

When quillemot populations collapsed in the Barents Sea in the winter of 1986–7, a lack of food was blamed. But did climate play a role in this collapse? Michel d. S. Mesquita and Kjell Einar Erikstad went looking for an answer

he winter of 1986–7 was perhaps the darkest in seabird ecology in Norway. The events that happened then and there would puzzle scientists for years to come. The mystery began with the discovery, in December 1986, of the carcasses of several common guillemots, an endangered species of seabird that lives in the Barents Sea. Dead seabirds washed ashore are not unusual in themselves, but as the weeks went on, reports of more quillemot deaths came in, and it was soon determined that these deaths were not isolated incidents. In the northern island of Hornøya, where common guillemots breed (see Figure 1, below, and Figure 2, page 30), only about 20% of the population survived that winter. A colony collapse on this scale had not been seen before (see Figure 3, page 30). Elsewhere, in other guillemot colonies, there were similar collapses.

A number of reports and publications were written at the time to try to explain these deaths. They pointed to one main cause: lack of food. It seemed that the birds had starved to death. One study, published three years ago, showed that there was a low density of main fish stocks in 1986-7.1 But why should this be? For a fuller picture of what had happened that winter, researchers would have to look elsewhere.

In 2013 a number of scientists – including the authors of this article – gathered in Tromsø to reopen this "cold" case. All the evidence at hand was analysed and statistical techniques, common to climate science, were used to put the puzzle

together. It was true detective work. The account presented here will discuss our forensic analysis, as well as the role of statistics in seabird ecology and the need for new statistical methods.

Case details

Let us start with the basics. Common guillemots weigh about 1kg and their appearance is that of a small penguin. They lay a single egg that is incubated for about 33 days; both parents feed the chick for three weeks before it leaves the colony, still flightless, together with its father. These birds begin breeding when they reach 5-7 years of age, and annual adult survival is high - close to 95% on average.

That was not the case in 1986–7, when the population collapsed, leading to the species being declared "endangered" in Norway (even though it is not considered endangered internationally). In trying to figure out what happened that winter, food shortages provided an important first clue: the winter of 1986-7 coincided with low stocks of prey species, such as capelin, young cod, and herring. In the years since the colony collapse, variation in fish stocks seems to explain some of the annual population variability. However, stocks of some fish have been at similarly low levels since 1986–7 without having such a disastrous effect on the common guillemot population. We therefore wondered whether there was a climatic component that could explain some of this variation in population growth rate.

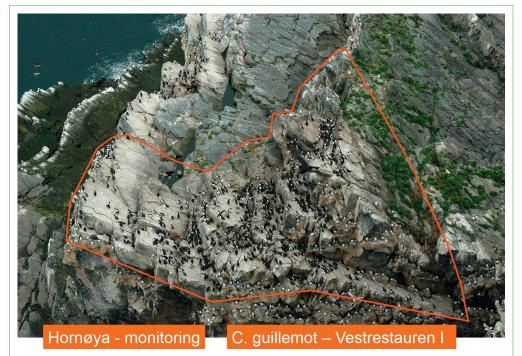


FIGURE 1 An example of a monitoring plot for the common guillemots at the colony on Hornøya in eastern Finnmark, Norway, counted from photos five times each year at different times of the breeding season to get credible estimates. There are 16 such plots in different parts of the colony, which then are used to model change in population size over the years. Photo: Robert T. Barrett



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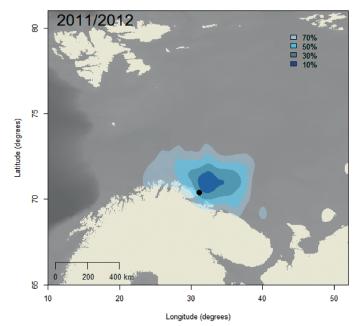


FIGURE 2 The wintering area (December and January) of adult common guillemots from Hornøya, based on positions from small geolocators that are attached to leg rings and fitted on a sample of birds. Geolocators give signals twice a day and the figure is based on more than 10 000 locations. Their distributions are shown by 10-70% kernel areas, which indicate densities of birds, where 10% is the area of highest density. Data from Erikstad et al. (in prep.)

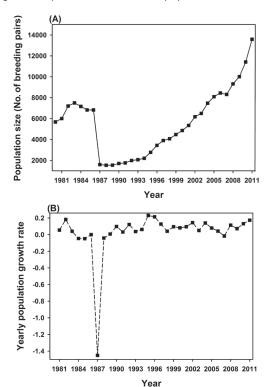


FIGURE 3 Dynamics of the common guillemot population on Hornøya, 1980–2011. (A) Counts and estimates of numbers of breeding birds. (B) Annual population growth rates r on a log scale (r = $ln(X_t - X_{t-1})$). Figure adapted from Erikstad *et al.*¹

There is more to climate than the NAO

In order to address this particular theory, we looked to statistical techniques that could identify a link between climate covariates and the population changes of the common quillemot to explain a causal relationship; but this could not be achieved without first considering the climate dynamical mechanisms underpinning any such links.

Interestingly, a number of seabird publications have focused on one climate covariate in particular – the North Atlantic Oscillation (NAO), which is an anomalous dipole of atmospheric pressure with centres over Iceland and the Azores. A dipole is a region of positive pressure juxtaposed with a region of negative pressure, such that they form two regions with opposite signs. Although the NAO has been shown to partially explain climate variability - meaning changes in the NAO are associated with changes in some climatic conditions - it does not explain everything. Unfortunately, the NAO has been (over)used as a proxy for climate variability in seabird ecology, such that other climatic processes are often overlooked.

Moreover, if one uses the NAO without providing a clear climate dynamics framework to explain its purported effect on an ecological variable, it could give a myopic view of climate variability. By focusing only on the NAO, some relevant climate variability information may be lost - which is analogous to not being able to see the forest for the trees. Thus, one has to resort to other techniques to look at the climate system in order to find covariates that make sense.

Climate analysis toolbox

The Norwegian meteorologist Jacob Bjerknes could arguably be called one of the twentieth century's great "detectives" of atmospheric science, and among his many contributions was the application of a technique called point maps (of correlation or regression) to understand the interactions between oceans and atmospheric conditions (see "On point maps").

One of his most famous contributions consisted of correlating the annual surface pressure in Jakarta, Indonesia, with the annual surface pressure of all available data points around the globe. Bjerknes noticed a gradient of temperature between the eastern (cold) and western (warm) Pacific, which causes an atmospheric circulation along the Pacific. It was named the "Walker circulation" by Bjerknes, after the work of Sir Gilbert Walker, and proceeds as follows. Cool dry air from the eastern equatorial Pacific flows to the west along the surface. When it gets there, the warm waters of the west heat the air and supply it with moisture. Thus, we have high pressure over the eastern Pacific and low pressure over Indonesia in the west. In the ocean, there is cold upwelling in the eastern Pacific, which brings nutrients to fish. In some periods, the cold water disappears and becomes warmer than normal: this we call "El Niño".

These atmospheric and oceanic events seemed unrelated until Bjerknes was able to put them together. In his point correlation map, Bjerknes found what we would now refer to as a "hotspot" – a strong negative correlation between the surface pressure in the eastern tropical Pacific region (centred



on Easter Island) and the annual surface pressure time series in Jakarta. This means that when the pressure in Jakarta is low, the pressure in the eastern Pacific region is high (and vice versa). As Wilks put it, this "correlation pattern is an expression in the surface pressure data of the El Niño-Southern Oscillation (ENSO) phenomenon".2

On point maps

The discussion of "point maps" is a reworking of the problem of model identification with potential spatial and temporal associations. A topic for statisticians would then be to distinguish subjective and objective methods for data and model selection. In spite of the many approaches available to climatologists, many still use simple approaches that may not take full account of the information the data set could provide. Hence, more could be achieved through a stronger collaboration between climatologists, statisticians, and mathematicians. Such collaboration would foster the creation of new and alternative methods for making sense of climate data. A number of networks already exist to try to achieve this objective. For instance, CliMathNet (climathnet.org), based in the UK, is a good example of a forum for discussion and collaboration focused on climate modelling. Seabird ecology would benefit greatly from the creation of a similar network, which could encompass a strong collaboration between statisticians, ecologists, biologists, and climatologists.

Point correlation and point regression maps are still widely used in climate science, as they help provide information that could lead to the understanding of teleconnection patterns that is, how a region in one part of the world can affect another. as seen in the example above. Also, through the use of climate theory, one can use these patterns to create an image of the dynamical processes that could be affecting conditions in other regions (temperature, rainfall, and wind, for example).

Another technique commonly used by climatologists is composite analysis. It involves creating typical climate states and using them to make inferences about dynamical conditions by studying similarities and differences between states.

In our forensic analysis, we used the aforementioned techniques to find hotspots and climate mechanisms to understand whether there was any relationship between the common guillemot population growth rate and mean sea-level pressure (i.e. the atmospheric pressure at sea level). Our point maps (see Figure 4, page 32) revealed some important features that helped unravel a few hypotheses for the climate dynamics effects:

(a) there were no hotspots that resembled a dipole in the Atlantic sector similar to the NAO, so we ruled out

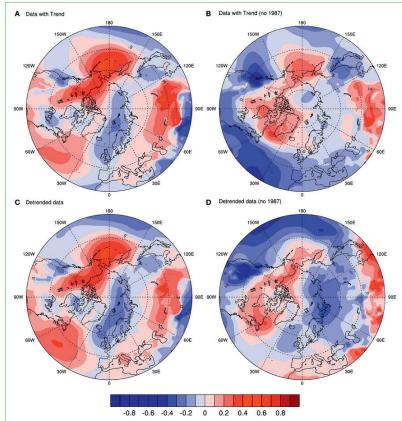


FIGURE 4 Illustration of the point correlation map approach we have used in our study. The figure shows the Pearson correlation coefficient (red is positive and blue is negative) of the correlation between the mean sea-level pressure (MSLP) and the guillemot population growth rate (r) based on the period 1980–2011. The correlation coefficient is calculated for each grid point. Also, since we wanted to check the correlation with and without the winter 1986-7 seabird crash, we have plotted the correlation with the winter of 1986-7 removed. The four plots display the correlation coefficient calculated as follows: (A) MSI P and raw r: (B) MSI P and r with the winter of 1986-7 removed from both series; (C) MSLP and detrended r; (D) MSLP and detrended r with the winter of 1986-7 removed from both series. Source: Mesquita et al.3

- the hypothesis that the NAO could explain the growth rate variability;
 - (b) there were coherent hotspots elsewhere, including the Pacific Ocean, so there could arguably be some teleconnection influence from remote areas - alternating positive and negative correlations could indicate wave propagation;
 - (c) one of the coherent hotspots was over the Barents Sea, where Hornøya is located, so there could be local processes modulating the climate variability in the region as well.

Thus, we proposed the following physical mechanism to explain the rise and fall of the common guillemot population (see Figure 5). Anomalous winter low-pressure systems over the Barents Sea are associated with higher population growth rates; low-pressure systems are associated with storms, which force upwelling mixing in the ocean (bringing nutrients to the surface that are important to fish stocks) and transport heat into the region. The opposite is true in years with anomalous high-pressure systems.

However, could these local changes in pressure help explain what happened in the winter of 1986-7? To answer this question, we applied composite analysis, which would tell us how atmospheric circulation behaves under different conditions. We isolated the winter of 1986-7, compared it against other periods, and verified that the winter in question did have an anomalous high-pressure system that was stronger than other periods. So, the anomalous high pressure would promote cold conditions and a lack of nutrients for the fish, which may have led to the lack of food that winter. Thus, the seabirds were weakened and the odds were against them.

But why were so many seabirds found dead on separate occasions? Carcasses were found washed ashore throughout late December 1986 and into January 1987. The answer to this question could be linked to the passage of polar lows that crossed the regions where the common guillemots were located. Polar lows are short-lived storms (with radii of 100-500 km and wind speeds above 15 ms⁻¹) that are sometimes compared to hurricanes. They provided another clue we needed for our analysis.

Yet one question still remained: how was the anomalous highpressure system in the Barents Sea created? This could arguably be accounted for by atmospheric activity from remote areas, as observed in the point maps. However, one element that is also important in the Barents Sea region is sea ice: it acts as a "lid", trapping heat that would otherwise be lost to the atmosphere. Fluxes of heat can perturb the atmosphere, for example, by providing energy to storms or by creating disturbances higher in the atmosphere which can then propagate to other regions. We investigated further and found that by regressing surface pressure against sea-ice concentrations in the Barents Sea, an anomalous high-pressure system was formed over the North Atlantic and Barents Sea sectors.

Putting the puzzle pieces together

As discussed earlier, the point maps did not show patterns that were characteristic of the NAO, so any correlation with the NAO would not be physically meaningful. Since a climate covariate was still needed in our population model, there was a need to create an index. This is also common practice in climate science: one selects a box (or a few boxes) around certain regions of interest. Then the average of the climate variable over that box (or boxes) would provide a time series that may be used as representative of local processes in the area.

More advanced statistical methods are needed in order to understand the full picture of how climate interacts with ecosystems

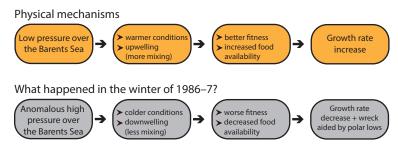


FIGURE 5 Hypothesised physical mechanisms of climate and population growth rate. (Top) An anomalous winter low-pressure system over the Barents Sea is associated with higher population growth rates: it creates warmer conditions and upwelling, brought by a synoptic-scale storm track into the region. This could lead to better fitness and increased food availability, which could partially promote an increase in growth rate of the common guillemot. The opposite would be the case in winters with an anomalous high-pressure system over the Barents Sea. (Bottom) The seabird crash in winter 1986-7 is partially explained by extreme conditions in the Barents Sea: a severe anomalous high-pressure system over the region and the presence of polar lows

Our point maps provided the location of hotspots from which we could select boxes for the creation of new indices. Three indices were created based on mean sea-level pressure and taking into account the sign of the correlation (whether positive or negative). The indices were: (a) IDX1, based on differences between the Barents Sea and the Northeast Atlantic regions; (b) IDX2, the difference between a box in the Pacific and another in the Alaskan region; and (c) IDX3, the sum of a box in the Pacific with the Barents Sea minus the sum of a box in the Northeast Atlantic with the Alaskan region. Note that some of the regions are remote, since teleconnectivity is something that could explain the variability in the growth rate of the common quillemot, and we wanted to test for that.

These covariates, as well as the NAO and a "null" model consisting of no covariates, were then tested in stochastic (or random) population models. The models were compared using the Akaike information criterion, corrected for small sample size, and the estimates were provided as means with their 95% confidence intervals. The population dynamics of the common quillemot on Hornøya are density-independent (see "Population model equation") and the analysis was conducted with and without the crash from 1986 to 1987.

The results of our population model showed that versions of covariates IDX2 and IDX3, which used detrended climate data, were the only ones that were significant (compared with versions that included a linear trend, IDX1, the NAO, and

Population model equation

$$\ln N_{t+1} = \ln N_t + \overline{r} - \frac{1}{2}\sigma_d^2 N_t^{-1} + \sum \beta_i X_{i,t} + \varepsilon_t$$

The equation parameters are as follows: N, is the population size in year t; \bar{r} is the long-term intrinsic population growth rate; σ_a^2 is the demographic variance; β_a is the slope of the ith environmental covariate X_i ; X_i , is the environmental covariate *i* in year *t*; and ε_i , represents the environmental noise at time t.

the null model). The fact that the NAO could not explain the population dynamics of the common guillemot confirmed our initial hypothesis and our climate dynamics analysis, which led us to suspect that other processes were at play, such as the local sea-level pressure conditions in the Barents Sea and their possible modulation through sea-ice conditions.

Case closed?

Our published forensic analysis explained in detail the climate dynamics mechanism that accounted for the death of common guillemots in the winter of 1986-7, the population dynamics of common guillemots, and the role of the atmosphere in modulating changes in the ocean and ecosystems.3 Simply put, we concluded that there seems to be an interaction between climate and prey stocks, which caused this collapse.

However, our work is not yet finished. Our attempts to unravel this mystery have highlighted the fact that new and more advanced statistical methods are needed in order to understand the full picture of how climate interacts with ecosystems, taking into account direct and indirect effects: and we hope that more and more statisticians will become interested in helping us make sense of the gamut of information we have at hand.

Seabird ecology presents a number of challenges, such as choosing climate covariates that make sense to use with a given ecological data set. Richardson et al. emphasise that "explicit statistical tests of congruence with a climate variable" are still needed in many publications.4 This highlights the need for closer collaboration with statisticians.

As we look to solve our next case – the synchronisation between multiple species in the Northern Hemisphere and climate - we hope to add more statistical sleuths to the investigating team.

Acknowledgements

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