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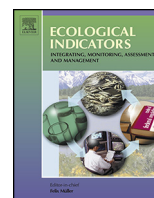


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Indicators of seabird reproductive performance demonstrate the impact of commercial fisheries on seabird populations in the North Sea



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ABSTRACT

In a world of growing anthropogenic pressures on biodiversity, effective indicators need to be specific and sensitive to the pressures in the ecosystem concerned, yet be simple enough to be interpreted by non-experts and straightforward enough to facilitate routine monitoring. Globally, seabirds are under increasing pressure as a result of anthropogenic activities and environmental variation. Traditionally, seabird indicators have been based on abundance at breeding colonies. However, as many species do not reach sexual maturity for several years, and may not attend the colony over this time period, such indicators may fail to capture the ecological complexity of the system concerned.

We constructed two indicators of the state of nine seabird species that breed along the UK coast of the North Sea: (i) abundance of seabirds at breeding colonies, and (ii) probability of seabird breeding failure. The indicators were significantly and strongly correlated with each other for eight out of nine species, but the abundance indicator typically lagged the indicator on seabird breeding failure by two to three years. We then considered a third indicator which compared kittiwake (*Rissa tridactyla*) breeding success to the levels expected given the underlying environmental conditions; changes in the abundance indicator also lagged this by three years. We investigate how sensitive each of these indicators was to the impacts of fishing. We found that the species which had seen the greatest increases in breeding failure rate over the study period were those species which were most sensitive to fisheries pressure.

By focussing on demographic parameters, and correcting for the underlying environmental conditions, we can detect potentially important population level changes at an earlier stage than by focussing on abundance alone. These indicators are able to more accurately capture the complexity of the ecosystem concerned and can be readily interpreted by policy-makers.

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1. Introduction

Globally, seabirds are under increasing pressure from anthropogenic activities, such as fishing, pollution and resource extraction (e.g. [Cury et al., 2011](#); [Furness, 2002](#); [Furness and Camphuysen, 1997](#); [Furness and Tasker, 2000](#); [Tasker and Becker, 1992](#); [Wiese and Ryan, 2003](#)). These pressures may exacerbate the impact of variation in environmental factors, such as climate ([Frederiksen et al., 2004a](#); [Gremillet and Boulinier, 2009](#); [Sandvik et al., 2005](#)). Consequently, there is an increasing recognition of the importance

of monitoring the impact of pressures on seabird populations ([Parsons et al., 2008](#); [Rogers and Greenaway, 2005](#)).

Monitoring population-level impacts of pressures on seabirds, however, presents a number of challenges. Counting the number of birds or breeding pairs attending colonies is relatively straightforward for most species ([Walsh et al., 1995](#)), but variation in the number of birds attending a colony may not necessarily reflect the influence of environment on population size. This is because, seabirds are long-lived and can delay breeding for several years following fledging. Adult birds may refrain from breeding in years when environmental conditions are poor ([Erikstad et al., 1998](#); [Oro and Furness, 2002](#)) and immature birds vary in the age at which they start attending the colony, and the age at which they start breeding ([Crespin et al., 2006](#); [Dittman and Becker, 2003](#); [Halley et al., 1995](#)). Consequently, a need has been identified to develop approaches to monitoring that allow the integration of processes acting at different levels ([Gremillet and Boulinier, 2009](#)). Evidence

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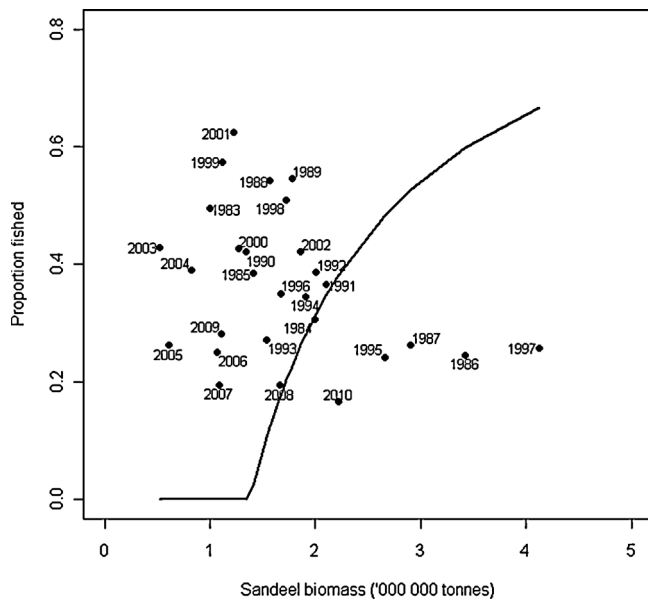


Fig. 1. The proportion of the sandeel population fished in each year in relation to total sandeel biomass in the North Sea. The black line shows the maximum proportion of the sandeel population that can be fished for any given population size whilst sticking to the “Third for the Birds” rule of Cury et al. (2011), that a third of the long-term maximum biomass of sandeel must be left by fisheries to support sustainable seabird populations in the North Sea.

suggests that reproductive performance of seabirds, rather than the number of birds attending a breeding colony, may be a better reflection of variation in environmental conditions (Erikstad et al., 1998; Piatt et al., 2007; Regehr and Montevecchi, 1997).

The United Kingdom (UK) provides a valuable case study with which to test indicators based on species breeding performance, because a wealth of monitoring data have been collected there over a number of years (JNCC, 2012; Lloyd et al., 1991; Mitchell et al., 2004). The UK is of great significance in terms of seabird conservation, hosting a large number of internationally important breeding colonies for several species (Mitchell et al., 2004). The implementation of the, legally binding, Marine Strategy Framework Directive (MSFD) across the European Union and in some neighbouring states requires an ecosystem-based approach to the management of human activities within the marine environment (EC, 2008). This means ensuring that “the collective pressures from human activities acting on the marine environment are kept at levels consistent with seas that are clean, healthy and productive, whilst providing for the sustainable use of marine goods and services by present and future generations” (EC, 2008). This legislation provides a strong policy driver to monitor seabird populations, to assess anthropogenic impacts on them, and to instigate management measures where necessary to reduce these impacts.

One of the main anthropogenic pressures on seabird populations, especially in UK waters, is caused by commercial fishing (Frederiksen et al., 2004b; Furness, 2002; Furness and Tasker, 2000). Commercial fishing can compete with seabirds over increasingly limited stocks of fish species. Based on data from seven seabird ecosystems, Cury et al. (2011) suggest that as a general rule, a third of the peak long term maximum stock size of forage fish should be left for birds in each year to ensure that seabird populations remain stable. For sandeel *Ammodytes* spp., key prey species for many seabirds in the North Sea (Rindorf et al., 2000; Wanless et al., 2005; Wright and Begg, 1997), this target was only met in five years between 1986 and 2010 (Fig. 1). We assess the impact that this pressure has had on seabird populations using long-term

monitoring data collected in a standardised fashion throughout the UK between 1986 and 2010.

We develop three indicators with which to assess the state of nine UK seabird populations. The first indicator examines annual variation in numbers of those nine species attending the breeding colonies and the second indicator examines the annual variation in breeding failure, defined as the probability of birds from that years’ cohort recruiting into the breeding population is close to zero, in these species. Furness and Tasker (2000) ranked species based on their sensitivity to reductions in sandeel abundance. If current levels of fisheries are having a detrimental impact on seabirds, we would expect this to be reflected in these indicators, with those species most sensitive to depleted stocks of prey species exhibiting the highest breeding failure rates and the most severe population declines. The third indicator focuses on the annual breeding success of a single well-studied species, kittiwake *Rissa tridactyla*, for which there are well established links between population trends and the availability of sandeel, a key prey species (Frederiksen et al., 2005, 2007; Harris et al., 1997; Lewis et al., 2001; Rindorf et al., 2000). Breeding success in the kittiwake has been shown to vary in relation to sea surface temperature in February and March of the previous year (hereafter SST₋₁, see Frederiksen et al., 2004a). This relationship reflects the availability of sandeel during the current breeding season because birds prey primarily on 1-group sandeels, whose abundance is related to water temperature in the spring of the previous year, when they hatch (Frederiksen et al., 2004a). This allows us to determine when breeding success has deviated from the level that would be expected under the observed environmental conditions at each kittiwake colony throughout our study period.

The potential for developing seabird indicators based on the breeding success has been widely discussed (Frederiksen et al., 2004a, 2008; Wanless et al., 2007) and there is a clear ecological rationale for doing so. Amongst long-lived species, which may not breed every year, changes in abundance and survival may not be apparent for several years. In contrast, changes in factors such as breeding success may be more responsive to environmental pressures. With this in mind, we may expect abundance-based indicators to lag those based on measures of breeding success or failure.

In order to assess the relative health of the seabird populations within North Sea and Celtic Sea, corresponding to the Greater North Sea and Celtic Seas OSPAR regions (Tromp and Wieriks, 1994), we compare the indicator values between these two regions. A key aim of these indicators is to assess the impact of commercial fisheries on seabird populations. The use of seabirds as quantitative indicators in this fashion has been questioned (Gremillet and Charmantier, 2010), with concerns over the plasticity of species response to change and the applicability of indicators beyond species breeding grounds (Dänhardt and Becker, 2011). We therefore examine whether the indicators are sensitive to changes in fish stocks and fishing pressure and discuss regional population differences between populations in relation to likely food stocks. Finally, we consider whether the inclusion of demographic parameters can improve our existing suite of indicators.

2. Materials and methods

2.1. Data collection

Seabird populations in Britain and Ireland are monitored on an annual basis at a range of colonies throughout Britain and Ireland as part of the Seabird Monitoring Programme (SMP, <http://jncc.defra.gov.uk/page-1550>). Data describing the number of pairs (typically estimated as either the number of adult birds present or the number of apparently occupied nests, sites or

territories, depending on species) and productivity (number of fledged chicks) at each colony are collected in a systematic fashion (Walsh et al., 1995). Productivity data are collected from colonies using a randomly sampled selection of nests or sites. The annual breeding success at each colony is then taken to be the mean number of fledged chicks produced per nest per year (Walsh et al., 1995). The survey covers a broad geographic area, largely relying on volunteer surveyors.

We used SMP data collected between 1986 and 2010. As is typical of many large-scale ecological datasets (e.g. Fewster et al., 2000), the time-series contained some missing values. We used a generalised linear modelling (GLM) framework within R 2.12.0 (R Development Core Team, 2012) to complete the time series, by modelling abundance and breeding success as a function of colony and year and using the resultant model coefficients to estimate the missing values.

Indicators were developed using abundance and productivity data for nine widespread and abundant species in the UK, which were representative of the wider seabird community – fulmar *Fulmarus glacialis*, shag *Phalacrocorax aristotelis*, kittiwake, Sandwich tern *Sterna sandvicensis*, common tern *Sterna hirundo*, Arctic tern *Sterna paradisaea*, little tern *Sternula albifrons*, guillemot *Uria aalge* and razorbill *Alca torda*. Separate indicators were developed for each region as differing pressures and prey stocks mean that seabird population trends differ between the east (North Sea) and west coasts (Celtic Seas) of the UK (Chivers et al., 2012; Cook et al., 2011; Frederiksen et al., 2005; JNCC, 2012).

2.2. Abundance indicator

To minimise the impact of year to year variation in coverage the colonies, which were sampled on an annual basis, the number of birds counted at each colony (site) in each year was modelled in relation to year and site factors using a GLM with a Poisson error structure and logarithmic link function (Fewster et al., 2000). The (back-transformed) coefficient for year was taken to represent the annual abundance index for each species, relative to its abundance in 1986. Site was fitted as a fixed-effect factor, rather than a random effect so that the individual coefficients fully reflect the actual data, rather than being constrained to follow a normal distribution.

So that no individual site had undue influence over the value of the coefficients, a jack-knife approach was used, dropping each site from the model in turn. Models were run for each species in each region in turn. The final indicator value presented for each species in each year is the mean index value calculated over all runs of the jack-knife.

2.3. Breeding failure indicator

Breeding success for each colony in each year was calculated as the mean number of chicks per nest, and where this value was below 0.1 chicks per nest, it was assumed that effectively no birds would be recruited into the population and the colony was assessed as having failed in that year. In years when breeding failure was not recorded, breeding success was typically in the region of 0.4–0.7 chicks per nest for each of the study species (JNCC, 2012).

The breeding failure indicator was calculated in a similar fashion to the abundance indicator. The probability of breeding failure being recorded at a colony follows a binomial distribution, in that in each year the colony can either fail or not fail. As with abundance, breeding failure was modelled within a GLM framework in relation to year and site, but with a binomial error structure and logit link function. The coefficient for each year was then taken to represent the probability of breeding failure occurring at any given site within that calendar year. Again, a jack-knife approach was used to ensure that no colony had undue influence over the final indicator

value. Models were run for each species in each region in turn. The final indicator value presented for each species in each year is the mean probability of breeding failure calculated from each run of the jack-knife.

2.4. Kittiwake breeding success indicator

Kittiwake breeding success has previously been shown to be related to SST₋₁, with warmer winters resulting in reduced sandeel recruitment, and consequently reduced sandeel availability for kittiwakes in the following year (Frederiksen et al., 2007). This relationship offers the potential to develop an indicator based on kittiwake breeding success that can be corrected for prevailing environmental conditions, making it possible to more accurately monitor the impact of anthropogenic activities, such as fisheries.

Kittiwake breeding success was monitored at over 100 colonies in the UK between 1986 and 2010 (JNCC, 2012). In order to ensure confidence in our models, we first used power analysis in the R package “pwr” (Champely, 2012) to determine that a minimum of 13 years data were required to detect a significant relationship between kittiwake breeding success and SST₋₁. Analyses were therefore restricted to the 29 colonies on the North Sea coast and 10 colonies on the Celtic Seas coast where kittiwake breeding success had been monitored for 13 years or more.

At each colony, a baseline level of breeding success was calculated using a mixed effect GLM. Colony was fitted as a random effect and SST₋₁, obtained from the Hadley Centre Sea Ice and Sea Surface Temperature (HadISST) dataset (Rayner et al., 2003), was fitted as a mean fixed effect with a random slope to account for colony specific differences in the relationship between SST₋₁ and breeding success, arising from processes such as density dependence. The number of young per nest did not follow a standard distribution, consequently, we modelled breeding success as the number of young produced per egg, which has a binomial distribution, as each egg will either produce a fledged chick or not, assuming a mean of two eggs per nest (range 0–3, e.g. Golet et al., 1998; Harris and Wanless, 1997). Weighting was introduced to account for the different number of nests in each colony. The predicted success rate per egg at each colony was then calculated from the model and transformed to give an estimate of breeding success per nest. Upper and lower 95% confidence limits were calculated around this prediction. Where the observed breeding success was greater than the lower limit around this estimate the indicator target was assessed as having been achieved at that colony in that year. Models were fitted using the “lme4” package in R 2.12.0 (Bates et al., 2011).

In deriving the final indicator value for each year, it was necessary to account for the fact that not every colony was monitored every year. To do this we followed the protocol described above modelling failure or success in achieving the indicator target within a binomial GLM framework in which year and colony were fitted as factors. The indicator value for each year is the proportion of colonies at which the observed level of breeding success was predicted to be below the lower confidence limit of the breeding success predicted given the underlying environmental conditions.

2.5. Impact of sandeel fisheries on seabird productivity in the North Sea

In order to examine whether the indicators were sensitive to changes in fish stocks and fishing pressure, fisheries data and sandeel stock assessment data were extracted for the North Sea from the ICES Stock Assessment Database (ICES, 2011). As fisheries data were only available for the North Sea subsequent analyses focus on this region.

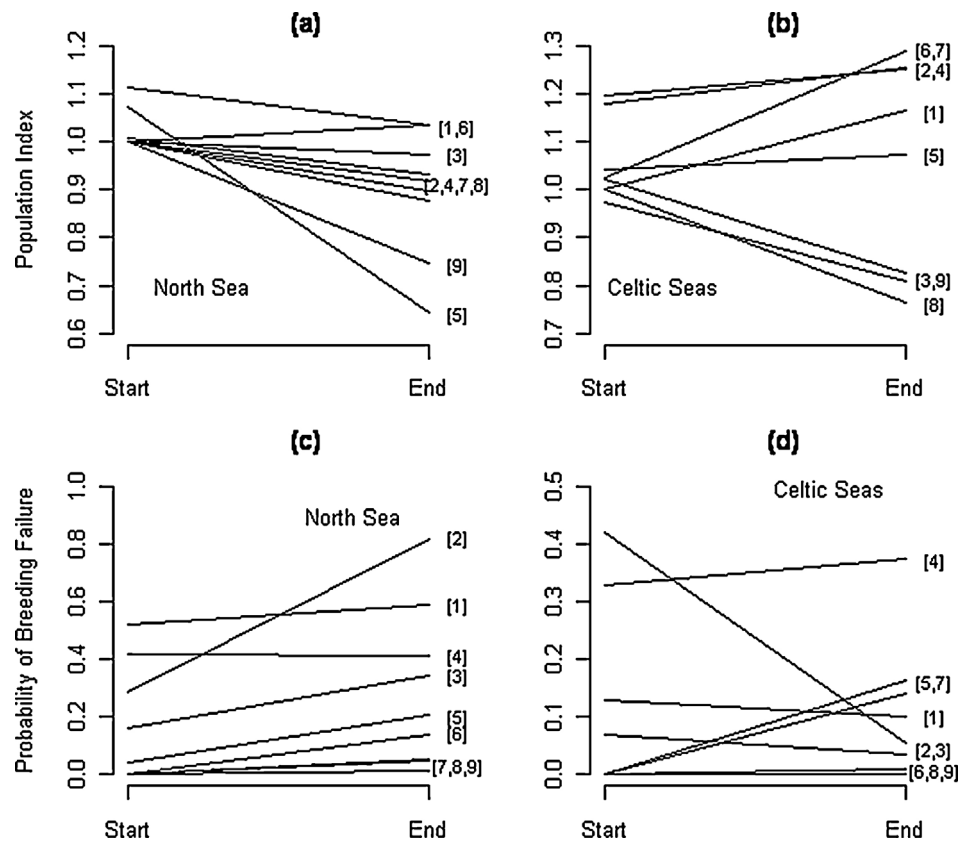


Fig. 2. Change in the median indicator value between the 'start' period 1986–1990 and 'end' period 2006–2010 for (a) the abundance indicator in the North Sea, (b) the abundance indicator in the Celtic Seas, (c) the breeding failure indicator in the North Sea and (d) the breeding failure indicator in the Celtic Seas. Species shown [1] Arctic tern [2] little tern [3] common tern [4] Sandwich tern [5] kittiwake [6] razorbill [7] guillemot [8] shag [9] fulmar, ordered according to their sensitivity to food shortages as assessed by [Furness and Tasker \(2000\)](#).

On an annual basis, the magnitude of the impact of sandeel fisheries may be dependent on the size of the stock during the year in question. [Cury et al. \(2011\)](#) suggest that a third of the long-term maximum population should be left for birds. This implies that it is possible to harvest a higher proportion of sandeel during years in which the stock is large, without having an impact on seabird populations. Consequently, to determine the impact of fisheries pressure on our study species, we modelled our annual indicator values in relation to sandeel population size and the proportion of sandeels harvested. In order to examine the impact of fisheries on our study species, we fitted an interaction term between sandeel population size and the proportion of stock harvested, rather than considering the total number of sandeel available to our study species. We then relate the model coefficients from each study species to their sensitivity to reductions in sandeel abundance, as assessed by [Furness and Tasker \(2000\)](#), and to the annual change in breeding failure.

3. Results

3.1. Abundance

Between 1986 and 2010 trends in seabird abundance differed strongly between the North Sea and Celtic Seas regions. In the North Sea ([Fig. 2a](#)), eight out of the nine study species appear to have declined in abundance; these declines have been particularly pronounced in the kittiwake and fulmar. Patterns were more variable in the Celtic Seas region, where only three species have declined, and populations of the remaining six have been stable, or increased ([Fig. 2b](#)).

3.2. Breeding failure rates

Breeding failure rates showed strong variation, between both species and regions. Between 1986 and 2010, the rate of colony failures increased amongst eight species in the North Sea ([Fig. 2c](#)). In contrast, in the Celtic Seas, breeding failure rates increased in only three species (Sandwich tern, kittiwake and guillemot), declined in a further three (Arctic tern, little tern and common tern), and remained around zero for the remaining species ([Fig. 2d](#)). Throughout the study period, colony failure rates were typically higher at North Sea colonies than at Celtic Seas colonies.

Breeding failure rates appeared to vary by species group. By 2010, the highest failure rates were recorded in terns and the kittiwake ([Fig. 2c](#) and [d](#)).

3.3. Kittiwake breeding success

In the North Sea, SST_{-1} had a significant, negative impact on kittiwake breeding success at the sample colonies (Effect Size -0.18 ± 0.05 , $P < 0.001$, $R^2 = 0.30$, [Fig. 3](#)). However, in the Celtic Seas the relationship was not statistically significant (Effect Size 0.07 ± 0.24 , $P = 0.77$, $R^2 = 0.25$). Use of the indicator was therefore restricted to the North Sea region, where the probability of breeding success being lower than expected at any given colony was assessed by comparing observed levels of breeding success to the lower 95% confidence limit on the value predicted given the observed SST_{-1} ([Fig. 3](#)).

The proportion of colonies at which breeding success was at or above what would be expected given the underlying environmental conditions fluctuated between 1986 and 1994 from 80% to

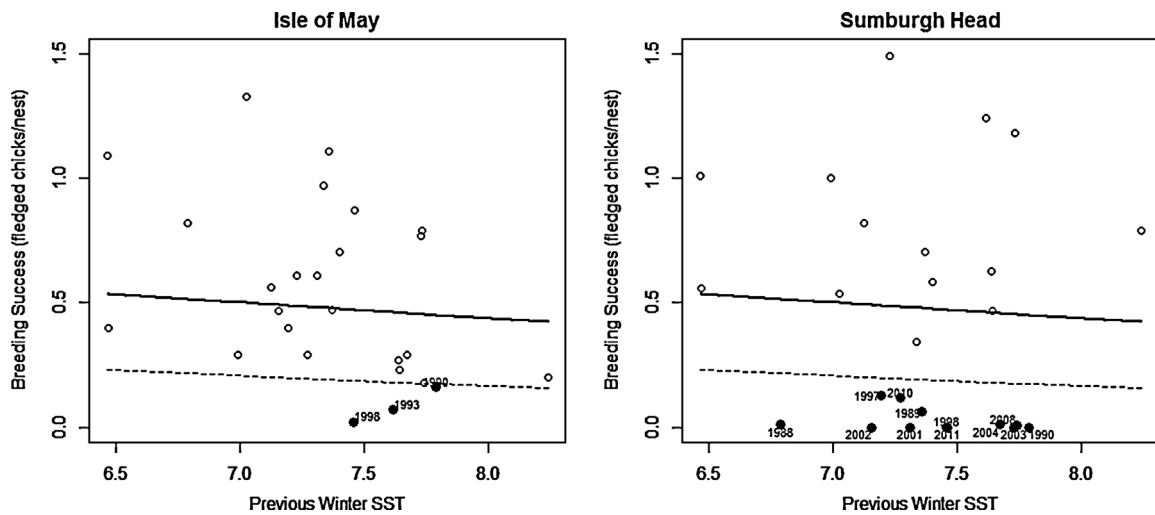


Fig. 3. Kittiwake breeding success indicator at Isle of May and Sumburgh Head colonies between 1986 and 2010. Solid line shows level of breeding success expected at each colony given the Sea Surface Temperature in February and March of the previous year. Where the recorded breeding success is below the 95% confidence limit surrounding this value, shown by the broken line, the indicator target is said to have been missed.

100% (Fig. 4). After 1994, the frequency with which colonies failed to achieve the target level of breeding success began to increase, with as few as 52% of colonies in 2004 and 54% of colonies in 2008 satisfying the target.

3.4. Comparison of indicator values

In the North Sea, the abundance indicator appeared to be at least as variable as the breeding failure indicator for all species except Sandwich tern (Fig. 5). This pattern was repeated in the Celtic Seas. Such variability makes it harder to discern a trend in the data from background noise.

In the North Sea region, there was a significant correlation between the indicator values for little tern, kittiwake and fulmar

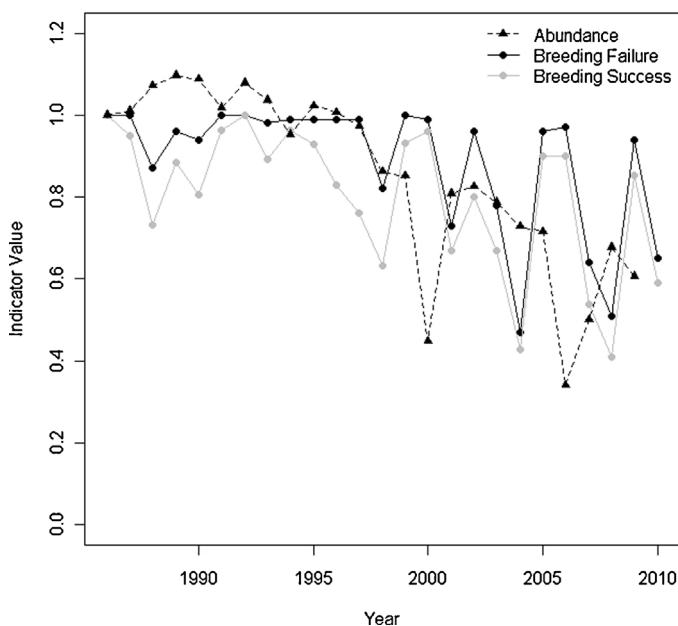


Fig. 4. Annual abundance, breeding failure and breeding success indicators for kittiwake in the North Sea. Abundance indicator shows population relative to 1986, corrected for differences in survey coverage, breeding failure indicator shows the proportion of colonies predicted to fledge more than 0.1 chicks nest⁻¹ and breeding success indicator shows the proportion of colonies at which breeding success is at the level expected given the underlying environmental conditions.

(Table 1). However, for eight of the nine study species the strongest correlations were observed between the abundance indicator and the breeding failure indicator one or more years previously. This pattern is particularly noticeable in the fulmar, European shag, kittiwake, guillemot and Arctic tern, where strong, negative correlations were recorded between abundance and the incidence of breeding failure two to three years previously (Table 1). Correlations between abundance and the proportion of kittiwake colonies achieving the required level of breeding success showed a similar pattern and were strongest when abundance was compared to the value of the breeding success indicator two years previously ($r=0.65$, $P<0.01$, Table 1).

A similar pattern was observed in the Celtic Seas region, where the strongest correlations were typically between abundance and breeding failure one to four years previously (Table 2). Again, the strongest relationship was between kittiwake abundance and the proportion of colonies achieving the required level of breeding success two years previously ($r=0.71$, $P<0.01$). However, amongst other species, relationships were less apparent, possibly the consequence of fewer colonies contributing data in the Celtic Seas region than in the North Sea region (Tables 1 and 2).

In the North Sea, the annual proportion of kittiwake colonies achieving the required level of breeding success and the proportion of kittiwake colonies where breeding failure was recorded were, not unsurprisingly, strongly, negatively correlated ($r=-0.95$, $P<0.01$, Fig. 4).

3.5. Impact of fisheries on seabird productivity in the North Sea

In years when the total biomass of sandeel in the North Sea was low, a higher proportion of the stock was harvested (Fig. 1). The proportion of sandeel harvested appeared to peak when total biomass was estimated at around 2 million tonnes. As total biomass rises above this figure, the proportion of the population harvested declines.

The breeding failure indicators and kittiwake breeding success indicator showed consistent negative relationships with fisheries pressure, represented by the interaction between sandeel population size and the proportion of the population harvested (Table 3). The magnitude of these relationships varied on a species-specific basis, being particularly strong in species like the little tern, kittiwake and razorbill, but weaker in others like the Sandwich tern

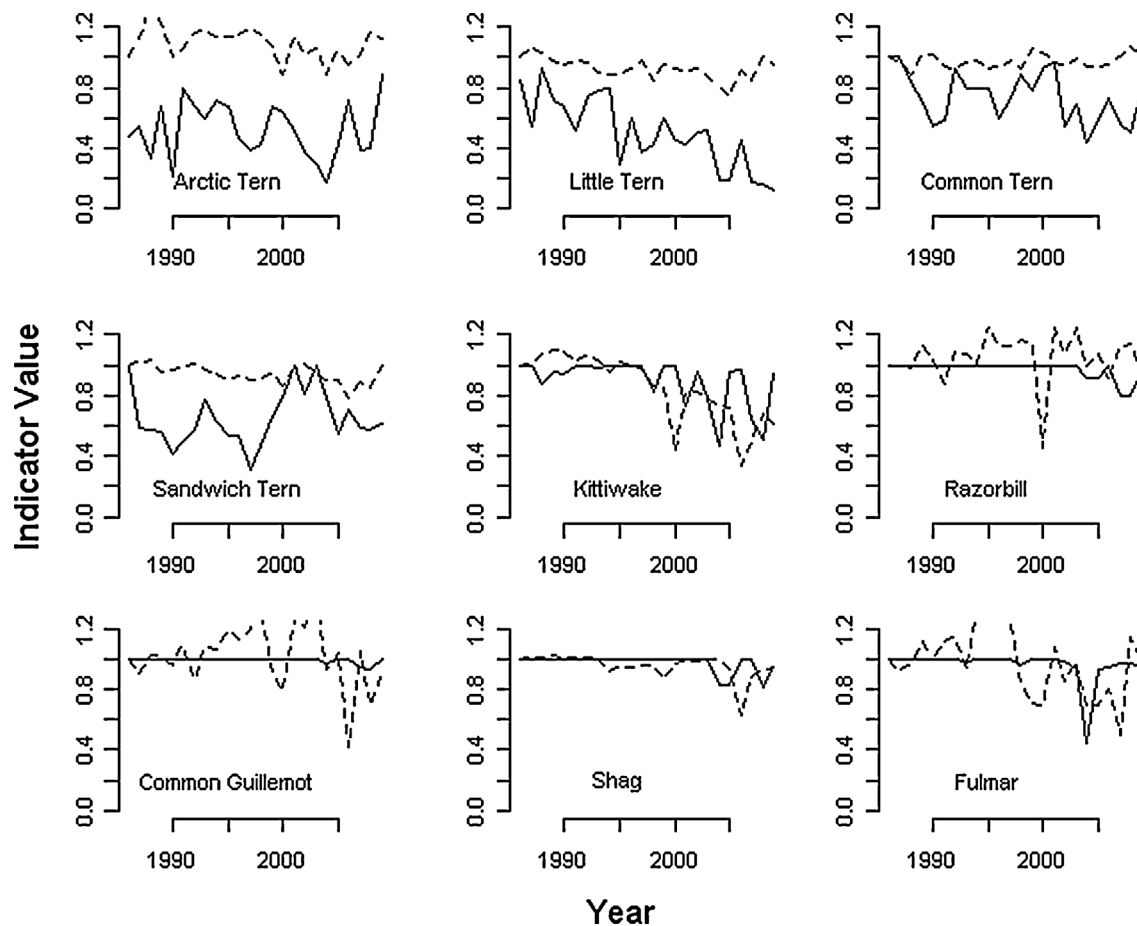


Fig. 5. Indicators for seabird breeding failure (solid line, shown as 1-proportion of colonies failing) and seabird abundance (broken line) in the North Sea between 1986 and 2010.

and guillemot. In contrast, the effect size for sandeel population size alone was typically much lower, indicating a weaker relationship.

The species which showed the strongest relationship between breeding failure rate and sandeel population size were weakly correlated with those assessed as being most vulnerable to reductions in sandeel abundance by Furness and Tasker (2000) (Fig. 6a). However, sensitivity to changes in food supply did not appear to account for the increases in breeding failure rate observed amongst these species in the North Sea over the study period (Fig. 6c). Instead, there appeared to be a strong correlation between increases in breeding failure and fisheries pressure when sandeel populations were depleted (Fig. 6d). It is noticeable that the data point for

little tern has high leverage in Fig. 6d, however, even with this point excluded there is still a strong, negative correlation between breeding failure rates and the effect size for fisheries pressure ($r = -0.87$, $p < 0.01$).

4. Discussion

4.1. Seabird indicators

Ecological indicators have a widespread appeal to scientists, environmental managers, politicians and the general public (Niemi and MacDonald, 2004). They act as a means of conveying

Table 1

Correlations between seabird breeding failure indicator and seabird abundance indicator between 1986 and 2010 in the North Sea.

| | No. of colonies | No lag | Year +1 | Year +2 | Year +3 | Year +4 | Year +5 | Age at first breeding |
|--------------------------------------|-----------------|----------------|----------|-----------------|----------------|---------------|--------------|-----------------------|
| Arctic tern | 41 | -0.12 | -0.12 | -0.42** | -0.32 | -0.04 | 0.21 | 4 |
| Little tern | 26 | -0.44** | -0.28 | -0.15 | -0.37* | -0.02 | -0.08 | 3 |
| Common tern | 45 | 0.08 | 0.10 | -0.14 | 0.17 | 0.40* | 0.22 | 3 |
| Sandwich tern | 17 | -0.15 | -0.18 | 0.03 | 0.24 | 0.44** | 0.47* | 3 |
| Kittiwake | 37 | -0.37* | -0.33 | -0.65*** | -0.49** | -0.26 | -0.42* | 4 |
| Razorbill | 5 | 0.11 | -0.07 | -0.17 | 0.14 | -0.03 | -0.14 | 4 |
| Common Guillemot | 11 | -0.28 | -0.28 | -0.44** | 0.03 | -0.34 | -0.12 | 5 |
| Shag | 11 | -0.01 | -0.55*** | -0.75*** | -0.16 | -0.02 | 0.01 | 4 |
| Fulmar | 30 | -0.34* | -0.36* | -0.26 | -0.44** | 0.10 | 0.03 | 9 |
| Mean correlation | | -0.17 | -0.23 | -0.33 | -0.13 | 0.03 | 0.02 | |
| Kittiwake breeding success indicator | | 0.35 | 0.32 | 0.65*** | 0.51** | 0.35 | 0.44 | |

Strongest correlation for each species in bold. Also shown is age at first breeding for each species, taken from Robinson (2005).

* Pearson correlation coefficients are shown for lags between abundance and breeding failure of between one and five years and are significant at $P < 0.1$.

** Pearson correlation coefficients are shown for lags between abundance and breeding failure of between one and five years and are significant at $P < 0.05$.

*** Pearson correlation coefficients are shown for lags between abundance and breeding failure of between one and five years and are significant at $P < 0.01$.

Table 2

Correlations between seabird breeding failure indicator and seabird abundance indicator between 1986 and 2010 in the Celtic Sea.

| | No. of colonies | No lag | Year + 1 | Year + 2 | Year + 3 | Year + 4 | Year + 5 |
|------------------------|-----------------|--------------------|----------------------|----------------------|----------|--------------------|---------------------|
| Arctic tern | 22 | 0.18 | −0.09 | 0.10 | −0.21 | −0.06 | −0.01 |
| Little tern | 4 | −0.23 | −0.23 | 0.14 | 0.02 | −0.13 | −0.16 |
| Common tern | 40 | −0.08 | −0.09 | −0.03 | −0.26 | −0.24 | −0.20 |
| Sandwich tern | 3 | 0.29 | 0.07 | −0.08 | −0.23 | −0.37 [*] | −0.50 ^{**} |
| Kittiwake | 15 | −0.35 [*] | −0.63 ^{***} | −0.71 ^{***} | −0.16 | −0.01 | −0.16 |
| Razorbill ^a | 2 | | | | NA | | |
| Common Guillemot | 3 | −0.08 | −0.13 | 0.02 | 0.01 | 0.01 | 0.01 |
| Shag | 17 | −0.05 | 0.01 | −0.20 | −0.19 | −0.29 | −0.04 |
| Fulmar ^a | 15 | | | | NA | | |
| Mean correlation | | −0.04 | −0.16 | −0.11 | −0.15 | 0.16 | 0.15 |

Strongest correlation for each species in bold.

^a Breeding failure not recorded in any fulmar or razorbill colony in the Celtic Sea over the study period so no correlations between indicators are possible for these species.^{*} Pearson correlation coefficients for lags between abundance and breeding failure of between one and five years and are significant at $P < 0.1$.^{**} Pearson correlation coefficients for lags between abundance and breeding failure of between one and five years and are significant at $P < 0.05$.^{***} Pearson correlation coefficients for lags between abundance and breeding failure of between one and five years and are significant at $P < 0.01$.

information about the condition of the environment, an early warning signal for potential ecological problems and as monitors for trends in ecological resources. Consequently, indicators are widely used within a legislative framework to determine progress towards meeting environmental (and other) objectives. However, to be effective, they need to capture the complexity of the ecosystem concerned, as well as being simple enough to be understood with a methodology that is both transparent and straightforward enough to facilitate routine monitoring, both in terms of data capture and cost (Dale and Beyler, 2001). For long-lived species, which may not reach sexual maturity for several years, simple abundance-based indicators (such as the number of birds attending a colony) may not fully capture the complexity of the ecosystem concerned.

The trends obtained from our abundance and breeding failure indicators highlight differences between seabird populations in the North Sea and Celtic Seas. In the North Sea, species abundance at breeding colonies is declining and breeding failure rates are increasing. In the Celtic Seas, the picture is more mixed, with some species declining, and others relatively stable or increasing. These differences may be related to food supply and the pressure from fisheries. SST₋₁ is believed to influence kittiwake breeding success through impacts on sandeel productivity (Frederiksen et al., 2004a).

In developing the abundance and breeding failure indicators, data were available from fewer colonies in the Celtic Seas than in the North Sea reflecting, in part and the distribution of several of our study species, and in part the distribution of surveyors. If the sample colonies were drawn from a single part of the Celtic Seas, there is a danger that they would not reflect patterns across the region as a whole (Cook et al., 2011). However, whilst for several species data were available from a limited number of colonies, these reflected the geographic extent of the region, minimising the probability of trends being influenced by data from a more localised area.

Table 3

Effect sizes from models of species breeding failure rates (and the kittiwake breeding success indicator) in relation to sandeel population size and the interaction between sandeel population size and the proportion of the population harvested. Species listed in descending order of their sensitivity to reductions in sandeel abundance as assessed by Furness and Tasker (2000).

| | Sandeel population size coefficient | Sandeel population size: fisheries coefficient | Model R ² |
|--------------------------------------|-------------------------------------|------------------------------------------------|----------------------|
| Arctic tern | 0.01 ± 0.06 | −0.12 ± 0.21 | 0.02 |
| Little tern | 0.09 ± 0.06 | −0.69 ± 0.21 | 0.30 |
| Common tern | −0.04 ± 0.05 | −0.16 ± 0.17 | 0.25 |
| Sandwich tern | 0.07 ± 0.06 | −0.03 ± 0.19 | 0.10 |
| Kittiwake | −0.01 ± 0.05 | −0.25 ± 0.16 | 0.18 |
| Razorbill | 0.03 ± 0.01 | −0.22 ± 0.06 | 0.41 |
| Common Guillemot | 0.01 ± 0.01 | −0.04 ± 0.02 | 0.24 |
| Shag | 0.01 ± 0.01 | −0.13 ± 0.06 | 0.27 |
| Fulmar | −0.02 ± 0.03 | −0.11 ± 0.12 | 0.12 |
| Kittiwake breeding success indicator | −0.01 ± 0.05 | −0.20 ± 0.18 | 0.12 |

In developing the kittiwake breeding success indicator, our analyses showed that the relationship between sandeel productivity and kittiwake breeding success held in the North Sea, but not the Celtic Seas. The lack of a relationship is consistent with another recent study that failed to detect a climatic effect on kittiwake productivity there (Lauria et al., 2012). The different relationships for the two regions may reflect differences in prey availability, with herring *Clupea harengus* a more important component of seabird diets in the Celtic Seas than in the North Sea (Chivers et al., 2012; Lauria et al., 2012). Kittiwake breeding failure in the North Sea was strongly correlated with the proportion of colonies at which breeding success was lower than would have been expected given the underlying environmental conditions (Fig. 4). However, taking environmental conditions into account meant important changes could be detected earlier than by focussing purely on breeding failure. The proportion of colonies at which breeding failure was recorded remained relatively stable between 1992 and 1997, with declines thereafter. However, when for environmental conditions are accounted for, the results suggest that breeding success may have started to decline as early as 1994 (Fig. 4).

4.2. Impact of fisheries

These indicators can be displayed in a manner which makes it possible to readily determine which colonies are failing, how frequently they fail and whether failures are localised, or occur more widely as indicated by the kittiwake breeding success indicator in Fig. 7. We can then make inferences about the pressures influencing these indicators and how these are changing over time.

Sandeel are a key prey species for many seabirds, and we show that the presence of an active fishery can have a detrimental effect on seabird populations (Cury et al., 2011; Frederiksen et al., 2004a,b, 2007, 2008; Parsons et al., 2008). Our study species had varying

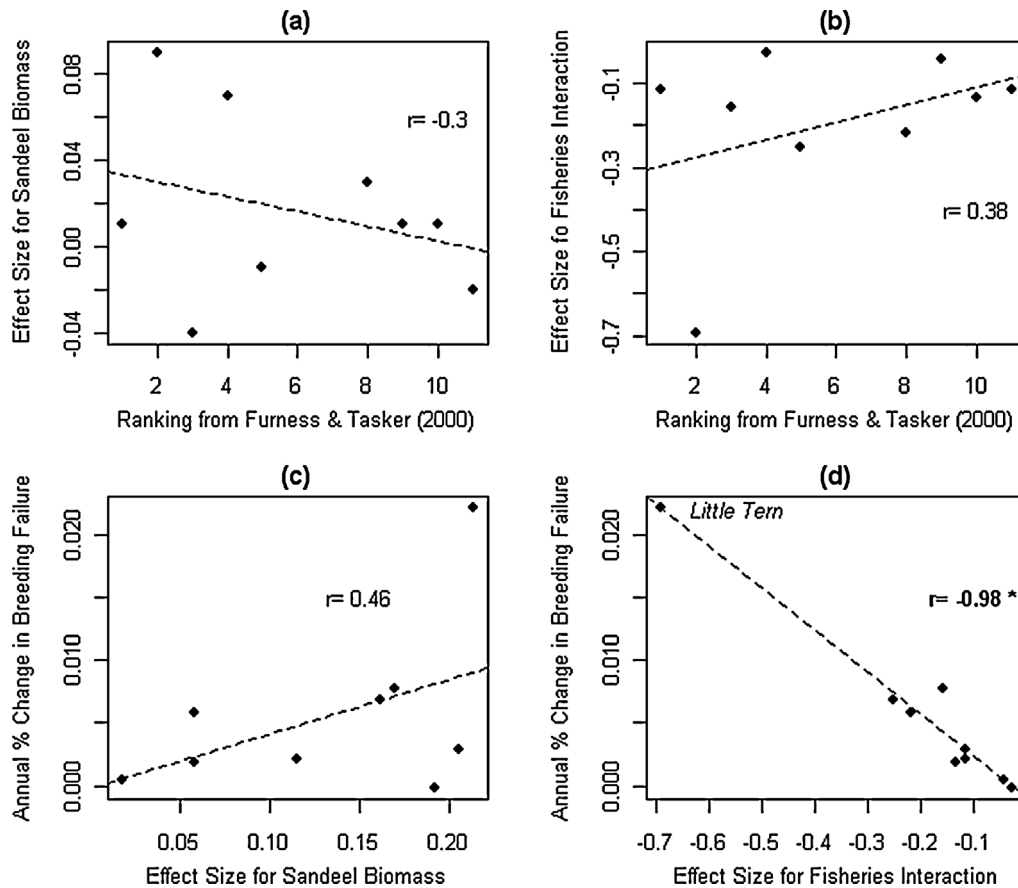


Fig. 6. Assessing the impact of sandeel fisheries on seabird breeding failure: (a) correlation between the effect size for sandeel biomass from models of seabird breeding failure rates and species sensitivity to reductions in sandeel abundance as assessed by Furness and Tasker (2000), (b) correlation between the effect size for fisheries interaction from models of seabird breeding failure rates and species sensitivity to reductions in sandeel abundance as assessed by Furness and Tasker (2000), (c) correlation between the annual change in breeding failure rate between 1986 and 2010 and the effect size from models of seabird breeding failure in relation to sandeel population size, (d) correlation between the effect size for the interaction between sandeel population size and fisheries effort from models of seabird breeding failure rates and annual change in breeding failure rate. Each point represents a study species. Annual change in breeding failure rate derived from change between median failure rate in 1986–1990 and median failure rate in 2006–2010. * Denotes significant correlation ($P < 0.05$).

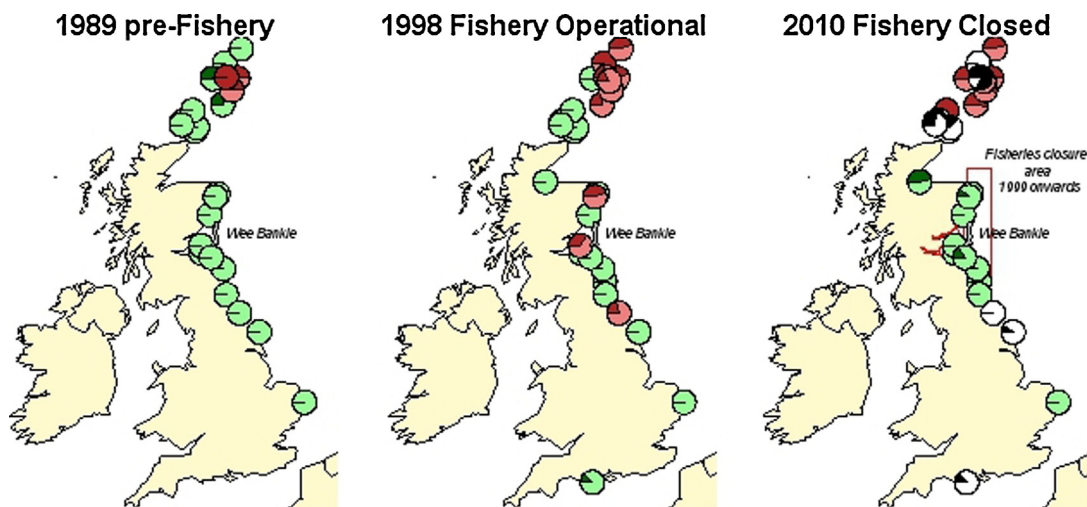


Fig. 7. Change in kittiwake breeding success indicator in relation to the presence of the Wee Bankie sandeel fishery. Following Frederiksen et al. (2004a) the sandeel fishery was assessed as present from 1990 to 1998. Each pie chart represents a kittiwake breeding colony, green indicates that breeding success reflected the underlying environmental conditions in the target year, red indicates that breeding success was lower than expected given the underlying environmental conditions and black/white indicates colony was not recorded in the target year. Darker segments indicate the proportion of the preceding years in which the target level of breeding success was not achieved in the pre-fishery (1986–1989), operational fishery (1990–1998) and closed fishery (1999–2010) periods. (For interpretation of the references to color in text, the reader is referred to the web version of this article.)

levels of dependency on sandeel (Furness and Tasker, 2000), but this did not reflect inter-specific differences in the breeding failure indicator. Instead, we found that changes in species breeding failure rates were strongly correlated with pressure from fisheries. The extent to which sandeel fisheries impact upon breeding seabird populations may be linked to how accessible different stocks are, and how readily larval sandeel can disperse between populations on different banks in the North Sea (Poloczanska et al., 2004; Wright, 1996). Whilst both the Wee Bankie and Shetland sandeel fisheries have been closed over part of our study period, the most intensive North Sea sandeel fishery operates on Dogger Bank (ICES, 2011). This area is within the foraging range of several of our study species from colonies on the east coast of the UK (Thaxter et al., 2013), and others may be willing to travel greater distances to exploit the predictable food resource it offers, particularly when local prey availability is reduced (Baudini and Hyrenbach, 2003; Bertrand et al., 2012; Hamer et al., 2001).

Whilst sandeel are largely sedentary, their larvae are capable of dispersing more widely (Christensen et al., 2007, 2008; Procter et al., 1998) and disruption to this dispersal can significantly affect local sandeel availability (Poloczanska et al., 2004; Wright, 1996). Consequently, intensive fisheries activity during the spawning period in areas like Dogger Bank, may reduce the supply of larvae elsewhere. The structure of North Sea sandeel populations means that this may be a particular problem in the east of England (Christensen et al., 2008), with a detrimental impact on species with restricted foraging ranges, like little tern.

Fisheries impacts may be direct or indirect. The Wee Bankie sandeel fishery operated between 1990 and 1999, although landings were small in 1990 and 1999 (Frederiksen et al., 2004a,b). Using the kittiwake breeding success indicator, given the underlying environmental conditions, it is possible to investigate the impact of the fishery on breeding populations of the kittiwake (Fig. 7). Following the start of the Wee Bankie fishery, the number of colonies failing to achieve the level of breeding expected given the underlying environmental conditions increased. These increases were particularly noticeable in areas close to Wee Bankie on the east coast of Scotland and North East of England. Following the closure of the fishery, colonies failing to achieve the desired level of breeding success became clustered around Orkney and Shetland, where great skua *Catharacta skua* predation makes a significant contribution to mortality (Oro and Furness, 2002; Votier et al., 2004, 2007). This may reflect an indirect impact of fisheries as predation rates are linked to the availability of different food resources (Votier et al., 2004).

The use of seabirds as biological indicators of environmental pressures in this fashion has been questioned (Gremillet and Charmantier, 2010). In particular, there is concern over the plasticity of behavioural characteristics, such as diet, which may blur functional relationships between the seabird indicator and the pressure they are monitoring. In the Celtic Seas alternative prey to sandeel may be available (Chivers et al., 2012; Lauria et al., 2012) and the resultant plasticity in diet may make seabirds more valuable as sentinels of wide-scale ecological processes, rather than quantitative indicators. However, in the North Sea there is a long-established link between sandeel stocks and seabird productivity, with declines closely linked to sandeel availability (i.e. Wanless et al., 2005, 2007). Our results further demonstrate the potential for using breeding success to assess the impact of fisheries on seabirds in the North Sea. If there is a direct impact of fisheries on breeding seabirds at a population level, we would expect two conditions to be satisfied; (1) failing colonies would be widely distributed, as seen in the kittiwake breeding success indicator in 1998 and (2) a greater proportion of the colonies of those species most sensitive to fisheries pressure, such as kittiwake, are failing than is the case for

species, such as fulmar, which are less sensitive to pressure from the North Sea sandeel fishery.

4.3. Setting targets

Indicators such as these are used to assess environmental conditions and monitor progress towards a target (Sanderson, 2006), in this case achieving “Good Environmental Status” in the North Sea and other European waters by maintaining biological diversity and ensuring species distributions reflect prevailing environmental conditions (EU, 2008). Such targets must reflect baseline levels of diversity, against which future changes can be assessed. Ideally, indicators should also account for prevailing climatic conditions so that they are sensitive to specific anthropogenic pressures rather than wider environmental changes. In terms of the impact of fisheries on seabirds, this means identifying species likely to be affected, understanding what both baseline levels of breeding failure/success and the demographic mechanisms of population change should be, determining the rate at which populations can recover and understanding how management can be used to achieve these targets (Bridgewater, 2011).

Determining the species negatively affected by fisheries and suggesting management measures to achieve targets, for example limiting fisheries take, can be reasonably straightforward. However, as a proportion of colonies may be expected to fail in any given year, irrespective of anthropogenic pressures (Poloczanska et al., 2004), defining baseline levels of breeding failure or success and population recovery rates is more complex. Indicator targets are set in a variety of ways. Sanderson (2006) suggests a four stage process (1) achieve demographic sustainability, (2) ensure sufficient recruitment to maintain breeding population, (3) ensure populations can withstand irregular disruption through factors such as disease or predation, (4) ensure populations can withstand regular disruption or catastrophic events. In the North Sea, breeding failure rates are increasing and targets therefore should focus on the first stage of this process, achieving demographic sustainability and ensuring that colonies do not fail repeatedly over short time periods.

Such targets will, by their nature, be arbitrary, but should account for species' differing ecologies. Using the breeding failure as an example, for those, like auks, where colony-level breeding failure is a rare event, ensuring this does not occur in consecutive years may be a reasonable target. In species, like terns, where breeding failure is naturally more common, a realistic target may be ensuring that it does not occur over more half the indicator reporting cycle (e.g. no more than three of the preceding six years). Focal species should be those for which the fisheries impact is greatest, such as kittiwake, little tern and razorbill. The spatial distribution of failing colonies should also be considered. Pressures like fisheries, which reduce food availability in shared foraging grounds, would be expected to impact populations over a broad spatial scale. Localised failures may reflect alternative pressures, like nest predation, which are less important, particularly where between-colony recruitment is likely.

4.4. Advantages of demographic indicators

There is a strong demographic and evolutionary rationale for the use of seabird indicators based on productivity. Most indicators for these species are based on abundance. However, abundance is a function of the distribution, survival and productivity of a species and consequently, often lagged in relation to environmental parameters (e.g. Sæther, 1997; Thompson and Ollason, 2001). Therefore, by focussing on abundance, we may miss events which impact upon a species' population. Demographic indicators allow a more immediate assessment of the state of a population. Monitoring seabird

survival can be difficult, as many species spend a significant portion of the year away from their colonies, and adults may skip breeding seasons (e.g. [Aebischer and Wanless, 1992](#); [Catry et al., 1998](#); [Harris and Wanless, 1995](#)), making re-sightings of marked individuals on annual basis difficult. Monitoring breeding success can be simpler, as tracking the progress of individual nests can be straightforward, and can often be achieved without having to enter the colony ([Walsh et al., 1995](#)).

Our results illustrate that by focussing on indicators of productivity, it is possible to detect important changes to seabird populations before they became evident at a population level. By correcting for environmental conditions, we can detect key changes even earlier. In the coming years, the way the marine environment is managed is likely to be subject to significant changes as a result of the expansion of offshore developments, changes to discard policy and the introduction of marine protected areas ([Bicknell et al., 2013](#); [Garthe and Huppopp, 2004](#); [Lascelles et al., 2012](#)). These rapid changes mean it is vital to have up-to-date information about impacts on the marine environment.

5. Conclusions

A key part of developing effective ecological indicators is that they must accurately reflect the complexity of the systems involved. By focussing on abundance in long-lived species, which may not reach sexual maturity for several years, important population level changes may be missed. Focussing on demographic parameters, like productivity which may be readily monitored amongst colonially breeding species, can more accurately capture this complexity. Demographic indicators can be further improved by accounting for known relationships with environmental parameters.

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References

- Aebischer, N.J., Wanless, S., 1992. Relationships between colony size, adult non-breeding and environmental conditions for Shags *Phalacrocorax aristotelis* on the Isle of May, Scotland. *Bird Study* 39, 43–52.
- Bates, D., Maechler, M., Bolker, B., 2011. lme4: Linear Mixed-Effects Models Using Eigen and S4 Classes. <http://cran.r-project.org/package=lme4>
- Baudini, C.L., Hyrenbach, K.D., 2003. Biogeography of procellariiform foraging strategies: does ocean productivity influence provisioning? *Mar. Ornithol.* 31, 101–112.
- Bertrand, S., Joo, R., Arbulu Smet, C., Tremblay, Y., Barbraud, C., Weimerskirch, H., 2012. Local depletion by a fishery can affect seabird foraging. *J. Appl. Ecol.* 49, 1168–1177.
- Bicknell, A.W.J., Oro, D., Camphuysen, C.J., Votier, S.C., 2013. Potential consequences of discard reform for seabird communities. *J. Appl. Ecol.* <http://dx.doi.org/10.1111/1365-2664.12072>.
- Bridgewater, P., 2011. SMART or CUTE – what makes a good target? *Biol. J. Linn. Soc. Lond.* 166, 240–249.
- Catry, P., Phillips, R.A., Hamer, K.C., Ratcliffe, N., Furness, R.W., 1998. The incidence of nonbreeding by adult great skuas and parasitic jaegers from Foula, Shetland. *Condor* 100, 448–455.
- Champely, S., 2012. pwr: Basic Functions for Power Analysis. <http://cran.r-project.org/package=pwr>
- Chivers, L.S., Lundy, M.G., Colhoun, K., Newton, S.F., Reid, N., 2012. Diet of black-legged kittiwakes (*Rissa tridactyla*) feeding chicks at two Irish colonies highlights the importance of clupeids. *Bird Study* 59, 363–367.
- Christensen, A., Daewel, U., Jensen, H., Mosegaard, H., St. John, M., Schrum, C., 2007. Hydrodynamic backtracking of fish larvae by individual-based modelling. *Mar. Ecol. Prog. Ser.* 347, 221–232.
- Christensen, A., Jensen, H., Mosegaard, H., St. John, M., Schrum, C., 2008. Sandeel (*Ammodytes marinus*) larval transport patterns in the North Sea from an individual-based hydrodynamic egg and larval model. *Can. J. Fish. Aquat. Sci.* 65, 1498–1511.
- Cook, A.S.C.P., Parsons, M., Mitchell, I., Robinson, R.A., 2011. Reconciling policy with ecological requirements in biodiversity monitoring. *Mar. Ecol. Prog. Ser.* 434, 267–277.
- Cresspin, L., Harris, M.P., Lebreton, J., Wanless, S., 2006. Increased adult mortality and reduced breeding success with age in a population of common guillemot *Uria aalge* using marked birds of unknown age. *J. Avian Biol.* 37, 273–282.
- Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J.M., Furness, R.W., Mills, J.A., Murphy, E.J., Österblom, H., Paleczny, M., Piatt, J.F., Roux, J.-P., Shannon, L., Sydeman, W.J., 2011. Global seabird response to forage fish depletion – one-third for the birds. *Science* 334, 1703–1706.
- Dale, V.H., Beyer, S.C., 2001. Challenges in the development and use of ecological indicators. *Ecol. Indic.* 1, 3–10.
- Dänhardt, A., Becker, P.H., 2011. Herring and sprat abundance indices predict chick growth and reproductive performance of common terns breeding in the Wadden Sea. *Ecosystems* 14, 791–803.
- Dittman, T., Becker, P.H., 2003. Sex, age, experience and condition as factors affecting arrival date in prospecting common terns, *Sterna hirundo*. *Anim. Behav.* 65, 981–986.
- EC, 2008. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environment policy (Marine Strategy Framework Directive). *Off. J. Eur. Union* L164, 19–40.
- Erikstad, K.E., Fauchald, P., Tveraa, T., Steen, H., 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* 79, 1781–1788.
- Fewster, R.M., Buckland, S.T., Siriwardena, G.M., Baillie, S.R., Wilson, J.D., 2000. Analysis of population trends for farmland birds using generalized additive models. *Ecology* 81, 1970–1984.
- Frederiksen, M., Wanless, S., Harris, M.P., Rothery, P., Wilson, L.J., 2004a. The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged Kittiwakes. *J. Appl. Ecol.* 41, 1129–1139.
- Frederiksen, M., Harris, M.P., Daunt, F., Rothery, P., Wanless, S., 2004b. Scale-dependent climate signals drive the breeding phenology of three seabird species. *Glob. Chang. Biol.* 10, 1214–1221.
- Frederiksen, M., Wright, P.J., Harris, M.P., Mavor, R.A., Heubeck, M., Wanless, S., 2005. Regional patterns of kittiwake *Rissa tridactyla* breeding success are related to variability in sandeel recruitment. *Mar. Ecol. Prog. Ser.* 300, 201–211.
- Frederiksen, M., Mavor, R.A., Wanless, S., 2007. Seabirds as environmental indicators: the advantages of combining data sets. *Mar. Ecol. Prog. Ser.* 352, 205–211.
- Frederiksen, M., Jensen, H., Daunt, F., Mavor, R.A., Wanless, S., 2008. Differential effects of a local industrial sand lance fishery on seabird breeding performance. *Ecol. Appl.* 18, 701–710.
- Furness, R.W., 2002. Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. *ICES J. Mar. Sci.* 59, 261–269.
- Furness, R.W., Camphuysen, C.J., 1997. Seabirds as monitors of the marine environment. *ICES J. Mar. Sci.* 54, 726–737.
- Furness, R.W., Tasker, M.L., 2000. Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Mar. Ecol. Prog. Ser.* 202, 253–264.
- Garthe, S., Huppopp, O., 2004. Scaling possible adverse effects of marine wind farms on seabirds: developing and applying a vulnerability index. *J. Appl. Ecol.* 41, 724–734.
- Golet, G.H., Irons, D.B., Estes, J.A., 1998. Survival costs of chick rearing in black-legged kittiwakes. *J. Anim. Ecol.* 67, 827–841.
- Gremillet, D., Boulinier, T., 2009. Spatial ecology and conservation of seabirds facing global climate change: a review. *Mar. Ecol. Prog. Ser.* 391, 121–137.
- Gremillet, D., Charmantier, A., 2010. Shifts in phenotypic plasticity constrain the value of seabirds as ecological indicators of marine ecosystems. *Ecol. Appl.* 20, 1498–1503.
- Halley, D.J., Harrison, N., Webb, A., Thompson, D.R., 1995. Seasonal and geographical variations in the diet of Common Guillemots *Uria aalge* off western Scotland. *Seabird* 17, 12–20.
- Hamer, K.C., Phillips, R.A., Hill, J.K., Wanless, S., Wood, A.G., 2001. Contrasting foraging strategies of gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. *Mar. Ecol. Prog. Ser.* 224, 283–290.
- Harris, M.P., Freeman, S.N., Wanless, S., Morgan, B.J.T., Wernham, C.V., 1997. Factors influencing the survival of puffins *Fratercula arctica* at a North Sea colony over a 20-year period. *J. Avian Biol.* 28, 287–295.
- Harris, M.P., Wanless, S., 1995. Survival and non-breeding of adult common guillemot, *Uria aalge*. *Ibis* 137, 192–197.
- Harris, M.P., Wanless, S., 1997. Breeding success, diet, and brood neglect in the kittiwake (*Rissa tridactyla*) over an 11-year period. *ICES J. Mar. Sci.* 54, 615–623.
- ICES, 2011. Report of the ICES Advisory Committee 2011. ICES Advice, Book 6. ICES, Copenhagen.
- JNCC, 2012. Seabird Population Trends and Causes of Change: 2012 Report. Joint Nature Conservation Committee, <http://www.jncc.defra.gov.uk/page-3201> (accessed 21.02.12).
- Lascelles, B.G., Langham, G.M., Ronconi, R.A., Reid, J.B., 2012. From hotspots to site protection: identifying marine protected areas for seabirds around the globe. *Biol. Conserv.* 156, 5–14.

- Lauria, V., Attrill, M.J., Pinnegar, J.K., Brown, A., Edwards, M., Votier, S.C., 2012. Influence of climate change and trophic coupling across four trophic levels in the Celtic Sea. *PLoS ONE* 7, e47408. [10.1371/journal.pone.0047408](https://doi.org/10.1371/journal.pone.0047408).
- Lewis, S., Wanless, S., Wright, P.J., Harris, M.P., Bull, J., Elston, D.A., 2001. Diet and breeding performance of black-legged kittiwaks *Rissa tridactyla* at a North Sea colony. *Mar. Ecol. Prog. Ser.* 221, 277–284.
- Lloyd, C.S., Tasker, M.L., Partridge, K., 1991. The Status of Seabirds in Britain and Ireland. T & AD Poyser, Calton.
- Mitchell, I.P., Newton, S.F., Ratcliffe, N., Dunn, T.E., 2004. Seabird Populations of Britain and Ireland. T & AD Poyser, London.
- Niemi, G.J., MacDonald, M.E., 2004. Application of ecological indicators. *Annu. Rev. Ecol. Evol. Syst.* 35, 89–111.
- Oro, D., Furness, R.W., 2002. Influences of food availability and predation on survival of kittiwakes. *Ecology* 83, 2516–2528.
- Parsons, M., Mitchell, I., Butler, A., Ratcliffe, N., Frederikson, M., Foster, S., Reid, J.B., 2008. Seabirds as indicators of the marine environment. *ICES J. Mar. Sci.* 65, 1520–1526.
- Piatt, J.F., Sydeman, W.J., Wiese, F., 2007. Introduction: a modern role for seabirds as indicators. *Mar. Ecol. Prog. Ser.* 352, 199–204.
- Poloczanska, E.S., Cook, R.M., Ruxton, G.D., Wright, P.J., 2004. Fishing vs. natural recruitment variation in sandeels as a cause of seabird breeding failure at Shetland: a modelling approach. *ICES J. Mar. Sci.* 61, 788–797.
- Procter, R., Wright, P.J., Everitt, A., 1998. Modelling the transport of larval sandeels on the north-west European shelf. *Fish. Oceanogr.* 7, 347–354.
- R Development Core Team, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna <http://www.R-project.org>
- Rayner, N.A., Parker, D.E., Horton, E.B., Folland, C.K., Alexander, L.V., Rowell, D.P., Kent, E.C., Kaplan, A., 2003. Global analyses of SST, sea ice and night marine air temperature since the late nineteenth century. *J. Geophys. Res.* 108, 4407.
- Regehr, H.M., Montevecchi, W.A., 1997. Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: indirect effects of fisheries activities and implications for indicator species. *Mar. Ecol. Prog. Ser.* 155, 249–260.
- Rindorf, A., Wanless, S., Harris, M.P., 2000. Effects of changes in sandeel availability on the reproductive output of seabirds. *Mar. Ecol. Prog. Ser.* 202, 241–252.
- Robinson, R.A., 2005. BirdFacts: Profiles of Birds Occurring in Britain and Ireland (BTO Research Report 407). BTO, Thetford <http://www.bto.org/birdfacts> (accessed on 15.08.13).
- Rogers, S.I., Greenaway, B., 2005. A UK perspective on the development of marine ecosystem indicators. *Mar. Pollut. Bull.* 50, 9–19.
- Sanderson, E.W., 2006. How many animals do we want to save? The many ways of setting population target levels for conservation. *BioScience* 56, 911–922.
- Sandvik, H., Erikstad, K.E., Barrett, R.T., Yoccoz, N., 2005. The effect of climate on adult survival in five species of North Atlantic seabirds. *J. Anim. Ecol.* 74, 817–831.
- Sæther, B.E., 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends Ecol. Evol.* 12, 142–149.
- Tasker, M.L., Becker, P.H., 1992. Influences of human activities on seabird populations in the North Sea. *Neth. J. Aquat. Ecol.* 26, 59–73.
- Thaxter, C.B., Lascelles, B., Sugar, K., Cook, A.S.C.P., Roos, S., Bolton, M., Langston, R.H.W., Burton, N.H.K., 2013. Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. *Biol. Conserv.* 156, 53–61.
- Thompson, P.M., Ollason, J.C., 2001. Lagged effects of ocean climate change on fulmar population dynamics. *Nature* 413, 417–420.
- Tromp, D., Wieriks, K., 1994. The OSPAR Convention: 25 years of North Sea protection. *Mar. Pollut. Bull.* 29, 622–626.
- Votier, S.C., Bearhop, S., Ratcliffe, N., Phillips, R.A., Furness, R.W., 2004. Predation by great skuas at a large Shetland seabird colony. *J. Appl. Ecol.* 41, 1117–1128.
- Votier, S.C., Beahop, S., Crane, J.E., Arcos, J.M., Furness, R.W., 2007. Seabird predation by great skuas *Stercorarius skua* – intra-specific competition for food? *J. Avian Biol.* 38, 234–246.
- Walsh, P.M., Halley, D.J., Harris, M.P., del Nevo, A., Sim, I.M.W., Tasker, M.L., 1995. Seabird Monitoring Handbook for Britain and Ireland. JNCC, RSPB, ITE, Seabird Group, Peterborough.
- Wanless, S., Frederiksen, M., Daunt, F., Scott, B.E., Harris, M.P., 2007. Black-legged kittiwakes as indicators of environmental change in the North Sea: evidence from long-term studies. *Prog. Oceanogr.* 72, 30–38.
- Wanless, S., Harris, M.P., Redman, P., Speakman, J.R., 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Mar. Ecol. Prog. Ser.* 294, 1–8.
- Wiese, F.K., Ryan, P.C., 2003. The extent of chronic marine oil pollution in southeastern Newfoundland waters assessed through beached bird surveys 1984–1999. *Mar. Pollut. Bull.* 46, 1090–1101.
- Wright, P.J., Begg, G.S., 1997. A spatial comparison of common guillemots and sandeels in Scottish waters. *ICES J. Mar. Sci.* 54, 578–592.
- Wright, P.J., 1996. Is there a conflict between sandeel fisheries and seabirds? A case study at Shetland. In: Greenstreet, S.P.R., Tasker, M.L. (Eds.), *Aquatic Predators and Their Prey*. Fishing News Books, Oxford.