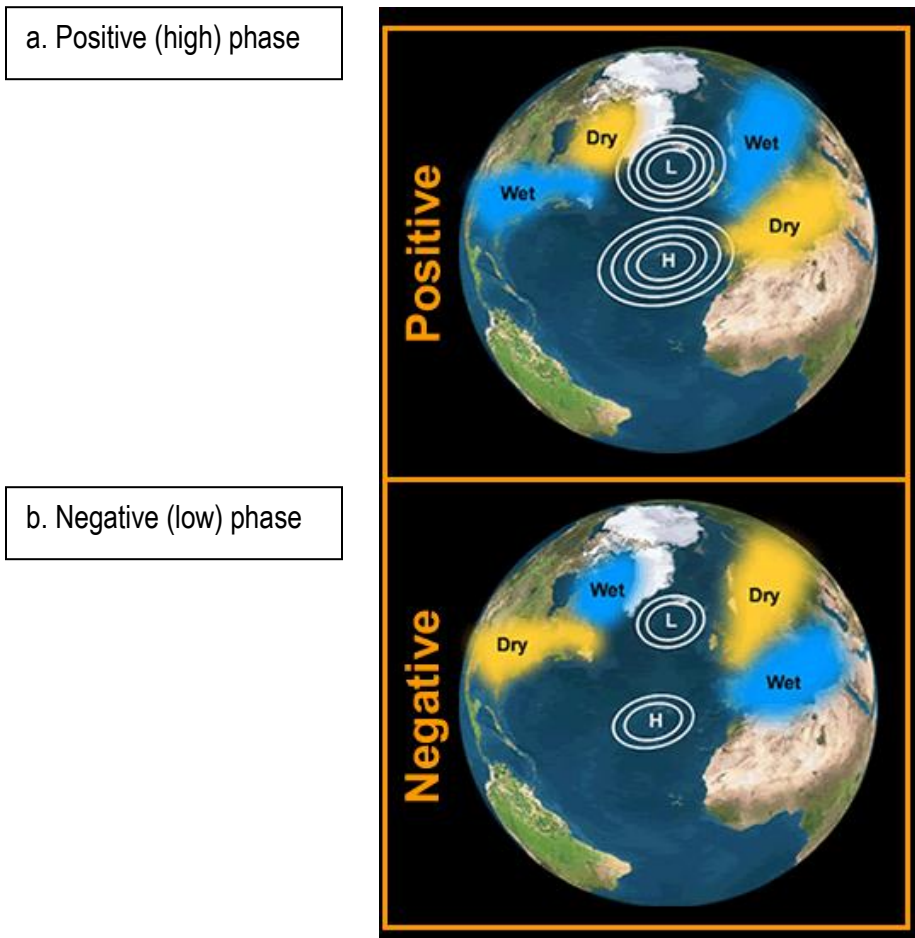


Figure 1: Image Source: University Corporation for Atmospheric Research (UCAR) via <http://www.windows2universe.org/earth/climate/nao.html>

- (a) During positive (high) phases of the NAO index, the prevailing westerly winds are stronger and move northwards causing increased precipitation and temperatures over northern Europe and south-eastern USA and dry anomalies in the Mediterranean region.
(b) Approximately opposite conditions occur during the negative (low) index phase

The NAO index is also known to affect the abundance and distribution of phytoplankton through advection and temperature changes (Drinkwater *et al.* 2003). This can have important consequences on higher trophic levels. For instance, the index is known to influence the dynamics and composition of several north Atlantic communities within the food chain upon which fulmars rely (Thompson and Ollason 2001). Fromentin and Planque (1996) observed a significant influence of the NAO on two *Calanus* species in the North Atlantic and the North Sea. Fluctuations in abundance of these two major prey zooplankton

was found to be directly related to variations in the NAO index. This would suggest marked subsequent effects on higher trophic levels.

Climatic Variation: Effects on behaviour

Foraging Behaviour and Prey Availability

Seabirds have evolved in a stochastic environment where environmental and oceanographic processes are unpredictable; as such seabird communities have developed substantial diversity in feeding behaviour and form. This includes pelagic surface-feeders (e.g. petrels (*Procellariiformes*)), coastal surface-feeders (e.g. terns (*Sternidae*)), coastal omnivores (gulls (*Laridae*)), benthic-feeders (cormorants (*Phalacrocoracidae*)), and specialised pursuit-divers (auks (*Alcidae*)) (Barrett *et al.* 2006). Foraging seabirds select habitats where prey is more predictable and more easily captured (Durant *et al.* 2004) as their highly vagile nature allows them to exploit favourable conditions for breeding and survival (Hedenström 1993). Raymond *et al.* (2010) found that the long distance foraging activity of Sooty Shearwater's (*Puffinus griseus*) was associated with areas of elevated prey availability.

Small pelagic fish (such as herring and anchovies) are widespread and key prey species for seabirds. They respond dramatically and quickly to changes in ocean climate and as such, are highly variable in abundance (Alheit and Niquen 2004). Oceanographic phenomena have been shown to concentrate prey for seabirds over both spatial and temporal scales (Shealer 2002). Availability of prey can be affected by environmental variation and consequently, type and frequency of prey caught can be affected. Monaghan *et al.* (1989) compared a successful (Coquet Island) and unsuccessful (Shetland) breeding colony of Arctic Terns (*Sterna paradisaea*). They found that males in Shetland brought larger fish to their mates than the birds on Coquet. However, Coquet Terns brought more energy-rich fish, made more foraging trips per hour and rate of energy transfer to their mates was also higher. This, in conjunction with the poor breeding success of the Shetland Terns (a factor attributed to Drent and Daan (1980) "optimal working capacity" theory) was suggested to have been caused by low sandeel abundance, changes in which may have been due to variations in local climate (delayed migration etc.) In contrast, Finney *et al.* (1999) found no evidence to suggest that the rate that prey was brought in by the Common Guillemot (*Uria aalge*) in south-east Scotland was affected by environmental conditions; however the type of prey delivered was affected in stormy weather. Data on dive behaviour in this study also suggested that birds were working harder when conditions were undesirable with the number of dives in a bout (hence the amount of time spent underwater) increased significantly and the interval between consecutive bouts decreased significantly. They concluded that if the current climate change prediction proves correct (i.e. increased intensity/frequency of storms), this could result in clear energetic costs for Common Guillemots in terms of foraging for adults and reduced energy intake for chicks.

Changes in temperature patterns (associated with the NAO) have also been found to affect direct predator-prey interactions. Bogstad and Gjørseter (1994) described an increase in the basic metabolic rate of cod associated with higher temperatures during years of high NAO values. This was found to result in increased rates of consumption of capelin by 100,000 tonnes per degree centigrade. Consequently, capelin available to seabirds prey was reduced and thus less abundant in the diets of many Atlantic and Arctic seabird species. Aebischer *et al.* (1990) also found that a delayed arrival of capelin due to colder than normal SSTs in the North Sea during negative NAO phases resulted in a one month migratory delay of the Kittiwake Gull. Similarly, Montevecchi and Myers (1996) also observed the effect of temperature on north-west Atlantic mackerel, an inhibited migratory pelagic species, which subsequently had negative effects on the reproductive success of surface feeding birds such as the Black-legged Kittiwake (*Rissa tridactyla*). This indirect effect of SST on key prey species has also been recorded in the Atlantic Puffin (*Fratercula arctica*) in Røst. Durant *et al.* (2003) found that sea temperature and food availability were correlated with fledging success and as such, the lower temperatures recorded affected the abundance of the population of the Norwegian Herring, their main source of prey. As a result, there were clear inconsistencies between the Atlantic Puffins' energy requirements and the actual availability of their food. Additionally, Irons *et al.* (2008) studied two congeneric species of Arctic seabird, the Thick-billed (*Uria lomvia*) and Common Murre (*Uria aalge*), during changes in sea surface temperature associated with climate shifts (associated with the Arctic Oscillation). They concluded that Thick-billed Murres foraged successfully in colder waters, whilst the foraging range of the Common Murre was generally in warmer waters. They surmised that relatively large climate shifts, irrespective of direction, may have negative consequences on Murre populations.

Flight: Energetic Consequences of Climatic Variation

Global climate warming is attributed to causing the intensity and frequency of storms to increase (IPCC I and II 2001). Flight is affected by variations in wind speed and direction (Spear and Ainley 1997, Durant *et al.* 2004), the cost of which depends on flight style (i.e. flapping vs. gliding). However, due to the difficulties associated with observing seabirds whilst at sea, few studies have been carried out.

Jouventin and Weimerskirch (1990) observed that Wandering albatrosses often sit on the sea in wait of higher wind levels to avoid the cost of flapping flight during calm periods. However, Furness and Bryant (1996) noted that Northern Fulmars (*Fulmarus glacialis*) could not take the "sit and wait" approach, instead suffering the increased cost of flight in low winds, a factor which may limit their breeding range and perhaps explain why birds spent more time at the nest during calm weather. Variations in winter colony attendance could also be attributed to the birds taking the opportunity to sit on the cliffs when lack of wind makes foraging more expensive, and so less profitable. Red-footed Boobies (*Sula sula*) and Great Frigatebirds (*Fregata minor*) also roost during low winds further

implying the increased costs of flight in low winds and suggesting diminished food availability (upwelling could potentially be reduced) (Schreiber and Chovan 1986).

Breeding Responses

Similarly, few studies have examined the direct relationship between climate and population performance; most recent papers instead model the likely impacts (Jenouvrier *et al.* 2003, Rolland *et al.* 2009, Rolland *et al.* 2010). For instance, Thompson and Grosbois (2002) found that variations in the winter NAO index were shown to influence both the probability that adults would breed in any particular year, and their subsequent success in fledging a chick. Both the probability of breeding and breeding success were highest in those years when the NAO was in its negative phase. However, Jenouvrier *et al.* (2003) studied Southern Fulmars (*Fulmarus glacialoides*) in Antarctica and reported a correlation between diminished breeding performance and low sea ice concentration. Breeding rate was variable which indicated a “strong environmental force on the decision to breed”. Adult survival also decreased in years with high SST and low sea ice concentration. Similarly, Trinder *et al.* (2009) studied the effects of climatic variation on the reproductive success of barnacle geese; the results of this study showed that weather conditions can influence the reproductive success of migratory populations, with wind speed and direction during northward migration having a significant effect on breeding performance. Additionally, Guinet *et al.* (1998) reported that episodes of warm SST associated with El Niño events can affect the breeding performances of Blue Petrels (*Halobaena caerulea*) as warm water anomalies reach their foraging grounds, inhibiting abundance of prey populations. Croxall *et al.* (2002) also found that breeding success of Snow Petrels (*Pagodroma nivea*) and body condition of fledglings were correlated strongly to higher levels of sea ice.

Thompson and Ollason (2001) found that the environmental changes associated with the NAO index influenced the breeding probability and ensuing reproductive success in Northern Fulmars (*Fulmarus glacialis*). A statistically significant negative relationship was found between the proportion of breeding adult fulmars present on Eynhallow each summer and the NAO index. Additionally, the success of summer fledging and summer hatching were both negatively correlated with the previous winter’s NAO index (Thompson and Ollason 2001). Breeding numbers were also found to have a significant relationship with the NAO for several species including fulmars, herring gulls (*Larus argentatus*), lesser black-backed gulls (*Larus fuscus*), common gulls (*Larus canus*), black-headed gulls (*Chroicocephalus ridibundus*), kittiwakes, sandwich terns (*Sterna sandvicensis*), guillemots and razorbill (*Alca torda*).

Individual species response to weather events can also differ. Shaffer *et al.* (2001) found that sexual segregation can occur in Wandering albatrosses (*Diomedea exulans*) in foraging zones due to differences in wing loading. Males

(with 12% greater wing loading than females) were found to feed in areas with highest wind levels.

Conclusions and implications for research

This review has highlighted that the effects of climatic/environmental variation on seabirds are not easy to quantify, and each study uses different life history characteristics as proxies for measuring these effects e.g. Durant *et al.* (2003) uses breeding success; Sandvik *et al.* (2005) uses adult survival. As such, it was difficult to view the studies alongside one another, as the measurements all varied. However, it was remarkably apparent that changing local and large-scale environmental factors were generally all having a negative effect on seabird populations, a significant accomplishment considering the range of morphological and physiological adaptations that have evolved over various seabird species.

It is also worth noting the quantity of published studies based on climatic variation and its effect on foraging/feeding and social responses (perhaps due to the ease of studying these behaviours; foraging/feeding can be viewed from land or boats and breeding/social responses can be observed easily in colonies) in comparison to flight. The studies which *have* been carried out on flight and its energetic costs in variable environmental conditions are often limited; the vast distances undertaken by most seabird individuals appear to make studying flight in volatile and constantly changing environmental conditions much more of a challenge. Thus, considering the major role of flight in any seabird's life, and the great importance it holds for survival, I feel further studies into this topic and the influence of changing global climate need to be implemented. It will be from ongoing research into this relatively limited field of study that we will gain an appreciation of the wide scale effects of climate variability on seabird populations as a dynamic community and expand upon the knowledge of their ecological important enabling us to identify the extent to which conservation and management are required.

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