Reconciling policy with ecological requirements in biodiversity monitoring

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ABSTRACT: Many of the breeding seabird populations in Britain and Ireland are of international importance; consequently, there is a statutory duty to protect these populations, as part of national biodiversity strategies and under Article 4 of the EU's Directive on the Conservation of Wild Birds (EC/79/409). As part of this process, populations have been monitored annually at a sample of colonies since the mid-1980s and (near) complete surveys have been undertaken twice. Results of this monitoring are currently reported regionally, in an effort to reflect the impact of spatially varying environmental drivers of change; however, there is concern that these regions reflect policy requirements rather than ecological relevance, particularly for mobile species. We used the monitoring data to identify a series of ecologically coherent regions in which trends in abundance and breeding success varied in a consistent fashion and examined how closely the annually sampled data matched the change quantified by the whole population surveys. The number of ecologically coherent regions identified varied from 2 for the northern gannet *Morus bassanus* and common guillemot *Uria aalge* to 7 for the great cormorant *Phalacrocorax carbo*. Trends imputed for ecologically coherent regions more closely matched those observed between whole population censuses and were more consistent than those identified for more policy-driven monitoring regions. By accounting for ecology in the design of monitoring regions, population variation in mobile species can be more accurately represented, leading to the design of more realistic monitoring regions.

KEY WORDS: Ecologically coherent monitoring · Policy-driven monitoring · Seabirds · Marine Strategy Framework Directive · OSPAR · Marine ecosystems · Population trends · Productivity

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INTRODUCTION

Globally, ecosystems are facing increasing threats as humans make ever increasing demands on the shared resources they harbour. The 1992 Convention on Biological Diversity brings in an international requirement to protect and monitor these ecosystems (United Nations 1992). However, often these requirements are carried out in relation to statutory and legislative processes whose boundaries may not be ecologically relevant, particularly when multiple taxonomic groups are concerned. As a result, there is a growing recognition of the importance of including knowledge of species' ecology in the monitoring and protection of ecosystems (i.e. Airame et al. 2003, Roberts et al. 2003, Hughes et al. 2005).

In recent years, marine ecosystems have been the focus of much interest into the impacts of a range of pressures from sources including fisheries, offshore wind farms, aggregate dredging, pollution and shipping (Piatt et al. 1990, Furness & Tasker 2000, Derraik 2002, Furness 2002, Garthe & Huppopp 2004, Cook & Burton 2010, Schwemmer et al. in press). Quantification of the impacts from these pressures has necessitated sustained environmental monitoring within many areas (Stewart et al. 2007, Drewitt & Langston 2008). Frequently, this is done within a Pressure-State-Response (PSR) framework, whereby the pressures or threats to the system are identified, the state of the system is quantified, and conservation or management responses are identified (e.g. Caddy 2004, Jennings 2005, Rogers & Greenaway 2005, Piet et al. 2007). This

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approach requires ecological information to be collated in a robust and coherent fashion, so that the uncertainty surrounding our knowledge of the system can be incorporated into the PSR framework in a transparent manner. However, as this monitoring is carried out within areas whose boundaries may not be ecologically relevant, impacts on some populations may be overlooked as they are not believed to be exposed to the pressure under consideration.

Comprehensive monitoring of the multitude of pressures acting on marine ecosystems is well beyond current methodological and budgetary constraints; consequently, there is widespread interest in the use of indicators to assess marine ecosystem health.

As top predators, seabirds are likely to provide an indication of the state of the marine ecosystem as a whole, and it is relatively easy to monitor their population status (Furness & Greenwood 1993). Seabird breeding success has been shown to be closely linked with prey quality and availability (Frederiksen et al. 2005, Wanless et al. 2005). Consequently, changes in the physico-chemical environment or in lower trophic levels are likely to manifest themselves as changes in seabird populations (Parsons et al. 2008). Furthermore, seabirds often occur with other top marine predators as part of multi-species feeding assemblages (Camphuysen & Webb 1999). These studies indicate that it may be possible to use changes in seabird populations to infer changes within other marine taxa. As a result, seabirds provide a useful group to test the wider applicability of existing, defined assessment regions.

The UK offers a valuable framework to investigate the ecological relevance of existing monitoring regions. As a home to several internationally important breeding populations (Mitchell et al. 2004), the abundance of seabirds at breeding colonies has been monitored in a standardised fashion since 1986 as part of the Seabird Monitoring Programme (SMP; Walsh et al. 1995). Uniquely, these annual data have been supplemented by periodic (near) complete censuses of all seabird colonies in the UK and Ireland. These data provide a valuable resource for investigating regional population trends and for assessing the validity of the annual monitoring programme, which is necessarily based on a limited sample of colonies due to logistic and financial constraints.

In the UK, monitoring of seabird populations is legislated by the UK Biodiversity Action Plan (UKBAP; Department of Environment 1994) and the recently adopted Marine Strategy Framework Directive (MSFD; Directive 2008/56/EC of the European Council). The UKBAP commits the UK to identify, conserve, protect and enhance biodiversity, whilst the MSFD brings in a statutory requirement to monitor biodiversity components within the marine environment with a view to

achieving 'Good Environmental Status' by 2020. To meet the requirements of the MSFD, assessments of environmental status are conducted at regional and sub-regional levels, with further subdivisions applied if necessary to monitor aspects of marine biodiversity. For the UK, the sub-regional levels used closely match those defined under the 1992 Oslo-Paris (OSPAR) Convention (Tromp & Wieriks 1994; Fig. 1a). However, Cochrane et al. (2010) recommended that a set of suitable ecological assessment areas be defined for each region, which adequately reflect both the scale of biological variation and the most appropriate scale for effective management measures. In the UK, these took the form of 8 Regional Seas (RS; DEFRA 2010; Fig. 1b), defined in a way that reflects the physical and biological features, such as tidal fronts and seabed flora and fauna, of the marine environment. However, there is a question as to whether the OSPAR and RS regions, designed with the biodiversity of marine habitats in mind, are appropriate for more mobile species, like fish, seabirds or cetaceans. Understanding the wider ecological applicability of these existing monitoring regions has often been hampered by a lack of detailed ecological data and appropriate analysis (Ardron 2008).

In this study we sought to identify a series of 'Ecological Assessment Area' (EAA) regions, within which population trends vary in a consistent fashion, for a range of seabird species with differing ecologies. The accuracy of imputed trends, both for EAAs and for existing monitoring regions, were assessed by comparison with changes observed between whole population censuses in 1985 to 1988 and 1998 to 2002 (Mitchell et al. 2004), the most reliable population estimates available. We then determined to what extent regional trends are representative of the individual colony-specific trends within each monitoring region.

MATERIALS AND METHODS

Seabird abundance has been monitored at colonies across the UK and Republic of Ireland in a standardised fashion since 1986 under the SMP (Walsh et al. 1995). For the purposes of this study, the term 'seabird' is used to refer to species that are primarily marine in their ecology, for example petrels, gannets, cormorants, skuas, gulls, terns and auks. By analysing abundance data for the 11 species for which the best quality data were available and which represented a range of foraging strategies (northern gannet *Morus bassanus*, northern fulmar *Fulmarus glacialis*, European shag *Phalacrocorax aristotelis*, great cormorant *P. carbo*, Arctic skua *Stercorarius parasiticus*, little tern *Sternula albifrons*, Sandwich tern *Sterna sandvicensis*,

Fig. 1. Existing (a) OSPAR and (b) Regional Seas monitoring regions. Doubled countour line marks the UK coastline and the boundaries of each of the monitoring regions, which take into account inter-tidal areas

herring gull *Larus argentatus*, black-legged kittiwake *Rissa tridactyla*, common guillemot *Uria aalge* and razorbill *Alca torda*), we sought to identify a series of EAAs in which trends in seabird populations varied in a consistent fashion.

Useful monitoring regions would be expected to show mean trends that are representative of trends at colonies throughout the region. If this is the case, it would be expected (1) that missing counts could be accurately imputed by considering trends in colonies elsewhere in the region, and (2) that trends at individual colonies would be consistent with the mean trend calculated for the relevant monitoring region. To this end, the accuracy (in terms of matching the population change recorded between the 2 whole population surveys) and consistency (colonies within a region exhibiting the same trend) of the newly identified EAAs were compared to the accuracy and consistency of the RS and OSPAR regions. For the purposes of monitoring seabirds, the boundaries of the UK RS regions were altered such that all of Shetland and the Western Isles were included in the Scottish Continental Shelf RS, whereas previously the east coast of each had been included in the Northern North Sea and Minches and

Western Scotland RS, respectively; these boundaries were followed in this study.

Identification of EAAs. Data used to identify the EAAs were colony counts obtained from the SMP between 1986 and 2008. As tends to be typical in large-scale bird surveys (Thomas 1996), these data included a high proportion of missing counts (~50%; Appendix 1). Data were available from all years for all species, apart from Arctic skua, for which data were only available in 10 yr. To minimise the impact of these missing counts, the dataset for each species was limited to colonies which had been surveyed in at least 10 yr. However, in the case of the northern gannet, little tern and Sandwich tern, this figure had to be reduced to 5 yr in order to have sufficient data to model, and in the case of the Arctic skua, this figure had to be reduced to 2 yr. As well as minimising the impact of missing counts, this has the advantage of excluding sites at which species have only occasionally been recorded to breed, and that therefore may not represent true breeding colonies.

As it is not possible to perform the multivariate analyses required for subsequent cluster analysis on data with missing values, it was necessary to impute values for these missing data. This was done by fitting

a General Linear Mixed Model (GLMM) to the data and using the output of this model to predict values for the dataset as a whole. For each species, a suite of candidate models was considered in which colony was fitted as a random effect and combinations of colony, latitude, longitude, year and a sine-transformation of year (to account for any non-linear trend) were fitted as fixed effects (preliminary modelling suggested non-linear terms were not needed for the other variables). Models were fitted using the `glmmPQL` function in R 2.11.0 (Venables & Ripley 2002, Bolker et al. 2009). By fitting colony as both a fixed effect and a random effect, it was possible to model the variation both within and between colonies (Gelman & Hill 2007). As the data were counts, Poisson, quasi-Poisson and negative binomial error structures were considered; however, these severely under-fitted the data, presumably reflecting the fact that the processes determining colony size are non-random. Consequently, counts were transformed by $\log(n + 1)$ and modelled with normal (Gaussian) errors; as the mean increases, the Poisson distribution is increasingly well approximated by a normal distribution. As PQL methods do not result in the full likelihood being calculated, it is not possible to perform model selection through the comparison of Akaike information criterion (AIC) values (Bolker et al. 2009), so models were selected by comparing pseudo- R^2 values. For each species, the model with the highest pseudo- R^2 value was selected. This model was then taken forward and used to impute the missing annual values for each colony.

In order to cluster colonies with respect to population change (rather than simply colony size), we re-scaled the time series for each colony, such that each colony had an index value of 100 in 1986 (the first year of the study). These index values were then used to cluster the colonies based on the similarity of the annual population changes using the `hclust` algorithm in R 2.11.0 (R Development Core Team 2010). To identify specific groups, the resulting dendrogram, constructed using Ward's minimum distance, was cut at a variety of heights, and each of the resulting groups was examined for spatial structure. The grouping level selected was that which provided the greatest number of groups whilst still retaining an element of consistent spatial structure with geographically adjacent colonies falling into the same groups. To verify the validity of the clusters, the analysis was repeated using available data describing breeding success, and the distribution of the resultant clusters was compared. Breeding data were less complete than abundance data, and in a number of cases, colonies were not common to both datasets.

To ensure that data imputed to account for missing values did not have an undue influence on the assign-

ment of colonies to clusters, regression analysis was used to determine whether there was a significant relationship between dendrogram height and the proportion of missing data within the dataset. The distance between colonies on a dendrogram increases as the degree of difference between them increases. Therefore, if imputed data were having an undue influence on the assignment to clusters, it would be expected that dendrogram height would be lowest for species with a high proportion of missing data.

Assessing the accuracy of regional trends. To assess the accuracy of trends from the sample data, we used the existing methodology employed by SMP (Thomas 1993, Marchant et al. 2004). Under this methodology, trends within regions containing missing data are imputed by combining population sizes in preceding years at colonies with missing counts with population trends elsewhere within the monitoring region. A key advantage of this methodology is that it allows for the implicit inclusion of ecological information from similar colonies in the calculation of missing data. Clearly, this assumes that colonies within the region are ecologically similar (hence it was not appropriate in defining the regions above).

To assess the accuracy of the imputed trends within each monitoring scheme, they were compared to the trends observed between the Seabird Colony Register census (all colonies counted between 1985 and 1988, Lloyd et al. 1991) and the Seabird 2000 census (all colonies counted between 1998 and 2002, Mitchell et al. 2004). These 2 censuses were undertaken at the start and end of the period considered here, and each aimed to provide complete counts of all colonies in the UK and Ireland, providing an independent means of assessing the accuracy of the population trend estimated from the annual sample data. For each region a linear trend was calculated covering the time period between whole population censuses. A second linear trend, covering the same time period was calculated using the imputed data. The trends in the imputed data were calculated as a percentage of the corresponding trends in observed data to determine accuracy. The significance of differences in the accuracy of trends between sets of monitoring regions was assessed using chi-squared tests.

Assessing the consistency of regional trends. For a regional trend to be viewed as accurate, it must be representative of the trends at the individual colonies within the region. We estimated the average rate of population change by fitting a GLM to the time-series of the (log-transformed) annual counts at each colony, with year as a continuous fixed effect. For each set of monitoring regions, colonies were assigned to their relevant region and a mean coefficient for each monitoring region was calculated. The consistency of the

trends within each monitoring region was assessed by calculating the coefficient of variation of these trends. The significance of differences in the consistency of trends between sets of monitoring regions was assessed using chi-squared tests.

RESULTS

For each species, the imputation models performed reasonably well, with pseudo- R^2 values ranging from 0.46 and 0.47 for the northern fulmar and little tern, respectively, to 0.85 and 0.86 for the northern gannet and Arctic skua (Table 1, Fig. 2), indicating that imputed data were a reasonable representation of the observed data. Populations of all species varied through time, although only for European shag was there any evidence that this pattern was non-linear over the period monitored (coefficient -0.28 ± 0.04 , $p < 0.01$). Arctic skua was the only species for which the best model contained colony as a factor; for all other species, latitude and/or longitude were sufficient proxies of colony location to impute counts. In addition, for each of these species, an interaction was fitted between year and latitude and/or longitude, indicating spatial variation in the magnitude of the population trends.

Identification of ecologically coherent regions

The number of EAAs identified for each species varied from 2 for the northern gannet and common guillemot to 7 for the great cormorant (Fig. 3). There was no significant relationship between dendrogram height and the proportion of missing data, either from the full dataset for each species or from the subset of data used for the analysis.

For all species, there was a separation between colonies on the east coast of Britain and colonies on the west coast and in Ireland, following the regions defined by the OSPAR Convention (Fig. 3). However, for most species there was evidence of finer-scale variation than that allowed for under the OSPAR regions.

The EAAs were often broadly similar to RS regions (Fig. 1b), although there were a number of key differences. Principally, the Scottish Continental Shelf RS region is typically split between 2 or more EAAs. Colonies within the Outer Hebrides typically showed variation more consistent with that observed on the

Table 1. Models used to impute missing values for each of the study species. In each case, colony was fitted as a random effect and species counts were $\log(n+1)$ transformed. The model selected was that which gave the highest pseudo- R^2 values from amongst a suite of candidate models. North/South (East/West): binary variable describing whether colony is in the northern or southern (eastern or western) half of the UK

Species	Model	Pseudo- R^2
Northern fulmar	$\sim \text{Year} \times \text{Longitude} + \text{Year} \times \text{North/South}$	0.46
Northern gannet	$\sim \text{Year} \times \text{Longitude} + \text{Year} \times \text{North/South}$	0.85
European shag	$\sim \text{Year} \times \text{Longitude} + \text{Year} \times \text{North/South} + \sin(\text{Year})$	0.61
Great cormorant	$\sim \text{Year} \times \text{Latitude} + \text{Year} \times \text{Longitude} + \text{Latitude} \times \text{Longitude}$	0.54
Arctic skua	$\sim \text{Year} + \text{Colony}$	0.86
Little tern	$\sim \text{Year} \times \text{Longitude}$	0.47
Sandwich tern	$\sim \text{Year} \times \text{Longitude} + \text{Year} \times \text{Latitude}$	0.55
Herring gull	$\sim \text{Year} \times \text{Latitude} + \text{Year} \times \text{East/West}$	0.58
Black-legged kittiwake	$\sim \text{Year} \times \text{Latitude}$	0.69
Common guillemot	$\sim \text{Year} \times \text{Longitude}$	0.62
Razorbill	$\sim \text{Year} \times \text{Latitude}$	0.70

Fig. 2. Imputed versus observed data from the models used to impute missing data for the northern gannet, Arctic skua, little tern and black-legged kittiwake. Also shown are pseudo- R^2 values for the model of each species

west coast of Scotland than that observed elsewhere within the Scottish Continental Shelf region. Furthermore, for the northern fulmar, herring gull and common guillemot, populations within Orkney, Shetland and the North of Scotland showed variation that was more consistent with east coast populations rather than populations elsewhere within the Scottish Continental Shelf region. Populations of European shag, great cormorant and Arctic skua on Shetland showed variation distinct from that observed elsewhere within the UK.

Fig. 3. Ecological Assessment Areas (EAAs) identified for each of the 11 study species by considering regions in which abundance at breeding colonies varies in a consistent fashion. (○) EAA 1, (■) EAA 2, (▲) EAA 3, (★) EAA 4, (△) EAA 5, (□) EAA 6, (◆) EAA 7. Figures refer to the EAA to which each colony is assigned. Black bars mark boundaries of the EAAs

The distinction made between the Western Channel and Celtic Sea and the Irish Sea RS regions was deemed to be superfluous by the EAAs for the herring gull, great cormorant, European shag and northern ful-

mar, with population trends for these areas clustering within the same group. However, these regions were distinct for the razorbill and black-legged kittiwake. Similarly, there seemed to be little distinction between

Fig. 4. Clusters identified using analysis of breeding success (BS) data for the European shag (final model: $BS \sim Year \times Latitude + Year \times Longitude$, pseudo- R^2 0.416), Arctic skua (final model: $BS \sim Year \times Latitude$, pseudo- R^2 0.19), little tern (final model: $BS \sim Year \times Longitude + \sin[Year]$, pseudo- R^2 0.20) and razorbill (final model: $BS \sim Year \times Latitude + Year \times East$ or $West$, pseudo- R^2 0.63). (●) Breeding cluster 1, (■) breeding cluster 2, (▲) breeding cluster 3. Figures and black bars as in Fig. 3

the population trends of colonies in the Southern North Sea and Eastern Channel RS regions for the little tern and black-legged kittiwake.

Clusters identified using the analysis of data from breeding birds showed a similar spatial distribution to those identified using abundance data (Fig. 4). However, there was a crucial difference in that an analysis of breeding data resulted in the identification of fewer coherent regions. Given the long-lived nature of seabird species, data describing breeding success might be expected to show a greater degree of annual variation than abundance data. Furthermore, it would be expected that this would be reflected in the identification of an equal or greater number of clusters than were identified through analysis of the abundance data. However, this was not the case in this instance. This may in part be because fewer data were available describing breeding success. However, it may also be because the breeding success data are 'noisier' and more prone to variation than the abundance data, and consequently more difficult to model. This is reflected in the lower pseudo- R^2 values obtained for models of breeding success than abundance (Fig. 4).

Accuracy and consistency of regional trends

The accuracy of the trends imputed using the different monitoring schemes was highly variable (Table 2). For 5 of the 11 study species, viz. northern fulmar, little tern, black-legged kittiwake, common guillemot and razorbill, the imputed trends were similar to the popu-

lation trends observed between the Seabird Colony Register and Seabird 2000 censuses. Imputed trends for the northern gannet, Arctic skua, Sandwich tern and herring gull proved to be a particularly poor match for the trends observed between the seabird censuses. The OSPAR regions provided more accurate trends than the EAAs ($\chi^2 = 38.61$, $p < 0.0001$) or RSs ($\chi^2 = 22.07$, $p = 0.0086$). However, a comparison of the finer-scale monitoring regions showed that the EAAs provided more accurate imputed trends than the RS regions ($\chi^2 = 18.23$, $p = 0.0325$).

Table 2. Mean accuracy of trends across all regions imputed using the Thomas (1993) approach, in comparison to the trends observed between the Seabird Colony Register and Seabird 2000 population censuses. Accuracy is assessed as the difference between the trends in each region as a percentage of the trend observed between population censuses. Insufficient data were available to impute trends at the level of the UK Regional Seas regions for the Arctic skua

	OSPAR	Regional Seas	Ecologically appropriate
Northern fulmar	17.82	18.96	13.41
Northern gannet	61.79	85.55	62.52
European shag	6.71	34.25	27.91
Great cormorant	13.21	20.78	34.58
Arctic skua	23.32		93.04
Little tern	9.04	24.84	18.96
Sandwich tern	48.90	142.17	66.56
Herring gull	40.74	67.51	53.05
Black-legged kittiwake	7.20	12.17	17.82
Common guillemot	5.19	15.74	16.20
Razorbill	11.39	20.14	21.42

Whilst it is important that monitoring regions can be used to accurately impute population trends, it is equally important that the trends they record are representative of the trends at individual colonies throughout the region. There were no significant differences in the consistency of trends within each set of monitoring regions. However, on average the EAAs (CV 1.31 ± 0.51) were more consistent than either the OSPAR (CV 1.45 ± 0.60) or RS (CV 2.18 ± 1.41) regions.

With the exception of the northern fulmar and great cormorant, the best performing regions in terms of consistency were the EAAs. The OSPAR regions performed relatively poorly in terms of consistency (Table 3), supporting the earlier hypothesis that the strong performance of these regions in terms of accuracy was the result of averaging the trends from a large number of colonies over a wide geographic area.

DISCUSSION

These results demonstrate that the existing monitoring regions are not necessarily the most appropriate scale at which to monitor populations of mobile species. Whilst the large OSPAR regions most accurately accounted for missing data in imputing annual trends, they lacked the cohesion of the finer-scale EAA or RS monitoring regions. Similarly, whilst trends within the finer-scale RS regions showed a greater degree of consistency than the OSPAR regions, the regions themselves proved of limited use for imputing trends with missing data. The most consistent trends were recorded within the EAAs, which also proved capable of imputing trends with missing data to a reasonable degree of accuracy. Consequently, the EAAs may prove the most useful in monitoring terms for seabirds.

Spatial variation in seabird population trends

The pressures to which seabird populations are exposed are likely to vary spatially. At a broad level, the distribution of breeding colonies is determined by the availability of suitable habitat within appropriate bioclimatic zones. However, variation in population trends between breeding colonies is likely to be affected by processes occurring at a finer scale, for example those that influence the distribution of prey species (Robinson et al. 2002). Populations of prey species can be influenced by processes acting at a highly localised scale, for example relatively subtle differences in temperature, salinity or sediment type (Lindley 1990, Halley et al. 1995, Rogers & Millner 1996, Maravelias 1997), but also pressures such as fisheries that act over a wider, regional level (Sherman et al.

Table 3. Coefficient of variation of trends in seabird abundance within the OSPAR (GNS: Greater North Sea, CS: Celtic Seas), Regional Seas (NNS: Northern North Sea, SNS: Southern North Sea, EC: English Channel, WCC: Western Channel and Celtic Sea, IS: Irish Sea, MWS: Minches and West Coast of Scotland, SCS: Scottish Continental Shelf) and Ecologically Appropriate Areas monitoring regions. Also shown is the weighted mean coefficient of variation within each set of monitoring regions. na = insufficient data available to calculate coefficient of variation. Bolded values = weighted mean coefficients of variation within each set of monitoring regions

Species	OSPAR			Regional Seas							Ecologically Appropriate Areas								
	GNS	CS	Mean	NNS	SNS	EC	WCC	IS	MWS	SCS	Mean	1	2	3	4	5	6	7	Mean
Northern fulmar	0.54	0.94	0.73	0.57			na	1.16	0.59	1.16	0.78	0.54	0.82	1.14					0.75
Northern gannet	1.18	1.51	1.36	0.80			na	1.24		1.09	1.08	1.18	1.51						1.36
European shag	1.31	3.23	2.25	1.23		na	na	0.86	1.41	0.77	1.11	1.41	1.09	1.28	0.76				1.16
Great cormorant	3.02	7.68	5.00	2.96	2.09	0.46	0.46	5.12	0.46	1.83	2.76	2.13	1.45	0.35	0.95	0.73	1.65	1.14	1.38
Arctic skua	na	0.94	0.94	na					na	1.03	1.03	0.59	0.42						0.48
Little tern	1.31	3.23	2.25	1.23		na	na	0.86	1.41	0.77	1.11	1.41	1.09	1.28	0.76				1.16
Sandwich tern	2.19	2.14	2.17	1.31	1.82	0.98		2.14			1.68	1.63	1.61	0.98	1.39	1.31			1.42
Herring gull	1.58	5.91	4.70	1.60	1.61			5.26	0.94	na	2.20	1.06	7.02	1.63	1.61				2.46
Black-legged kittiwake	1.45	1.08	1.31	1.27	0.08	1.02	0.47	0.92	0.21	1.52	1.11	1.41	0.77	1.27	1.76	0.55	0.76		1.18
Common guillemot	1.16	1.39	1.32	1.07		na	na	1.30	na	1.50	1.26	1.38	1.08						1.30
Razorbill	2.12	2.00	2.04	2.12			na	1.79	na	na	1.91	1.47	2.12	1.65	1.84				1.82

1981, Jansen et al. 1994, Wright & Begg 1997, Wanless et al. 1998, Furness & Tasker 2000, Tasker et al. 2000). Seabird species may also exhibit regional differences in their foraging behaviour in response to the availability of a predictable food source, such as an oceanic front (Begg & Reid 1997, Gremillet et al. 2006) or fisheries discards (Hudson & Furness 1988, 1989, Furness et al. 1992, Garthe 1997, Hamer et al. 1997).

It is these sources of variation that are likely to determine to what extent population trends at a regional level accurately and consistently represent the population trends at individual colonies within the region. By considering only static variables, such as habitat type, at the expense of these more dynamic variables, for example populations of prey species, important sources of variation in the population trends of seabirds are overlooked. As a result, the scale and number of EAAs may in part reflect the foraging range and preferences of each study species.

Species such as the northern gannet and northern fulmar are typically thought of as more pelagic foragers (i.e. Hamer et al. 1997, 2001, Gremillet et al. 2006, C. Thaxter unpubl. data), whilst others such as the terns and great cormorant are thought of as inshore foragers (i.e. Gremillet 1997, Wanless et al. 1998, Perrow et al. 2006, C. Thaxter unpubl. data). As the northern gannet and northern fulmar are able to forage over wide areas, they are likely to be less prone to local variation in prey availability. This is borne out by the relatively large size of the EAAs identified for these species, in contrast with species such as the Sandwich tern, for which a larger number of smaller regions were identified. Consequently, in these species, population trends may be influenced by processes occurring over a wider area than trends in species with a more restricted foraging range.

It is important to note that these results are based on data from the breeding season, when processes influencing seabird populations are generally well understood. Over-winter survival is likely to strongly influence population trends. However, habitat use over winter by seabirds is poorly understood, and consequently it is not possible to incorporate this information into the modelling at this stage.

Adapting existing monitoring to reflect ecological relevance

In an ideal world, monitoring regions would be representative of all species which occur within them. In practice, differences in species ecologies mean that this is unlikely to be possible. As a result, it is important to consider how regions can be adapted for use with other species. In many cases, there was significant

overlap between EAAs for multiple species. For example, the east coast of the mainland of Britain represented a single EAA for the northern fulmar, northern gannet, European shag, common guillemot and razorbill. This area is broadly contiguous with the Greater North Sea OSPAR region. Similarly, for the northern fulmar, great cormorant, European shag, little tern, herring gull and Sandwich tern, colonies in the west of Britain and Ireland are split between 2 EAAs, broadly contiguous with the Minches and Western Scotland and Irish Sea RSs. In each of these cases, only minor modifications are required to the existing monitoring region(s) in order to reproduce the EAAs. These results demonstrate that existing monitoring regions, defined using static variables, can be refined to take into account mobile species.

CONCLUSIONS

Marine top predators, such as seabirds, are often highly mobile and subject to a broad range of pressures across their range. Effective monitoring regions must be designed with these pressures in mind, as their impacts may vary at different spatial scales. Consequently, a '1-size-fits-all' approach to the monitoring of marine top predators is unlikely to provide reliable and consistent population trends. However, by considering the similarities in different species' foraging requirements, it should be possible to design monitoring schemes appropriate to multiple species.

Under the terms of the MSFD, governments are permitted to implement monitoring at a fine scale in order to account for the specificities of any given area, so long as when combined, these monitoring regions are compatible with the sub-regions set out in the directive. The existing RS and OSPAR monitoring regions provide a useful basis for this, as in most cases, EAAs defined for seabirds are broadly similar to regions within 1 of these schemes. This study highlights the importance of taking species' ecologies into consideration in the design of monitoring regions. By considering how different species' populations are likely to vary on a regional basis, rather than constraining monitoring to regions that are uniform across all species, it is possible to generate trends that provide a more accurate picture of the populations they represent. This is key to understanding the mechanisms underlying population change and hence the overall health of the marine ecosystem.

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Appendix 1. Distribution and proportion of missing data from both individual species datasets and the subsets of those datasets used for analysis

Species	Total colonies (n)	No. of colonies missing a percentage of data					Total proportion of missing data (%)	No. of colonies used in analysis	Proportion of data missing from subset used for analysis (%)
		>80 %	60–80 %	40–60 %	20–40 %	<20 %			
Northern fulmar	1015	982	10	3	6	14	93	33	3
Northern gannet	21	8	8	2	1	2	70	13	59
European shag	297	250	13	11	13	10	82	47	14
Great cormorant	171	112	18	8	16	17	65	59	21
Arctic skua	52	51	1	0	0	0	94	6	20
Little tern	67	24	6	2	6	29	40	43	10
Sandwich tern	48	18	2	0	0	28	38	30	5
Herring gull	450	388	11	14	26	11	83	62	21
Black-legged kittiwake	407	353	21	11	9	13	82	54	15
Common guillemot	377	346	14	4	6	7	88	31	16
Razorbill	292	264	10	5	6	7	88	28	15