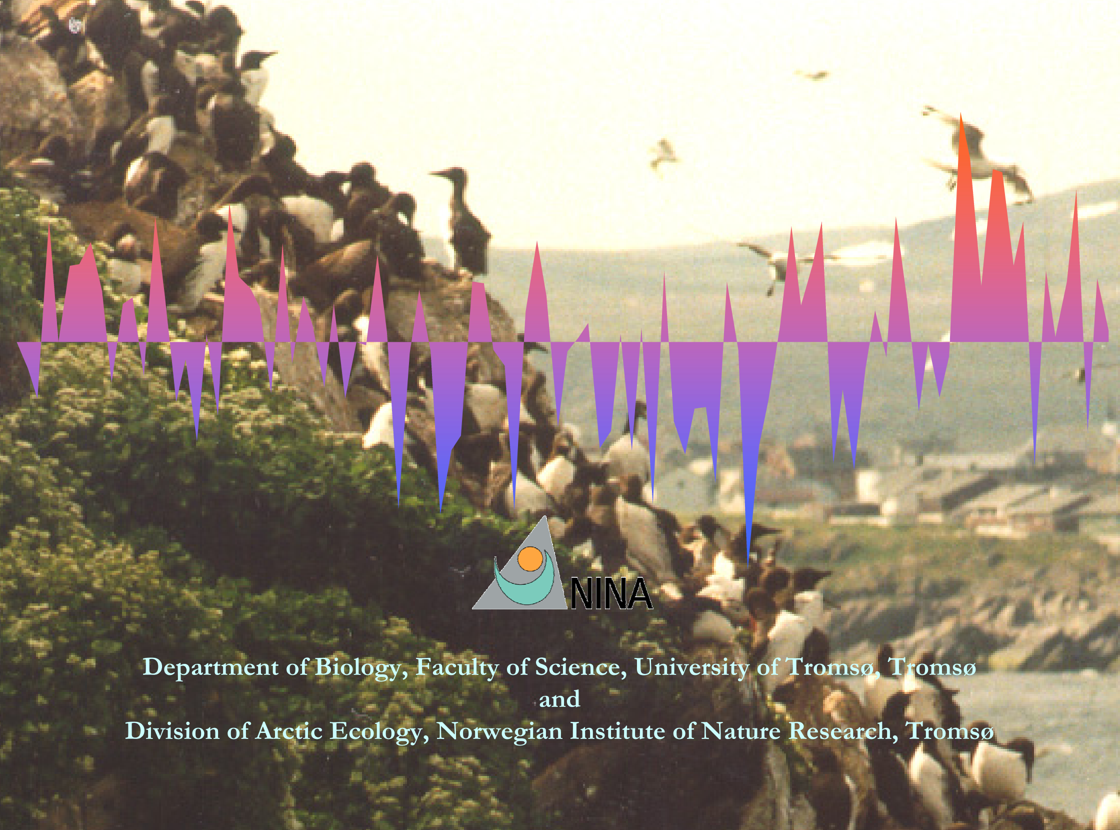
A DISSERTATION FOR THE DEGREE OF DOCTOR SCIENTIARUM

Life-history and breeding biology of seabirds in a changing environment: a comparative approach

Hanno Sandvik

August 2004



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Cover illustration:
View of the guillemot colony at Hornøya (photo by Hanno Sandvik), and NAO index

Citation:
Sandvik H (2004) Life-history and breeding biology of seabirds in a changing environment:
a comparative approach. Dr.scient. thesis, Universitetet i Tromsø, Tromsø, Norway

Printed on recycled paper
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and
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[All papers are so far unpublished manuscripts]

Preface

The completion of this thesis does not only mark that the end of my doctoral studies but also of the Tromsø era in my life. Thank you to all you people who made me come here and who made it worth staying here – both friends, colleagues, mentors and students!

To keep it short – in a desperate attempt not to become too sentimental: without Tromsø my life history (Lack 1947; Williams 1966; Stearns 1992; Hatch et al. 1993; Poiani and Jermiin 1994; Purvis and Harvey 1995; Poulin 1996; Daan and Tinbergen 1997; McHugh and Rouse 1998; Kozłowski 1999; Brommer 2000; Kirk et al. 2001; Roff 2002) would have been poorer, not only in terms of academic degrees but also in terms of friends, adventures, the accent of my children, mountains, experiences and arctic light conditions. I will certainly miss all that. And the view of Bentsjordtind from my office window.

As for the doctoral studies: guess who is glad that the "final spurt" is over now! Thank you, Hedda, Katja and Ivar, for your support during those years. It would have been simply impossible without.

Kjell Einar Erikstad was my supervisor. I did not ask for much help, I am afraid, but when I really needed him, he was always there – with advice, encouragement, a joke and/or assistance. I am extremely grateful for this supervision. Besides, I would probably have stayed in my "final spurt" phase for another humpteen months, had it not been for him.

Further support (financial) came from the Research Council of Norway. Also the University of Tromsø and the Norwegian Institute for Nature Research sponsored my activities.

I was so privileged to belong to two worlds, the Department of Biology at the University of Tromsø, and the Division of Arctic Ecology of the Norwegian Institute for Nature Research, both with great and helpful administrative staff and with equally great and competent scientists. It was exciting to follow NINA Tromsø's and NINA•NIKU Tromsø's and NINA and NIKU Tromsø's development from a somewhat chaotic organisation during the wild days at the "Station" (marine lab) via Storgata 25 to a serious participant in the Polar Environmental Centre;

and to follow the evolution of the IBG at the "Temporary Building" to IB at the "Building of Natural Sciences". Thanks to the people at both places for exchange, help and fun.

And thanks to all people in Berlin, Braunschweig and Tromsø, students and professors alike, who have shared, amplified and reinforced my (our) enthusiasm for ecology and evolution.

I would like to dedicate this thesis to the
Storsteinnestindan (1016 m, Kvaløya),
both because they remind me of the
Serles (2717 m, Stubaier Alpen)
and because they are beautiful
in their own rights.

Abstract

The climate of the earth has started to change as a result of human activity, and further changes in the means and variances of meteorological and climatological parameters have been predicted. Effects of both natural and anthropogenic climatic variability have also been documented in many biological species at all trophic levels. Seabirds constitute a group of marine top-predators with life-history characteristics that make them especially vulnerable for environmental changes: they are comparatively long-lived and have low fecundity. This means that even small changes in adult survival can drastically reduce life-time reproductive success. In the analyses presented in this thesis, I attempted to go beyond simply enumerating the species affected. If there are any characteristics in the ecology or life history of species that predisposes them to respond more strongly to climate variability than other species, those characters can only be revealed by interspecific analyses.

The articles that are part of this thesis include one theoretical and two empirical papers, the first of which is a case study carried out at a seabird colony in the Barents Sea, and the latter of which is a comparative analysis of the data available on all North Atlantic seabirds. The theoretical paper contributes to the methodology of phylogenetic-comparative analyses, which is the tool used by biologists to reveal lawfulness in nature.

The case study from Hornøya is the first to document an effect of climatic variability on the adult survival of North Atlantic seabirds. Especially alarming was the clearly negative effect of warm seawater conditions, a situation that will become more common in the future.

Effects of climate were also widespread in the interspecific data base analysed. While climatic responsiveness in population size was not accounted for by any of the explanatory variables investigated, comparative analyses showed that responsiveness of offspring production and adult survival to climatic variability exhibit patterns that are compatible with life-history theory: responsiveness tended to be higher in species with higher fecundity and/or lower survival. The bearings of these findings and proposals for future research are discussed.

Introduction

Animal populations are affected by climate. That observation is neither new nor controversial (Alheit and Hagen 1997; Ottersen et al. 2001; Walther et al. 2002). Understanding the causal pathways of this relation is quite a different matter, however. Climatic effects can be direct, i.e. caused by adverse weather conditions, or indirect, for instance mediated through the food chain. In the latter case they can be more or less immediate or lagged by several years. They can act on distribution or behaviour as well as morphology or life history (Ahas 1999; Post et al. 1999b; Post and Stenseth 1999; Walther et al. 2002). It is the last effects, the ones that climate exerts on the life history of species, that are relevant for whether the populations affected increase or decrease over time, and that are the focus of this thesis.

Background

Seabirds are comparatively long-lived animals: maximum ages of up to 60 years are documented (*Diomedea epomorpha*; Schreiber and Burger 2002a), and higher ages certainly occur. The corresponding high annual survival rates of well above 90% for many species, are one of the reasons that make this group interesting for students of the evolution of life history strategies (Jouventin and Mougin 1981).

Following George C. Williams's (Williams 1966) refinement of David Lack's (Lack 1947) principle of the optimum clutch size, it has been realised that the life expectancy of birds weighs heavily in their reproductive decisions (Goodman 1974; Wooller et al. 1992; Charlesworth 1994): the longer-lived a species is, the larger is the potential future reproduction in comparison to any particular actual reproductive event, and the more should natural selection be expected to favour investment in adult survival over investment in offspring. In the terminology of life-history theory, this results in adult survival being the life-history trait of seabirds which has the highest elasticity, where elasticity is a measure of "the percentage change in [the population increase rate] λ brought about by a percentage change in mortality [or any other life-history trait]" (Stearns 1992:34).

In many contexts, species are placed along a "fast–slow" axis

(Bennett and Owens 2002), where the "fast" species grow rapidly, mature early, produce much offspring per breeding bout, and survive poorly. This extreme has also been referred to as a "high reproductive effort" strategy (Owens and Bennett 1995). "Slow" or "low reproductive effort" species correspondingly grow slowly, mature later in life, produce little offspring per breeding season, but have long reproductive life spans. Compared to most other bird taxa, seabirds as a group are to be found towards the "slower" end of this continuum (Weimerskirch 2002), however there are also significant differences in placement along this axis among seabird species (Jouventin and Mougin 1981; Erikstad et al. 1998). Both aspects are relevant when we look at population trends in seabird species:

- That they are all comparatively long-lived, implies that already small changes in their annual adult survival rates will have unusually large effects on the life-time reproductive success and thus, ultimately, on the survival of the populations, and species as a whole.
- That there is considerable variation among seabirds on the other hand, means that the life-history of a seabird species may be used as a cue as to how vulnerable the species is in the face of changing environmental conditions.

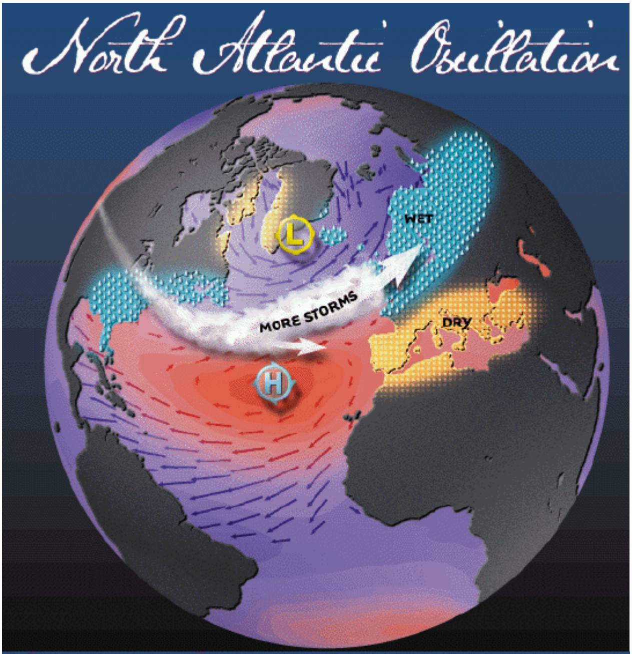
Seabirds live in, and are adapted to, highly stochastic environments. It is thus not the variability of environmental conditions per se that is of concern for long-term population trends. Rather it is changes in the variances or the long-term means of these conditions. Different models have made substantially diverging predictions as to how the different strategies within the long-lived spectre of life histories will respond to changes in the mean or variance of environmental conditions (Ricklefs 1990; Erikstad et al. 1998), and empirical evidence is still scarce.

One way to quantify environmental fluctuations is by means of climatic parameters. Climate effects seabirds directly, mainly through temperature, precipitation and wind during the breeding season, and by heavy winds outside the breeding season (Finney et al. 1999; Schreiber 2002; Durant et al. 2004). Most so-called seabird wrecks have been associated with winter storms (Hudson 1985). However, there is evidence that indirect climate effects are still more important. Sea surface temperature, wind direction and the speed of oceanic currents are known to influence the abundance and distribution of seabird prey (Fromentin and Planque 1996; Heath et al. 1999; Stiansen et al. 2002). The most well-known effects of climate on seabirds, the El Niño years at the western coast of South America where breeding failures may be total (Guerra et al. 1988; Mellink 2000) and adult survival severely impaired (Schreiber and Schreiber 1984; Massey et al. 1992), are caused by a break-down of the Peruvian upwelling system, which in turn is a consequence of a shift in climatic and oceanographic processes (Barber and Chavez 1983; Cane 1983; Philander 1990).

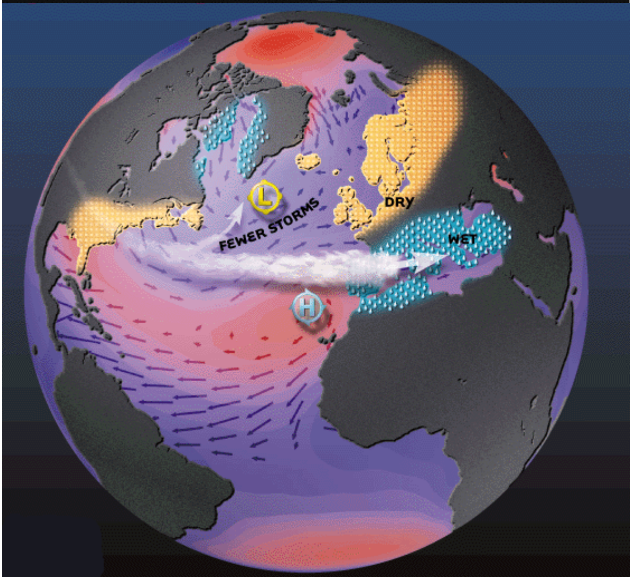
Global climate change is predicted to affect both means and variances of a variety of climatic parameters (IPCC 2001). In will not be possible to predict the response of animal populations to those changes unless the responses to the naturally occurring fluctuations are better understood. Although the effect of the El Niño (and Southern Oscillation; Trenberth 1984; Philander 1990) extends well beyond the South Pacific (La Cock 1986; Ainley 1990; Crawford et al. 2003), the climate to which North Atlantic seabirds are exposed, is governed by another large-scale oscillation pattern:

The North Atlantic Oscillation (NAO) as a phenomenon has been named exactly eighty years ago (Walker 1924). It describes a so-called teleconnection across the North Atlantic Ocean, i.e. the fact that meteorological parameters on both sides of the North Atlantic are highly correlated which each other, a pattern aptly termed “seesaw” (van Loon and Rogers 1978) because temperatures go up on one side when they go down on the other and vice versa. Many more parameters than air temperature have been show to correlate with the NAO, such as sea surface temperature (SST) and wind speed (Fig. 1; Hurrell et al. 2003; Hurrell and Dickson 2004). However, those correlations are not simply expressed by one number because they vary in well-defined spatial patterns (which is exactly what makes them a seesaw).

NAO conditions are now conveniently expressed by the NAO index (Fig. 2; Hurrell 1995). Because the NAO is a fluctuation of atmospheric mass between the Icelandic low-pressure centre and the Azores high-pressure centre, its classical definition was the normalised difference in sea level pressure between Stykkishólmur (Iceland) and Ponta Delgada (Açores). In NAO^+ winters (Fig. 1a), the Icelandic low and the Azores high are strong and canalise heavy westerly winds towards northern Europe, resulting in relatively warm and wet conditions. The Norwegian Atlantic Current is speeded up and transports warm water masses and zooplankton into the Barents Sea. Winters in the Mediterranean are cold and dry. In NAO^- winters (Fig. 1b), the westerlies are weakened


North Atlantic Oscillation
L
WET
MORE STORMS
DRY
H

(a) NAO$^+$


L
FEWER STORMS
DRY
WET
H

(b) NAO$^-$

Fig. 1 (opposite page). The North Atlantic Oscillation. Schematic illustration of the main climatological and oceanographic features of typical NAO$^+$ and NAO$^-$ years. © 2000, Martin Visbeck. Reproduced from http://www.ldeo.columbia.edu/NAO with M. Visbeck's kind permission.

and have more southerly trajectories, leading to warm and wet conditions in southern Europe and severe winters in northern Europe. The NAO is mainly a winter phenomenon, that is to say that the correlations mentioned are strongest during the months December–February.

As can be seen from this short, and not exhaustive, list, many of the parameters correlated with the NAO are utterly relevant for animal populations in general, and marine ones in particular (reviews in Ottersen et al. 2001; Stenseth et al. 2002; Ottersen et al. 2004). Nevertheless, it was in terrestrial habitats that many of the biological effects of the NAO have been described first, such as influences on flowering time of

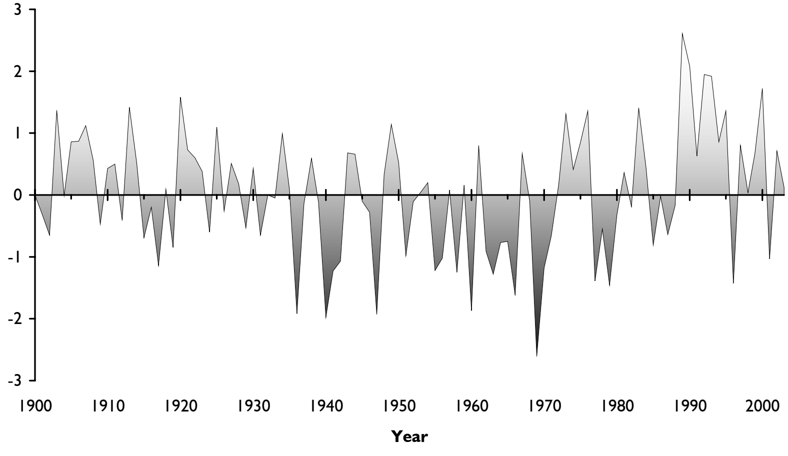


Fig. 2. Oscillations of the North Atlantic Oscillation index from 1900 to 2003. The last 15 years have seen unusually many NAO$^+$ years. NAO index values can be measured at any point in time or calculated for any period of time. The index shown here is the extended winter principal-component based NAO (i.e., the mean for the period December previous year–March). This is the index used in this thesis, because correlations between NAO and meteorological phenomena is strongest in winter. Furthermore, principal-component based indices better represent areas far removed from the stations used to measure station-based NAO indices. However, all different measures of NAO are strongly correlated with each other.

vascular plants or the sex ratio and birth weight of vertebrates (Post et al. 1999a; Post and Stenseth 1999). However, also effects on marine plankton (Fromentin and Planque 1996; Heath et al. 1999), fish recruitment rates and stock biomass are by now well-documented (Stiansen et al. 2002; Hjermann et al. 2004), both of which effect seabirds through the food chain.

What also might have become clear, is that one will not expect animals to respond to the NAO per se, as it is defined in terms of air pressure differences. It is the meteorological or oceanographic patterns correlated to NAO which affect animals. As such, the NAO is not more than "a proxy for a variety of climatic processes" (Ottersen et al. 2001:2). However, it is one of the best proxies that is currently at hand. Using it, one has to bear in mind that its correlations to other phenomena vary in both space and time.

32 out of roughly 330 seabird species recognised are endangered or critically endangered, a further 60 are vulnerable (Schreiber and Burger 2002b). The response of seabirds to climatic fluctuations, both naturally occurring and anthropogenically induced ones, is therefore of special concern. Only an understanding of which seabirds are expected to be especially vulnerable and by what factors and in which life-history trait they will be affected, will enable conservation biologists to conserve threatened species from extinction, and to prevent others from becoming threatened.

Limiting the magnitude of global change by reduction of CO_2 emissions should still have priority over all other measures (the conundrum of why so many scientists, including many at the Polar "Environmental" Centre, take a car to job is only mentioned in passing). However, also in the short run, conservation measures can relieve species that are threatened by climatic change, even if it takes considerably longer time to improve this prime extinction threat. Possible examples are albatrosses which suffer from long-line fishing (Inchausti and Weimerskirch 2001) as well as ocean warming (Weimerskirch et al. 2003), or bird populations negatively affected by introduced predator species (Pascal et al. 2004). Concentrating efforts at reducing those factors that *can* be influenced in the short term (such as fishing techniques or predator eradication), will have positive effects on threatened populations, even though the climatic conditions themselves cannot be influenced in the short term.

It is the wish to contribute to a better understanding of the mechanisms underlying population responses to climatic fluctuations, that has motivated these studies.

Objectives

Having thus sketched the framework of my studies – life-history theory and climatic variability – I will now explicate the aims of my analyses.

- Climate is known to affect adult survival of seabirds in the South Pacific and some other oceanic regions. In the North Atlantic, effects of climate have so far been only documented on other life-history traits such as reproduction. Is this absence of documented climate effects on survival in North Atlantic seabirds a real phenomenon, or is it caused by the fact that no-one has looked for it earlier?
- Theory suggests close relationships between the life-history strategies of species and their response to changes in environmental conditions. Are there any corresponding patterns in population dynamics of seabirds that apply across species? In other words, can the life history of species be used to predict their responsiveness to climate change?
- Which parameter is most informative as a shortcut to climatic variability? The NAO is not by itself relevant to seabirds, however other parameters such as SST require knowledge of where the seabirds are at any given time. What does this have to say for the choice of explanatory variables for analyses of seabird responses?
- Given that the main concern is lawful generalisations across different seabird species, how is the evidence available best analysed? More specific, which methodology can be used to address interspecific questions were the environmental variable is a continuous one (e.g., meteorological parameters) and the biological variable a discrete one (e.g., clutch size)?

The questions posed are both factual and methodological. Correspondingly, the papers addressing them are both empirical (Papers II and III) and theoretical (Paper I, and to a certain degree, Paper III). One of the methodological aspects, related to interspecific analyses, may need some more explanation:

The Comparative Method in Ecology

Ecology, just as biology as a whole (Mayr 1988), is a science that encompasses both idiographic and nomothetic aspects. Even though a naïve reading of Popper (e.g., Popper 1934, 1944/45) has lead some researchers to disparage idiographic or historic science as "pseudoscience", both branches of enquiry are equally important (Ghiselin 1997) and should ideally complement each other (Sandvik 2000). Idiographic aspects of ecology are for instance the unravelling of the trophic, symbiotic or competitive relations between certain species, or scenarios of how particular communities have been assembled through time. Nomothetic ecology aims at finding lawfulness in the living world. While the patterns thus revealed would be referred to as *laws of nature* in physics, ecologists normally prefer to call them *rules* (such as Allen's rule, Bergmann's rule, Cope's rule), mainly because they are of a probabilistic nature rather than being absolute laws. Whatever name is chosen, lawfulness does exist even in systems as hopelessly complex as ecosystems. Deriving generalisations across the constituents of those systems, i.e. species, is at the heart of all nomothetic activities in ecology.

The method employed in all nomothetic activities in biology is called the comparative method. In short, any interspecific study, i.e. any investigation including more than one species, addresses a comparative question. To make inferences from interspecific datasets, however, one has to realise that species are neither biologically nor statistically independent of each other. This fact is by now acknowledged as a triviality as far as the independence of individual organisms is concerned: including several measurements of the same individual in an intraspecific analysis violates assumptions of most standard statistical tests and should be avoided or corrected for (Machlis et al. 1985). That the same is valid for species, has been known for a long time (at least since 1857, see Ridley 1992). However, methods to deal with this situation have not been developed before the 1980s (Ridley 1983; Felsenstein 1985).

Figure 3 illustrates what is meant by the (in)dependence of species. Any statistical test that is carried out using single species as data points, implicitly "assumes" that the phylogenetic relationships of the species involved are the ones depicted in Figure 3a: an unresolved bush. In the real world, phylogenies never are unresolved bushes, however. Species share certain amounts of their evolutionary history with each other, and they do so to differing degrees, depending on the time elapsed since their most recent common ancestor lived (Fig. 3b). Ignoring this can have many undesired consequences, such as type I errors because an overestimation of the sample size, or type-II errors because the underlying microevolutionary processes have been misrepresented (Martins and Hansen 1996b).

Luckily, several methods have been proposed that can take account of the phylogenetic relationships between the species studied (reviewed by Martins and Hansen 1996a). A common feature of those methods is that it is evolutionary events rather than species that are considered independent data points, and that they require knowledge of the phylogeny of the species of concern. Such tests are therefore referred to as phylogenetic-comparative analyses.

The text raising attention to this methodology for a broader audience, unfortunately received the somewhat inappropriate title *The comparative method in evolutionary biology* (Harvey and Pagel 1991) – "unfortunate" because the comparative method is relevant not only for evolutionary biology but for any biological discipline which attempts answering interspecific hypotheses (Ridley 1989). By now, most journals also in the non-evolutionary fields of biology require interspecific analyses to be based on phylogenetic-comparative methods. This list gives an (incomplete) survey of the ecological questions that already can be addressed phylogenetic-comparatively:

- How can biodiversity be quantified? (Faith 1994; Owens and Bennett 2000; Faith 2002)
- Have the species of host–parasite or mutualistic relations co-speciated? (Page 2003)
- Which taxa deserve priority in conservation? (Moritz 1996)
- Which ecological requirements does a poorly known species in need of protection have? (Brooks et al. 1992; Jennings et al. 1999)
- How was an ecological community assembled and why by those species? (Losos 1996)

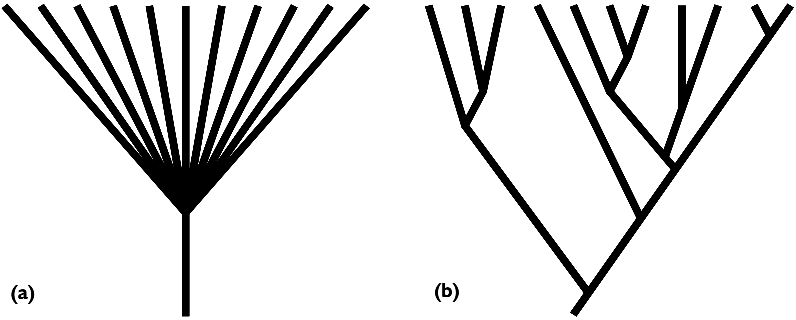


Fig. 3. Not taking phylogeny into account in interspecific analyses amounts at assuming an unresolved bush-like "star phylogeny" **(a)**. In reality, species share different amounts of their evolutionary history with each other **(b)**.

Table 1. Overview over phylogenetic-comparative methods developed in order to analyse the correlated evolution of two characters (or of one character and an environmental variable). The tabulation is according to the nature of the variables. The impression that methods dealing with two variables of the same kind are dominating, is confirmed by Fisher's exact test ($p < 0.040$).

Environmental variable	Dependent variable	
	discrete	continuous
discrete	Ridley 1983, Maddison 1990, Sillén-Tullberg 1993, Pagel 1994, 1997	Grafen 1989, 1992
continuous	Paper I	Felsenstein 1985, Huey and Bennett 1987, Grafen 1989, 1992, Lynch 1991

- Is the presence or quality of a character (i.e., has its evolution been) correlated to the environmental conditions faced by the species?
- Is the occurrence or quality of two characters correlated?

The last two kinds of question are probably the most frequent ones in comparative ecology. The methods proposed to answer them are shown in Table 1.

The aim of my studies was to derive lawful generalisations ("rules") of how seabirds respond to changing climatic conditions (Paper III). The questions posed where thus interspecific in nature, and required a phylogenetic-comparative framework. Furthermore, one of the types of questions relevant to my analyses could not be dealt with by existing methods: as can be seen from Table 1, no method existed to address questions where the environmental variable is continuous and the species character is a binary or a class variable. To fill this gap, was another aim of my studies (Paper I).

Results and Discussion

As normally methodological issues have to be settled first, before applying them to data, I start with the methodological contributions. Paper I outlines my solution to the case where an interspecific dataset to be analysed consists of an continuous explanatory variable and a discrete dependent variable. The method draws upon methods developed by Maddison (1990) and Pagel (in Harvey and Pagel 1991:94–100) for analyses of purely discrete datasets. Paper I illustrated the method using a worked and a real example taken from the literature. It had been my hope to also apply the method to the climatological problems I addressed in the other papers. However, in Paper III Felsenstein's (1985) independent contrasts were more appropriate because all variables were continuous. I hope that this only means that I have postponed application of my method to my data to a later paper.

Another methodological finding was a way to analyse re-sighting data of ringed birds in the presence of ring loss. I am not aware that this solution has been proposed earlier, although Vladimir Grosbois (pers. comm.) has found the same solution independently of me. Estimates of adult survival rates are based on re-sightings of marked individuals (see Paper II for references), and ring loss poses therefore a severe problem. In the case described in Paper II, each bird had been ringed with a total of two or three rings on each leg, one of which was a numbered metal ring which is very rarely lost. However, upon loss of one of the colour rings, a whole series of other colour ring combinations is invalidated unless one is able to read the ring number of the bird in question. Excluding all birds belonging to this series from the dataset would dramatically reduce the sample size of such studies (by 63% in one case in Paper II). Still, in the absence of other methods, this is the only defensible thing to do. Birds of the same colour ring series which have not lost any ring and have been observed after a ring loss was stated, obviously cannot be the individual that lost its ring. Nevertheless, not excluding those birds would introduce a systematic error. That is because birds that have not been observed with complete ring combinations can be either of two things: dead or partly ring-less. Birds that *have* been observed with complete ring combinations are obviously alive. Excluding the former but not the latter therefore biases survival estimates upwards.

The solution proposed must still discard all re-sightings of those birds *after* the ring loss, however it allows to use them up to (and excluding) the year in which the ring loss was discovered. The approach presupposes knowledge of how the computer program MARK (White 2003) works, so I refer to the Methods section of Paper II for more details. The advantage of the method is that many years of observation can be retained even for birds that become "problematic" at a later time. Considering the difficulties of obtaining sufficient sample sizes for reliable estimation, this is a clear improvement over discarding problematic birds altogether.

As for the empirical aspects of my PhD, I analysed one case study of seabird survival at a north Norwegian seabird colony, viz. Hornøya (Paper II), and a interspecific dataset of demographic data of diverse seabird species throughout the North Atlantic (Paper III). In both studies I found clear evidence of an effect of the NAO on the parameters considered.

In four of the five species studied at Hornøya (common and Brünnich's guillemot *Uria aalge* and *U. lomvia*, razorbill *Alca torda*, and Atlantic puffin *Fratercula arctica*), the survival model incorporating NAO was better, or in one case only very nearly as good and just about as parsimonious, than any models without environmental explanatory variables. Based on knowledge of the winter distribution of those species, it was also possible to test for the effect of another, more geographically constrained, climatic variables, viz. SSTs. In most species SST models were still better than NAO models, and the variance in survival accounted for by those parameters was unexpectedly high (13–54%). Given that already small changes in survival of these long-lived species have dramatic effects on the life-time reproductive success, the large effects of SST are alarming. Similar findings have so far only been reported from the Southern Ocean (Barbraud et al. 2000; Barbraud and Weimerskirch 2001, 2003; Jenouvrier et al. 2003) and the Pacific (e.g., Jones et al. 2002). The pattern found in those studies and my own is identical: adult survival and SST are negatively correlated. The prospects for the species affected are thus not very bright in light of the expected (IPCC 2001) – and already documented (Levitus et al. 2000; Gille 2002) – increase in oceanic temperatures.

In the studies carried out in the Southern Ocean, the availability of food (krill) was discussed as the main cause of this negative correlation (Barbraud et al. 2000; Barbraud and Weimerskirch 2001, 2003; Jenouvrier et al. 2003). This seems likely for my system as well, especially given recent evidence (Hjermann et al. 2004) that warm water conditions favours the herring (*Clupeus harengus*) at the cost of other species (especially the capelin *Mallotus villosus*) which are both more numerous (Hjermann et al. 2004) and seem to be more easily accessible for seabirds (Barrett and Krasnov 1996; Barrett 2002). Attempts to corroborate the effect of prey abundance using estimates of the Barents Sea stocks, had only very mixed success. The effect of prey abundance on survival was nearly never significant, and did not have high explanatory value. The widespread distribution of the seabirds during winter, in regions were estimates of the Barents Sea stock are not representative for prey availability, is likely to be part of the reason.

Also in an interspecific analysis of more than 500 previously published studies of either population size, productivity (chicks fledged) or adult survival, the effect of NAO was apparent. Because the studies used came from the whole North Atlantic, I used the coefficient of determination (r^2) between the NAO and the species' demographic parameters as a measure of climatic responsiveness. The reason to chose r^2 rather than the correlation coefficient itself (r) was that the latter varied grossly and seemingly at random across the studies used. This is in accordance with earlier findings that NAO can have highly variable effects on animal populations even on relatively small geographic scales (Mysterud et al. 2000; Sæther et al. 2003). r^2 has the advantage of always being positive, but still measuring climate effects.

In approximately 18 out of 38 species included, an effect of NAO on population size was recovered at one or several time lags. The same applied to offspring production in at least 5 out of 22 species, and to adult survival in 6 out of 15 species, It thus seems that responses to climate, even in an aggregate parameter as population size, are anything but exceptional. This is especially impressive as most of the original studies used were not concerned with climate at all; the effects found are thus hardly the consequence of a publication bias.

In the final step of analysis, the attempt was made to explain the distribution of responsiveness to climate across species. The expectations derived from life-history theory were tested on this dataset in a truly phylogenetic-comparative manner. As far as responsiveness of population sizes to climatic variation was concerned, the variation in this variable could not be explained by any of the life-history traits considered. Responsiveness of chick production and of adult survival, on the other hand, showed clear patterns in favour of my expectations: responsiveness in survival was for instance lowest in species at the low fecundity end of the life-history strategy gradient. This result corroborates the theoretical assumption (Schaffer 1974) and empirical finding (Lindén and Møller 1989; VanderWerf 1992) that animals with lower fecundity are less prepared than higher-fecundity species to incur survival costs that may follow from reproduction.

Table 2. Effect of a reduction in annual adult survival rates by five percentage point in two different seabird species, the common guillemot (*Uria aalge*) and the little tern (*Sterna albifrons*). ϕ is adult survival (as derived from Paper II and Hongell 1989, respectively); RLS is the reproductive life span measured in years, approximated (following Botkin and Miller 1974) as $0.5 \cdot (1 + \phi) / (1 - \phi)$.

Conditions	Common guillemot		Little tern	
	ϕ	RLS	ϕ	RLS
"Normal"	0.96	24.5	0.77	3.8
Changed	0.91	10.6	0.72	3.1
Difference	0.05	13.9	0.05	0.8
Decrease	5%	57%	6%	20%

However, this finding does not in itself reveal much about the vulnerability of the species concerned. A decrease in adult survival of five percentage points is much more dramatic for a bird with an annual rate of 96% (e.g. the common guillemot; Paper II) than for a bird with an annual survival rate of 77% (e.g. a little tern *Sterna albifrons*; Hongell 1989). Table 2 explicates what this difference means in terms of the species' reproductive life spans: It is more than halved in the guillemot and only reduced by a fifth in the tern.

In order to predict vulnerability of a species, the effect on survival has consequently to be scaled in some way for the effect a given change exerts on the reproductive life span and thus life-time reproductive success of the species. This is a rewarding topic for future research.

Conclusion and Outlook

Both the case study (Paper II) and the comparative analysis (Paper III) have revealed the prevalent existence of climate effects in seabird population size and/or demographic parameters. The effects of reduced survival which Table 2 exemplifies, are in the order of magnitude which have been documented at Hornøya, and they are to a large extent attributable to warm sea water conditions (Paper II), a situation that will occur more frequently in the future. Even though the longest-lived seabirds respond the least to climatic variability (Paper III), their responses may nevertheless be more dramatic. Whether this indeed is the case, will be an important question to be addressed by future studies. This requires some investigations into how the different parameters should be scaled in order to make effects comparable across different species.

There are several other fields that are promising for future research:

- As mentioned earlier, the signs of correlations with climate vary unpredictably. This only means that the cause has not yet been identified, however. In an elegant study on red deer (*Cervus elaphus*), Mysterud et al. 2000 (2000) were able to identify the reason for opposite relationships of sex ratio with NAO on small geographical scales: the key factor was altitude, because the precipitation, the quantity of which is influenced by the NAO, falls as rain below c. 400 m and as snow above. It is possible that a similar key factor governs responses in marine systems. Identifying it would be a major advance. Part of the solution may be to take a closer look at SSTs rather than climatic index values. I have done so successfully in Paper II, however in a comparative context (Paper III) this approach is complicated by incomplete knowledge of where seabirds are outside the breeding season, i.e. most of the year.
- It would be most rewarding to compare other oceans with the North Atlantic. Paper III was confined to the North Atlantic because NAO was used as a shortcut to climatic conditions. A problem with interoceanic comparisons is that different climate indices are not comparable across different oceans. Also here, SSTs may be a promising parameter to use.
- A necessary condition for phylogenetic-comparative analyses is the knowledge of the phylogenies of the species of interest. In comparative analyses of seabird it is a great impediment that the phylogeny of the terns (Sterninae) is as yet entirely unknown. This taxon encompasses 45 species, some of which are quite intensively studied, however they had to be represented by an unresolved bush in my analyses, so that much information was lost. So please, tern specialists: reconstruct the phylogenetic tree of this group!
- Density dependence has not been taken account of in my studies. However, it has been argued on theoretical grounds (Chan and Stenseth 2002; Ottersen et al. 2004) that climate and density dependence do not need to affect population sizes in an additive manner, it may well be density dependence, rather than population size itself, which is the parameter affected by climate. Recent empirical evidence has verified the existence of density-dependent effects of climate (Barbraud and Weimerskirch 2003; Sæther et al. in press).

- The same applies to nonlinear relationships: most studies – mine included – have simply assumed relations between climate and ecological parameters to be linear. That this does not have to be the case, has been impressively demonstrated by Mysterud et al. (2001) and by Ellis and Post (2004).
- Finally, in addition to focusing on changes in means of meteorological parameters, more research on the effect of changing variances is clearly needed. Changes in variances can have at least as important effects on population dynamics as changes in means (Mearns et al. 1997; Erikstad et al. 1998; Sæther et al. in press).

As usual, the number of questions seems to grow more rapidly than the number of answers. I choose to interpret this as a good sign: we have started unravelling something – the findings might be somewhat provisional yet, but the results show clearly that there *are* patterns waiting for an explanation. Obviously other interpretations are conceivable for some of the findings. However, given that nobody had been looking for those patterns previously at this scale and interspecifically, exposing them has certainly been an important step.

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Paper I

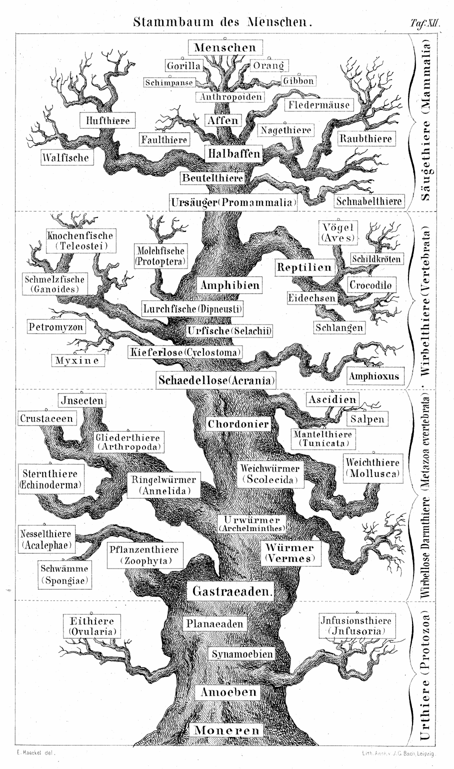

Illustration (source, Haeckel 1874):
One of the first truly phylogenetic trees, Haeckel's *Stammbaum des Menschen*.

Analysing The Correlated Evolution of Discrete and Continuous Traits: A Phylogenetic Comparative Method

Hanno Sandvik

Abstract A phylogenetically informed method for the analysis of interspecific data with a continuous independent variable and a discrete dependent variable is proposed. The test compares two hypotheses built upon a continuous-time Markov model of evolution. The first (null) hypothesis assumes that the transition rates of the discrete character are dependent on branch lengths. The alternative hypothesis assumes that the transition rates are a function of the amounts of change in the continuous variable. Using likelihood ratio tests or Akaike's Information Criterion it can be decided which model is better at explaining the data. The evolutionary and statistical assumptions of the method are made explicit and compared to other approaches.

Keywords Binary characters, categorical characters, comparative analysis, continuous characters, maximum likelihood, phylogeny

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It has become standard, at least in most of the well-reputed biological journals, to require that interspecific analyses be carried out by taking into account the phylogeny of the species investigated. A diversity of methods has been proposed, which have been reviewed by Harvey and Pagel (1991) and Martins and Hansen (1996).

The methods have in common that they can be used to answer interspecific questions such as: do two characters show correlated evolution across species, or is the evolution of one character correlated to the environmental conditions faced by the species. A major distinction between the various phylogenetic comparative methods is according to the nature of the characters analysed: some models deal with pairs of continuous characters, while others are designed to process pairs of discrete, i.e. binary (0 vs. 1) or multi-state (e.g. 0, 1, 2 etc.), characters. However, few methods allow to deal with one continuous and one discrete trait (Grafen 1989; Lynch 1991), and in none of these methods can the continuous character be the independent variable.

Obviously, comparative biology is in need of a method that can deal with the latter situation. In this paper, I propose a solution to this problem. It can be applied to address a wide range of questions in all fields of biology, such as whether a certain trait (absence/presence of secondary sexual characters, endo- vs. ectothermy, etc.) or life-styles (parasitic vs. free-living, marine vs. freshwater, etc.) is correlated with another trait (size, basal metabolic rate, range, etc.) or environmental variable (temperature, precipitation, etc.).

After having explained the approach in detail and by using an example tree, I will make explicit its assumptions and mention some possible modifications. I will then re-analyse an existing data set to illustrate how the method can be implemented. Finally, I discuss other possible approaches to solve the same problem.

Background

Ridley (1983) was the first to suggest a phylogenetic-comparative method for the analysis of two binary variables. It consists, essentially, of tabulating changes in both characters in a 2 × 2 contingency table, and using a χ^2 test or Fisher's exact test to establish whether changes (or states) in one character are associated with changes (or states) in the other. Figure 1 exemplifies this approach with two simple phylogenetic trees, in which branch colour symbolises the presence of the first character, and black squares the evolution of the second character. Both tree topologies result in the same contingency table (viz., ((4, 0), (0, 2))) and, consequently, test results ($\chi^2 = 2.34$, $p = 0.063$; Fisher's exact test, $p = 0.067$).

Maddison (1990) developed an alternative method which allows to pose more specific questions of the kind: are gains or losses of one character concentrated in certain parts of a phylogenetic tree? Here, "certain parts of a tree" refers to branches that are in one or the other character state of a second binary

Paper II

Illustration (© 2004, Katja Sandvik):
The upper levels of the Barents Sea food web, or *A kittiwake and its prey*

Dependence of adult survival on climate in five species of North Atlantic seabirds revealed by capture-recapture analysis

Hanno Sandvik, Kjell Einar Erikstad,
Robert T. Barrett and Nigel G. Yoccoz

Abstract In long-lived species, annual survival is the single most important life-history trait. Better knowledge of the effects of non-catastrophic climate variation on the adult survival of long-lived seabirds is therefore important. However, documentation of such effects is still rare. Using capture-mark-recapture methodology, we modelled the annual survival rates of five species of seabirds, the common guillemot (*Uria aalge*), Brünnich's guillemot (*Uria lomvia*), razorbill (*Alca torda*), Atlantic puffin (*Fratercula arctica*) and black-legged kittiwake (*Rissa tridactyla*). The data span fourteen years of observation at the species' breeding colony on Hornøya, off Northern Norway in the western Barents Sea. The estimated survival rates are higher and less variable than most estimates for the same species from other colonies.

The effect of different environmental variables on seabird survival was investigated, including the North Atlantic Oscillation (NAO) index, sea surface temperatures (SST), and abundance indices of important prey species. In most of the species, models incorporating climatological variables were considerably better supported than models with constant survival, time-dependent survival or prey effects. SSTs tended to explain more of the variability in seabird survival than did the NAO. Nevertheless, the evidence suggests that it is not meteorological parameters per se that cause seabird mortality, but indirect effects, possibly mediated by the food chain. This conclusion rests on the observations that most NAO effects are lagged, and that survival rates decreased with increasing SSTs. The importance of prey availability was evident in some of the species, however prey abundance was generally a poor predictor of survival. This may partly be because the estimates of fish stocks available are not representative of the prey availability in the wintering areas.

Keywords Adult mortality, Alcidae, Barents Sea, North Atlantic Oscillation, Fish stock biomass, Sea surface temperature

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Many aspects of seabird life history respond to climatic conditions (Ainley and Divoky 2001; Schreiber 2002; Durant et al. 2004). The most dramatic examples in this regard come from the effect of the El Niño-Southern Oscillation, which regularly causes total breeding failure and high mortality (e.g., Barber and Chavez 1983; Schreiber and Schreiber 1986; Duffy 1990; Wilson 1991; Chastel et al. 1993). The effect of the El Niño-Southern Oscillation is most pronounced in the south-eastern Pacific Ocean, however other parts of the Pacific (Ainley 1990; Ainley et al. 1994), the Southern Ocean (Guinet et al. 1998) and even the Indian Ocean (Barbraud and Weimerskirch 2003; Crawford et al. 2003) and Southern Atlantic (La Cock 1986; Duffy 1990) are affected. Other, less pronounced climatic oscillations are known from other oceanic regions, the most well-studied of which is the North Atlantic Oscillation (NAO; e.g., Hurrell 1995; Hurrell et al. 2003). However, those oscillations do not entail phenomena as catastrophic as El Niño years. It may be partially for this reason, that documentation of climatic variability on seabird life histories is rarer in the North Atlantic.

Some recent reviews have attempted at summarising the effects of the NAO on life-history traits of Atlantic seabirds (Reid et al. 1999; Durant et al. 2004). However, no clear pattern has emerged. Several life-history traits have been shown to vary with climatic conditions also in the North Atlantic (Montevecchi and Myers 1997; Barrett 2001a; Durant et al. 2003), however adult survival has not been among these. Aside from the South Pacific and Southern (Indian) Ocean (Barbraud et al. 2000; Barbraud and Weimerskirch 2001, 2003; Jenouvrier et al. 2003), responses of seabird adult survival

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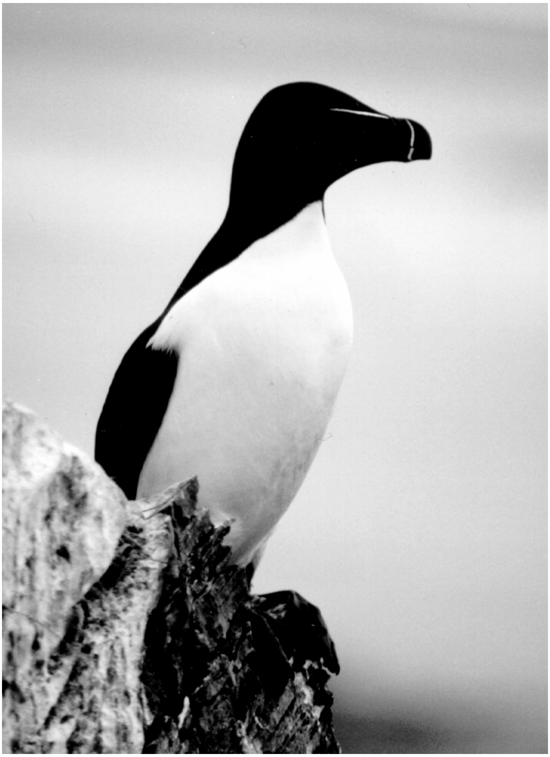

Illustration (© 1996, Hanno Sandvik):
The ratherbill, definitely one of the coolest representative of the seabird guild

Seabird life histories and climatic oscillations: a phylogenetic-comparative time series analysis of North Atlantic seabirds

Hanno Sandvik and Kjell Einar Erikstad

Abstract In the light of the predicted changes in climate as a consequence of global warming, it is a major concern how animal species will respond to the altered meteorological and oceanographic conditions. Seabirds constitute a diverse group of marine top predators which have relatively low fecundity and high annual survival rates. This makes them especially vulnerable because even small changes in survival will have huge effects on the life time reproductive success of individuals, and on the prospects of whole populations and, ultimately, species. In order to predict effects of climate change, it is a necessary precondition to first understand responses to naturally occurring climatic fluctuations. While the effects of the El Niño-Southern Oscillation have received much attention in the past, the responses of seabirds in oceans affected by other climatic systems is still little understood. We analyse several hundred previously published time series of seabird population sizes, offspring production and adult survival rates in the North Atlantic in order to detect climatic signals in this data base. Using the correlation of these parameters with the North Atlantic Oscillation (NAO) as a measure of responsiveness to climatic variability, we find widespread effects of climate on all parameters considered. As our analyses are phylogenetic-comparative, we are able to search for patterns across species, which may be used in predicting especially vulnerable species. Our expectation was that life-history characteristics of the species should have explanatory value for climatic responsiveness. Based on the elasticity of different life-history traits it is expected that the longer-lived a seabirds is, the most reluctant it is in responding to climatic variability. We are able to corroborate this for the responsiveness in adult survival and in chick production, but not in population sizes.

Keywords Adult survival, Breeding success, Climate response, NAO, North Atlantic Oscillation, Population size

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Global change is predicted to change both the mean and variance of many climatological and oceanographic parameters (Trenberth 2001b; Karl and Trenberth 2003) which are relevant to animal populations (Aebischer et al. 1990; Ainley and Divoky 2001; Walther et al. 2002). In several areas, the signal is already apparent, as shown by increases in water temperature in the Southern Ocean (Gille 2002) or the North Atlantic (Levitus et al. 2000). Climatic and oceanographic systems are highly complex, not to speak of their interaction with biota, both on the scale of particular species (Kitaysky and Golubova 2000) and of ecological communities (Hjermann et al. 2004). The understanding of the naturally occurring fluctuations and their influence on animal populations is a crucial step towards an understanding of how global change will affect different species.

Of those naturally occurring large-scale patterns, the El Niño-Southern Oscillation (ENSO; Philander 1990; Trenberth 1997, 2001a) has received most attention, mainly because the effects it executes on marine animals are so dramatic (Barber and Chavez 1983; Schreiber and Schreiber 1984; Ainley et al. 1988). Recently, however, other climatic oscillations have gained increasing attention (Stenseth et al. 2003), among which the North Atlantic Oscillation (NAO; Lamb and Peppler 1987; Hurrell et al. 2001) may be the one most intensely studied (Hurrell et al. 2003b). While earlier research has focused mainly on vascular plants, terrestrial vertebrates and marine and limnic invertebrates (see reviews by Ottersen et al. 2001; Stenseth et al. 2002), the focus has currently been shifting to marine vertebrates. Many of the results, summarised by Hurrell et al. (2003) and Stenseth et al. (2004), have important direct and indirect implications for population dynamics of seabirds. A fine example by Hjermann et al. (2004) illus-