

The use of biologically meaningful oceanographic indices to separate the effects of climate and fisheries on seabird breeding success

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An important issue when considering seabird breeding success is what factors affect prey availability. If availability reflects absolute prey abundance, different species preying on the same prey population should show synchronized variation in breeding success. If, on the other hand, species-specific foraging techniques coupled with prevailing oceanographic conditions result in differential access to prey, then, breeding success is likely to vary asynchronously between species. Furthermore, for each species, long-term variation in breeding success should be predictable using appropriate oceanographic covariates. Currently, commercial fishing quotas are set on the assumption that prey abundance is the only important factor for multi-species management. Therefore, it is essential to understand prey availability in the context of both climate change and fishing pressure. This requires an integrated approach and in this chapter we demonstrate the potential of combining long-term demographic data from seabirds with output from a one-dimensional physical–biological model. Using data from the North Sea, we examine relationships between breeding performance and biologically meaningful indices of the physical environment during a period of years with and without an industrial fishery. We speculate how the contrasting responses shown by two seabird species might reflect differences in prey availability mediated by foraging technique.

Over the last 20 to 30 years, seabirds in the North Sea have shown considerable temporal variability in breeding success (Ratcliffe 2004). These

changes have frequently been attributed to variation in feeding conditions, in particular availability of lesser sandeels (*Ammodytes marinus*), the principal prey of many seabirds during the breeding season (Furness & Tasker 2000). In general, surface-feeding species such as the black-legged kittiwake (*Rissa tridactyla*) have been more severely affected than diving species such as the common guillemot (*Uria aalge*) (Monaghan 1992). The lesser sandeel is also the target of the largest single-species fishery in the North Sea, and the impact of industrial fishing on seabird populations has been a major conservation and fisheries issue (Furness 2002). More recently, attention has shifted to the potential impact of climate change on the North Sea ecosystem and how this might disrupt predator–prey relationships (Edwards & Richardson 2004). One of the best-studied parts of the North Sea is the area around the Firth of Forth off the coast of southeast Scotland. An industrial fishery has operated in this area for some of the time that data on seabird demography and environmental conditions have been collected (Rindorf *et al.* 2000). This area is thus an ideal setting, not only for investigating relationships between predator performance and the physical environment, but also for separating out the effects of climate and fisheries.

NORTH SEA SEASONAL OCEANOGRAPHIC CYCLE

Oceanographic conditions prevailing during the time of seabird reproduction (April to July) are most likely to exert a direct influence on the availability of seabird prey and hence the birds' breeding success. It is thus necessary to consider the timing of seasonal events in the North Sea. As a shallow sea less than 200 m in depth, the seasonal cycle of the North Sea is relatively simple to understand and model in oceanographic terms (Otto *et al.* 1990, Turrell 1992). The North Sea's physical characteristics are dominated by tides, winds and solar radiation (Otto *et al.* 1990). During the winter months, the lower levels of radiation together with the stronger winds and tidal friction leave the water column completely mixed. In the spring, increasing amounts of sunlight and less windy conditions allow a decrease in vertical mixing. In those areas that are deep enough or have weaker tidal currents such that the effect of tidal mixing does not reach the surface, the surface layer begins to warm up (Pingree *et al.* 1978, Mann & Lazier 1996). This warming creates a difference in density between the upper and lower layers of the water column called 'stratification' (see glossary in Box 4.1). The onset of stratification allows plankton to remain above the 'critical depth' (see Box 4.1) needed for population growth. Consequently, the timing of

Box 4.1 Glossary

Bank regions. Large banks in the seabed topography off southeast Scotland, typically rising 20 to 40 m above the surrounding seabed, and measuring 10 to 30 km east–west and 50 to 100 km north–south.

Critical depth. If phytoplankton are continuously mixed between the sea surface and the critical depth, the light energy they receive is just sufficient to compensate for respiratory losses. If they are mixed in a region shallower than the critical depth, then growth exceeds respiratory losses and biomass can increase. If they are mixed deeper than the critical depth, then respiratory losses exceed growth and phytoplankton begin to die.

Primary production. The growth of phytoplankton in the ocean. Phytoplankton are single-celled plants, typically between 5 and 100 μm in size, and requiring both sunlight and nutrients in order to photosynthesize and grow. They are the ocean's primary producers, forming the base of the marine food chain.

Shallow sea front regions. These are also known as 'tidal mixing fronts' or 'shelf-sea fronts'. These fronts separate areas of shelf sea that are permanently vertically mixed (shallow water and/or strong tidal currents) from areas that thermally stratify during summer (deeper water and/or weaker tidal currents). They mark the boundary where the tendency towards summer stratification driven by solar heating is just countered by the tendency to redistribute heat through the water column by tide-induced turbulent mixing.

Spring bloom. As the solar irradiance increases in spring there is more light available for phytoplankton photosynthesis and more heat available for stratifying the water column. If the tendency towards stratification is able to overcome the mixing by tides and winds, the development of a warm surface layer isolates some phytoplankton, along with dissolved nutrients, in the surface layer. The stratification prevents these phytoplankton from being mixed into the deeper, darker water, and with ample light and nutrients they grow (bloom) rapidly. The bloom peaks quickly, but while the light in the surface layer continues to increase the nutrients are used up and cannot be easily re-supplied from the deeper water because of the inhibiting effect that the stratification has on mixing. The phytoplankton become nutrient-limited and, along with losses to grazing by herbivorous zooplankton, the bloom decays.

Stratification. A water column is stratified when the density of the water has some vertical variability. This could be because the surface water has been warmed (reducing its density compared with the deeper water), and/or because the surface water has a lower salinity. Stratification inhibits vertical mixing of heat, nutrients, phytoplankton, etc. and is a key process in controlling the light and nutrient environments experienced by phytoplankton.

stratification is generally believed to herald the beginning of the seasonal flush of ‘primary production’, referred to as the ‘spring bloom’ (see Box 4.1) (Miller 2004).

VARIABILITY IN THE SPRING BLOOM

The variability both in timing of the spring bloom and in the seasonal cycle of primary production at a given location in the North Sea is driven by the degree of mixing of the water column (Pingree *et al.* 1975, Simpson 1981, Fèvre 1986). Therefore, as the depth and speed of tides at any location are predictable (Pingree *et al.* 1978, Simpson & Bowers 1981), the variation in mixing, and hence primary production, is due to the inter-annual differences in the amount of wind, radiation and freshwater input received at that location. Thus, local meteorological forcing, such as daily wind speeds and the amount of sunlight and rain, drive variation in the timing and amount of production at the lowest trophic levels.

THE SPRING BLOOM AS AN INDICATOR

Almost 100 years ago, a hypothesis was formulated that the timing of the spring bloom, and therefore the availability of appropriate food, would greatly influence the survival of larval fishes (Hjort 1914). This idea was expanded upon by Cushing (1975), who coined the match–mismatch theory stating that high survival of fish larvae is expected in those years when the timing of spawning and hatching is such that larvae overlap appropriately with the timing of the spring bloom. Only recently has a study confirmed that fish recruitment does indeed increase when such an overlap occurs (Platt *et al.* 2003). However, the lack of support for the match–mismatch theory does not stem from a scarcity of studies addressing this question. Instead, it reflects the difficulties associated with sampling marine ecosystems repeatedly over appropriate temporal and spatial scales required to

simultaneously establish the timing of the spring bloom and estimate its effect on fish survival and growth.

Although the environmental features that trigger spring blooms have long been well understood in a general sense (Mann & Lazier 1996, Miller 2004), it is only recently that physical oceanographic modelling has advanced sufficiently to capture accurately the biological dynamics of these events at the temporal and spatial scales appropriate to the feeding behaviour of individual animals (Franks 1992, Sharples 1999, Waniek 2003). These types of models, in particular the one-dimensional physical–biological coupled model of Sharples (1999), allow the monitoring, in one location, of daily or hourly changes in vertical structure of the water column and the amount of primary production arising at any given depth at that location. However, marine ecologists are still some way from understanding the impact of between-year variation in the seasonal production cycle on higher trophic levels. This is because it is prohibitively expensive to continuously and simultaneously sample phytoplankton, zooplankton, and larval and adult fish. Therefore, a way to improve our understanding of marine-ecosystem functioning is to combine the quantitative predictions of these coupled physical–biological models with concurrent measurements of the foraging behaviour and breeding success of highly visible top predators such as seabirds. If the top predators can be shown to be good integrators of important signals being amplified as they move up the trophic levels, then we will have more reliable and immediate indicators of the current state of the ecosystem (Bertram *et al.* 2001, Gjerdrum *et al.* 2003).

OCEANOGRAPHY OF THE STUDY AREA AND REGION-SPECIFIC ONE-DIMENSIONAL PHYSICAL–BIOLOGICAL MODELLING

Our study area (Firth of Forth, 55° 30′ to 57° N, 3° W to 0° 30′ E) contains two of the hydrographic regions found within the North Sea (Otto *et al.* 1990): ‘Bank regions’ and ‘Shallow sea front regions’ (see Box 4.1). Both these water types are important foraging areas for seabirds breeding on the Isle of May, one of the main colonies in the area (see Daunt *et al.* (Chapter 12 in this volume) and Camphuysen *et al.* (Chapter 6 in this volume), for a description of the foraging distributions of these seabirds).

We used a one-dimensional physical–biological coupled model (Sharples 1999, see Box 4.2) to derive the inter-annual variability in the seasonal primary production patterns within these two regions (see Box 4.3). The one-dimensional model was parameterized using daily,

Box 4.2 The one-dimensional physical–biological model

The one-dimensional physical–biological coupled numerical model is based on that of Sharples (1999) and Sharples *et al.* (in press). The physical component of the model is driven by tidal forcing, surface heating and surface winds, calculating the vertical water column structure of currents, temperature (i.e. stratification) and light. A turbulence closure scheme (Canuto *et al.* 2001) is used to calculate the rates of turbulent mixing driven by tidal and wind stresses. The biological component calculates the response of a single phytoplankton species (in terms of chlorophyll concentration) to the light and nutrient environment, with the turbulent mixing controlling the vertical fluxes of phytoplankton and dissolved inorganic nutrients.

The model has been re-written with a graphical interface, allowing user input of all physical, chemical and biological parameters required to drive the modelled processes. The model was initially calibrated using the current- and temperature-profile information provided by the moorings at the two sites between March and July 2001, yielding a reliable agreement between modelled and observed tidal currents, vertical temperature structure and primary production. Meteorological information from 1974 to 2003 (see Box 4.3) was then used to calculate physical and biological time series over the 30-year period.

Box 4.3 Collection of fine-scale oceanographic, meteorological and bird breeding success data**Moorings**

In order to monitor at fine temporal and vertical resolution and to collect the data needed to parameterize the one-dimensional physical–biological model for the study area, moorings were placed in two regions in which seasonal production cycles were expected to differ: the bank region (depth 45 m, 56° 15' N, 02° 00' W) and the shallow sea front region (depth 65 m, 56° 15' N, 01° 15' W). The moorings provided information, at a 10-min resolution, on the changes in vertical structure (at 5- to 10-m intervals), such that it was possible to define the depth of the surface mixed layer and

the strength of the thermocline at any point in time. The mooring in the shallow sea front had two current meters, one fluorometer and eight mini-loggers (temperature recorders). The mooring in the bank region had one current meter, one fluorometer and seven mini-loggers. Each mooring was in operation from March to October for both 2001 and 2002.

Meteorological data

The most appropriate daily meteorological data for the study area, as needed to run the one-dimensional model, were collected from the Leuchars and Mylnefield meteorological stations, Scotland, UK. The database consists of hourly and daily weather indices for the last 30 years including wind speed, wind direction, irradiance, dew-point temperature and freshwater input (rain and river runoff). The data were obtained from the British Oceanographic and Atmospheric Data Centres (BODC and BADC).

Seabird breeding success

Standardized data on seabird breeding success were collected at the Isle of May, southeast Scotland ($56^{\circ} 11' \text{ N}$, $02^{\circ} 34' \text{ W}$). Breeding success, measured as the mean number of fledged chicks per pair, was estimated from 1982 to 2003 for the common guillemot (a pursuit-diver) and from 1985 to 2003 for the black-legged kittiwake (a surface-feeder).

local meteorological information and can therefore be used to recreate oceanographic conditions as far back in time as such data are available (see Box 4.2 and Box 4.3). The daily output of the model (Fig. 4.1) includes top and bottom temperatures and chlorophyll levels, as well as numerous other physical and biological variables, and allows calculation of the annual timing of the onset of stratification (taken as the time when the difference between top and bottom temperature exceeds 0.5°C) and the timing of the start of the spring bloom (when chlorophyll levels exceed 2 mg m^{-3}).

SANDEEL LIFE-HISTORY STAGES AND SEASONAL OCEANOGRAPHIC CYCLE

Primary production during the spring bloom provides food for zooplankton populations which, in turn, are the main food source of sandeels (Covill 1959, Monteleone & Peterson 1986). Therefore the timing, length

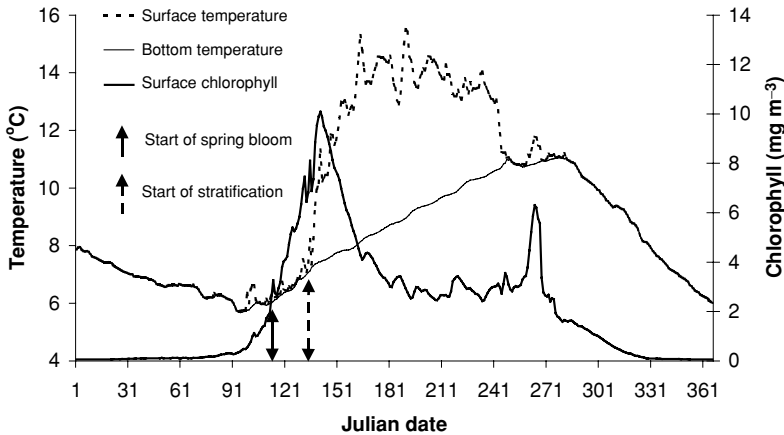


Fig. 4.1 An example of daily output of surface chlorophyll, surface temperature and bottom temperature from the one-dimensional physical-biological model for 1992. The solid arrow marks the timing of the start of the spring bloom, defined as the date when chlorophyll levels exceed 2 mg m^{-3} and stay above that value for five consecutive days. The dashed arrow marks the timing of the start of stratification, defined as the date when the difference between top and bottom temperatures exceeds $0.5 \text{ }^{\circ}\text{C}$ and stays above that value for five consecutive days.

and intensity of the bloom are all potentially important factors in determining food availability and hence the time spent foraging by larval, juvenile and adult sandeels. Sandeels in the North Sea spend the vast majority of their life buried in the sand (Reay 1970, Winslade 1974a, 1974b, 1974c, Pearson *et al.* 1984). In the Firth of Forth area they may only come out of the sands to feed between April and September (Worsøe 1999). In addition, the breeding component of the population emerges to spawn in late December and early January, and the eggs hatch by late February (Reay 1970, Winslade 1974b). Once hatched, the distance over which the larvae may be advected from spawning locations appears to be variable and dependent on wind speeds, wind directions and how fast the larvae attain the ability to make vertical migrations (Proctor *et al.* 1998, Munk *et al.* 2002, Jensen *et al.* 2003).

As soon as sandeels leave the protection of the sands and forage within the water column, they are subject to predation by a wide range of predators – such as larger fish (Greenstreet (Chapter 15 in this volume)), seabirds (Daunt *et al.* (Chapter 12 in this volume)) and marine mammals. Therefore, for sandeels to leave the substrate, the gain from food intake must override predation and starvation risks. In fact, it has been shown experimentally that low food availability significantly increased the time sandeels remained

buried in the sand (Winslade 1974a). Thus, it is reasonable to assume that the timing of the spring bloom will influence the timing of emergence of adult sandeels as well as the growth and survival of larvae and juveniles.

THE SANDEEL FISHERY

An industrial sandeel fishery targeting predominately adult sandeels was in operation in the Firth of Forth from 1990 to 1999. The fishery operated mostly in June but also extended into May and July in some years. Total annual catches ranged from 20 000 to over 100 000 t (Rindorf *et al.* 2000). The fishery was closed in 2000, but a catch of 3000 to 4600 t has been allowed each year up to the present (2004) for scientific purposes (P. Wright, FRS Marine Laboratory, Aberdeen, personal communication).

SEABIRD BREEDING SUCCESS IS LINKED TO AVAILABILITY OF SANDEELS VIA THE SPRING BLOOM

The breeding season is the most energetically demanding part of the seabird life cycle, and a successful outcome is critically dependent on the availability of sufficient amounts of high-quality food. If the initiation of the annual increase in primary production is the driving factor for the emergence of adult sandeels, timing of the spring bloom may be very important for the birds. The availability of adult sandeels at the right time is important in the early stages of the breeding season (egg laying and incubation) and thus may be a critical factor determining annual breeding success in seabirds (ICES 2004). During the chick-rearing period (typically in June), adult sandeels seemingly become less available as they disappear out of the diets of both kittiwakes and guillemots (Harris & Wanless 1985, Lewis *et al.* 2001). A likely explanation is that adult sandeels spend more time in the sands as the availability of their own food is declining; by this time of the year, primary production is falling rapidly due to the lack of free nutrients for phytoplankton growth (Miller 2004). Therefore, the birds must now depend more on juvenile sandeels and other prey species (such as sprat *Sprattus sprattus*) to feed their chicks and themselves. Spring conditions and their effect on the timing of primary production will have influenced the growth and survival of juvenile fish. It is therefore reasonable to assume that fledging success is also influenced by the timing and location of spring blooms. In short, spring-bloom timing is expected to influence all components of breeding success.

TIMING OF STRATIFICATION AND THE SPRING BLOOM IN THE BANK AND SHALLOW SEA FRONT REGIONS

To investigate annual variability in the timing of stratification and the spring bloom for the two regions, we ran the one-dimensional physical–biological coupled model over 30 years (1974–2003). In the bank region, we found that the mean date on which the spring bloom started was 19 April with a standard deviation of only 4.1 days. This constancy was maintained despite the amount of wind mixing in the weeks leading up to the bloom varying by an order of magnitude between years (mean amount of force of mixing from winds, wind stress, for March ranges from 0.02 to 0.20 N m⁻²). The mean start date for the bloom in the shallow sea front region was similar (21 April ± 5.4 days) and dates in the two regions were highly correlated ($r_p = 0.74$, $p < 0.001$).

Differences in water depth in the two regions resulted in consistent differences in the timing of the spring bloom relative to stratification. Thus in the shallower bank regions, the critical depth required for the modelled phytoplankton to achieve net growth is greater than the water-column depth and, on average, the spring bloom occurs 9 days before stratification (mean stratification date 28 April ± 12.3 days). In contrast, in the deeper shallow sea front region the spring bloom occurred at the same time as the water column became stratified (21 April ± 11.4 days). Any annual difference in the date of the spring bloom between the bank and the shallow sea front regions is therefore linked to the greater dependence on the development of stratification within the deeper region. Because stratification is not a prerequisite for growth in the shallower bank region, the initiation of the bloom is more simply related to increasing solar irradiance. This phenomenon has also been found in the southern North Sea (Haren *et al.* 1998) and may well be a feature of bank regions throughout the North Sea. The reliance on seasonal solar radiation levels for the timing of the spring bloom, in either region, explains the consistency of bloom dates and their proximity to the spring equinox.

SEABIRD BREEDING SUCCESS, TIMING OF THE SPRING BLOOM AND THE SANDEEL FISHERY

We compared the breeding success of kittiwakes and guillemots on the Isle of May to the timing of the spring bloom and stratification in the bank and the shallow sea front regions (see Box 4.3). For both species, results were similar for the two oceanographic regions and for both indices of timing.

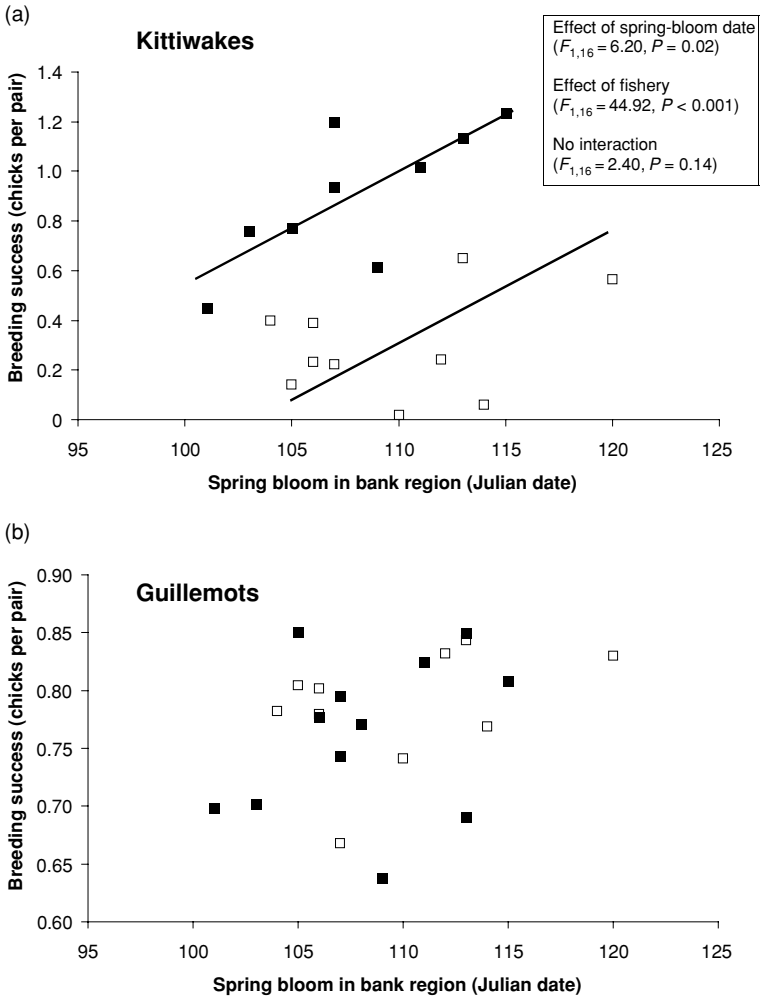


Fig. 4.2 Breeding success of (a) black-legged kittiwakes (1985–2003) and (b) common guillemots (1982–2003) on the Isle of May in relation to the start date of the spring bloom in the bank region, as estimated by the one-dimensional physical–biological model. Years with no commercial fishery for sandeels are represented by filled squares and years with a fishery with open squares.

To avoid unnecessary repetition, we therefore present quantitative results for the bank region and the timing of spring bloom only. Kittiwakes bred more successfully in the years when the spring bloom and stratification in either region occurred later. Breeding success increased by 0.13 chicks per pair for every 5 days delay in timing of the spring bloom (Fig. 4.2). There

was no evidence that the effect of date of the spring bloom on breeding success was different in fishing and non-fishing years (interaction: $F_{1,16} = 2.40$, $p = 0.14$), but breeding success was 0.33 ± 0.05 (mean \pm SE) chicks higher in years without fishing than in years with fishing ($F_{1,16} = 44.92$, $p < 0.001$). The final model containing both the effects of spring-bloom date and the sandeel fishery explained 74% ($p < 0.001$) of the variance in breeding success. Separating years with or without a fishery, the effect of climate alone explained 56% of the variance in breeding success in years without a fishery and 10% of the variance in years with a fishery. This suggests that important climatic variables are more easily identified in the absence of the confounding effects of a fishery.

A similar analysis carried out for guillemots, revealed that neither the timing of the spring bloom, nor stratification in either oceanographic region, had a significant effect on breeding success (Fig. 4.2).

DISCUSSION

With the use of a detailed one-dimensional physical–biological model we have shown how integrated and biologically meaningful region- and year-specific oceanographic variables can provide new insights into the mechanisms that link multiple meteorological conditions with seabird breeding success. In particular, we have used the timing of stratification and the spring bloom as possible indicators of sandeel availability. While previous studies have demonstrated statistical relationships between larger-scale oceanographic or climatic variables and seabird performance (e.g. Aebischer *et al.* 1990), our approach allows identification of proximate factors that directly affect seabird prey availability. In a system where experimental manipulation is impossible, this type of model is an extremely promising tool in the search for causal relationships among ecosystem components.

Information on the breeding success for seabirds with contrasting foraging strategies in an area where an industrial sandeel fishery has operated intermittently, and which has experienced large climatic changes (Edwards *et al.* 2002), provides a rare opportunity to investigate the effects of both climate and fishing activities. Our results suggest that breeding success of kittiwakes is higher in years when the spring bloom occurs relatively late throughout the study area. Because kittiwakes are surface-feeders and are more dependent on prey being present in the upper water column, this finding leads us to speculate that a later spring bloom increases the availability of prey in the upper water column during the breeding season. We

suggest that the mechanism by which this is achieved is through a slowing down in the growth of juvenile sandeels, possibly coupled with a delay in the emergence of adult sandeels. With elevated levels of food occurring relatively late in the season, the trade-off between predation and feeding may force fish to take longer to acquire adequate levels of food needed to survive the next winter. Either the slowing of fish growth, or the extension of the time window during which sandeels are feeding actively in the water column, could potentially provide an increase in prey availability, especially to surface-feeders.

These results accord well with those of Rindorf *et al.* (2000) who found that breeding success of Isle of May seabirds was higher when sandeel abundance peaked later in the season. They also help interpret the findings of Frederiksen *et al.* (2004) that kittiwake breeding success at the Isle of May was reduced when local winter sea temperature was high in the previous year. There is a weak negative correlation between winter sea temperature and the timing of the spring bloom in the current as well as the previous year ($r_p = -0.22 - 0.27$ respectively). Although spring-bloom timing here is modelled rather than measured, it is a more proximate and thus a much more interpretable correlate of breeding success than a single weather variable such as sea temperature. Using this biologically meaningful and locally specific index we have confirmed the conclusion of Frederiksen *et al.* (2004) that, under similar climatic conditions, kittiwakes suffer an additional reduction in breeding success in years when a commercial sandeel fishery is operating. Our approach allows us to quantify fishing and climate effects separately and indicates that the presence of a local sandeel fishery decreases breeding success of Isle of May kittiwakes by 0.33 chicks per pair whereas every 5-day delay in the date of the spring bloom increases breeding success by 0.13 chicks per pair.

For guillemots, annual variation in breeding success was not explained by the timing of spring blooms, stratification or the presence of a sandeel fishery (Fig. 4.2). Guillemots are pursuit-divers and are therefore less constrained in their foraging depths than kittiwakes (see Daunt *et al.* (Chapter 12 in this volume)). They thus have access to sandeels in the whole water column and are probably less likely to encounter food limitation. This contrast in how oceanographic factors affect the mechanism of prey availability helps explain why annual variations in breeding success of different species at the same colony may not be in phase (guillemot and kittiwake breeding success were not significantly correlated: $r_p = 0.26, p > 0.2$), and also why breeding success fluctuates less from year to year for guillemots than for kittiwakes (Fig. 4.2).

Although we have found here that for some species breeding success is linked to annual variation in the timing of spring blooms, seabird population growth is also affected by other demographic parameters. Indeed, because seabirds are long-lived, population growth rate is most sensitive to variation in adult annual survival (Croxall & Rothery 1991). Outside the breeding season, Isle of May seabirds range much more widely than our study area, in some cases over the entire North Atlantic Ocean. Seabirds only recruit into the breeding population when they are several years old, and during the pre-breeding period they range even more widely than adults. As encouraging as our present results are, identifying, measuring and modelling oceanographic variables at the appropriate spatial and temporal scale to understand interactions between seabird survival and recruitment still presents a major challenge.

More studies of this kind involving the use of one-dimensional physical–biological models as tools for connecting past and predicted changes in climate to higher trophic levels will bring us closer to identifying critical linkages within ecosystems. In a constantly changing environment, where future climate change is likely to have profound consequences for marine ecosystems, these models could prove invaluable tools for understanding and predicting impacts on higher trophic levels.

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