Introduction: a modern role for seabirds as indicators

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A key requirement for implementing ecosystem-based management is to obtain timely information on significant fluctuations in the ecosystem (Botsford et al. 1997). However, obtaining all necessary information about physical and biological changes at appropriate temporal and spatial scales is a daunting task. Intuitively, one might assume that physical data are more important for the interpretation of ecosystem changes than biological data, but analyses of time series data suggest otherwise: physical data are more erratic and
often confusing over the short term compared to biological data, which tend to fluctuate less on annual time scales (Hare & Mantua 2000). Even so, biological time-series may also be confusing when coexisting marine species respond differently to ecosystem variability. For example, while warming temperatures in the Gulf of Alaska following the 1976 to 1977 regime shift favored an increase in gadoids and flatfish, a variety of forage fish and pandalid shrimp species virtually disappeared (Anderson & Piatt 1999). Zooplankton communities in the Gulf of Alaska also demonstrated similar patterns of response (Francis et al. 1998). At the basin scale, favorable conditions for salmon in Alaska following the regime shift were matched inversely by poor conditions in the California Current (Francis et al. 1998). In marine birds, subtropical species increased, while subarctic ones decreased during a warming phase in the southern California Bight. Clearly, no single index can tell the whole story accurately. Multi-species, multi-region, and multi-trophic level approaches are needed to quantify fluctuations in marine ecosystem processes and in the distribution and abundance of its inhabitants, to determine critical parameter thresholds and to use this information in management and marine conservation.

**Using seabirds as indicators.** Seabirds can contribute to this approach, offering unique insights into ecosystem status and change. In terms of marine species, seabirds offer many advantages for study. They are highly visible animals in an environment in which most other plants and animals are completely hidden under water. They are easily enumerated as they travel or forage in productive marine hotspots (Sydeman et al. 2006). Most species are colonial and gather annually in large numbers at relatively few locations in order to reproduce, a convenient occurrence that allows one to census populations and monitor trends of multiple coexisting species at various trophic levels simultaneously. Furthermore, some species are easy to observe and capture at colonies, allowing measurements of a wide variety of demographic, behavioral and physiological parameters. Given their relative ease of study, seabirds have frequently been identified as useful indicators of the health and status of marine ecosystems (see reviews by Montevecchi 1993, Furness & Camphuysen 1997).

For example, breeding failures in Peruvian guano birds (booby, pelican, cormorant) heralded the collapse of the anchoveta *Engraulis ringens* fishery during the 1950s and 1960s; reproductive failures of the Atlantic puffin *Fratercula arctica* presaged the collapse of herring *Clupea harengus* stocks off Norway during the 1970s; the near-instantaneous crash of common murre *Uria aalge* populations in the Barents Sea during the 1980s signaled the collapse of the capelin *Mallotus villosus* in the Barents Sea; and widespread failures in breeding of the black-legged kittiwake *Rissa tridactyla* in the North Sea during the late 1980s indicated the collapse of sand eel *Ammodytes* spp. stocks and a widespread change in environmental conditions in the North Sea.

The concept of seabirds as indicators of fish stocks was well established by the early 1980s (Cairns 1987, Montevecchi 1993). Efforts over the next 2 decades focused on gathering data on a wider variety of demographic, behavioral and physiological parameters. At sea, concurrent studies of seabirds and forage fish allowed investigators to quantify functional predator–prey relationships for the first time. At colonies, researchers examined behaviors related to the acquisition of prey at sea. After prey were delivered to chicks at the colony, questions focused on how food was assimilated and how feeding rates influenced breeding biology and ultimately population demography (e.g. Croxall et al. 1999). With a variety of technological advances we can measure time budgets (time–activity recorders, Cairns 1987), foraging effort (time–depth recorders), energy expenditure (doubly-labeled water), stress levels (corticosteroid hormone concentrations), diet trends (stable isotope and fatty acid analyses) and a number of other parameters which provide insight into how seabirds respond to changes in their environments.

The importance of scale became increasingly obvious while looking for spatial patterns in pelagic distribution data. Processes influencing the distribution and abundance of seabirds at sea are themselves scaled, from the patches of prey that persist for only minutes or hours over meters in the water column, to seasonal prey aggregations found along current boundaries or shelf-edges, to fluctuations in climate over annual, decadal or longer time periods and the influence of ocean basins and current regimes at the largest spatial scales. Ultimately, scale is important as we search for concordance in demographic trends across large regions and evaluate the effects of climate variation on local populations (Montevecchi & Myers 1997).

**Seabirds and the climate–ecosystem nexus.** Seabird data has been useful in recent years for the study of climate change and regime shifts in marine ecosystems. A pivotal paper by Aebischer et al. (1990) revealed a remarkable parallel in long-term (decadal) trends across 4 trophic levels, including, specifically, phytoplankton, zooplankton, herring, and kittiwakes, and the frequency of westerly weather in the North Sea. This work supports two important hypotheses: (1) that higher trophic level animal populations are largely controlled by bottom-up processes and (2) that seabirds or their biological attributes (in this case breeding phenology, clutch size and chick production by
kittiwakes) are accurate indicators of ecosystem status and change, at least at those temporal and spatial scales. On the other side of the world, retrospective analysis of seabird data provided some of the earliest evidence that a shift in the physical regime of the Gulf of Alaska during the late 1970s had a major impact on higher vertebrate communities of fish and wildlife (Francis et al. 1998). Contemporaneous changes in diet composition of 5 abundant seabirds in the Gulf of Alaska, from diets dominated by high-energy capelin to the low-energy pollock Theragra chalcogramma, pointed a finger at climate variability as the ultimate cause of diet and demographic changes in seabird populations (Piatt & Anderson 1996).

With longer time-series, more precise annual data, and more parameters under scrutiny, seabirds offer ever-expanding insights into the effects of climate change on marine ecosystems. For example, marked changes in the diet and reproductive output of 11 species of seabirds in the California Current reflect low-frequency climate changes (Sydeman et al. 2001). Indeed, seabird diets can reveal the influence of climate at many time scales, including seasonal, annual, multi-annual (e.g. El Niño Southern Oscillation [ENSO] frequency), decadal and centurial scales (Montevecchi & Myers 1995). And these temporal scales are linked: it appears that annual variability of within-year timing of the seasonal cycles of primary and secondary productivity has a pronounced effect on productivity of marine fish and birds, owing to match–mismatch effects (Bertram et al. 2001). In addition to the more conspicuous effects of extreme climate change on adult survival (e.g. adult mortality at tropical seabird colonies during strong ENSO events in the Pacific, Chavez et al. 2003), demographic parameters, such as production and population trends, can be strongly correlated with large scale indices of ocean climate, such as temperature or the Southern Oscillation Index (Lee et al. 2007).

**Seabirds as indicators for management.** Ecosystem indicators are used in one part of a larger process to develop policy-level goals for ecosystem management (Kruse et al. 2006). However, in order to use indicators effectively, we need to determine how ecosystem science relates to ecosystem-based fisheries management policies (Christensen et al. 1996, Mangel et al. 1996) by elucidating the mechanisms that link climate variability, oceanographic processes, trophic level production and fisheries (Carpenter & Folke 2006). Indicator species or processes also need to be vetted for independent secular or cyclical changes and the possibility that indicators themselves may disappear from the system. It may not be useful to focus on single, sentinel species as indicators of ecosystem-level changes, but to broaden our thinking by looking at aggregate indicators, such as the biomass of a class of consumers.

Indicators are used currently as a heuristic tool to reflect key ecosystem processes and patterns. Linking indicators to decision criteria remains a key challenge. While scientists point to complexities of ecosystems, managers require defensible environmental information in order to take actions that may have economic consequences. Ecosystem-based indicators are often conservative in the sense that they only show if the ecosystem is strongly affected, leaving management to take narrowly-focused actions without benefit of more specific data in hand.

Indicators can be classified as strategic or tactical (Kruse et al. 2006). Tactical indicators are used to measure immediate, short-term management responses, such as estimated stock biomass. Management action does not follow immediately when indicators such as these show change, but information about their trajectories might provide context for future management actions. Strategic indicators of future ecosystem response (‘sentinels of climate change’) depend on past performance being a good predictor of the future. If climate variability changes the rules by which ecosystems function, then the use of some long-term predictors becomes problematic. If species are to be useful as sentinels of change, then their responses need to be calibrated to changes in ecosystem function.

In the long term, our use of indicators needs to shift from the purely contextual to include predictive or management indicators, although clearly both types are needed. Contextual (or ‘audit’) indicators provide background context and may index conditions over which humans have no direct control. Management (or ‘control’) indicators report on conditions over which humans have some direct control, so they could be used to monitor the results of management actions. In ecosystem-based fisheries management, the objective is not to find the best indicator, but rather a relevant suite of indicators that respond in known ways to ecosystem change. Selected indicators should be relevant, integrative, sensitive, correct, defensible, vetted and economical.

Analysis of existing datasets often reveals ecosystem shifts in hindsight, pointing to correlated indicators that tend to be data-driven rather than process-oriented. The question is: how reliable are the indicators? Once historical time-series of indicator values have been developed, the next step should be to reconstruct the management decisions that would have resulted from these data. Four outcomes are possible in indicator evaluation: (1) hit (something should have been done and the indicator said take action); (2) true negative (no management response was needed and the indicator said status quo okay); (3) miss (something should have been done but the indicator did not say action...
was needed); (4) false alarm (nothing needed to be done but the indicator called for management intervention). A perfect indicator has no misses or false alarms. One approach to the use of ecosystem indicators (Kruse et al. 2006) explicitly acknowledges that the costs associated with misses and false alarms are not the same. It allows users to choose a decision point on an indicator (‘reference point’) that minimizes the overall error rate or controls the ratio of misses and false alarms in a manner that reflects their relative costs to management of the resource (see Kruse et al. 2006 for details).

Although seabirds are useful ecosystem indicators, calibration is required to know exactly what they indicate at any one time and place or how to interpret variability in their biology over different temporal and spatial scales. Marine ornithologists have generally provided more qualitative than quantitative indices of ecosystem change, and they have often neglected to effectively highlight their work in the realm of fisheries science (Cairns 1987, but see Hatch & Sanger 1992, Roth et al. 2007). Only a few functional (possibly predictive) relationships between seabird indicators and ecosystem properties have been developed. Often due to the temporal limitations of datasets, we tend to develop simple correlations between ecosystem properties (e.g. temperature, abundance of a particular prey species) and some measure of seabird breeding biology, where predictive equations would be most valuable in a management context. Previous work has also failed to address the nature of these relationships: Are they linear or non-linear? With or without thresholds? Cairns (1987) argued on theoretical grounds that different seabird demographic and life history measurements should have mostly non-linear relationships to ecosystem and food web fluctuations, but to date this has rarely been tested. There is also confusion over which parameters may serve as the most sensitive ecosystem indicators (i.e. have a high signal to noise ratio).

**A modern role for seabirds as indicators and predictors.** With this backdrop and with encouragement from the North Pacific Research Board (NPRB), we convened an international symposium on ‘Seabirds as Indicators of Marine Ecosystems’. The NPRB, created by the US Congress in 1997 to recommend and fund research initiatives in the Northeast Pacific, is charged with building a clear understanding of North Pacific, Bering Sea and Arctic Ocean ecosystems that enables effective management and sustainable use of marine resources. The NPRB recognizes that seabirds may serve as cost-effective indicators of the health and status of these ecosystems and allocates about 10 to 15% of its annual research budget (now ca. US$8 to 10 million) to marine bird research. To synthesize the current state of knowledge for NPRB, we held the symposium from 19 to 21 February 2006, under the auspices of the Pacific Seabird Group (PSG) and during their 33rd annual meeting. A total of 22 invited speakers from both coasts of the United States and Canada, as well as from Great Britain, Japan, Russia and France were asked to provide insight on the role of seabirds as ecosystem indicators from diverse ecosystems in the North Atlantic, North Pacific and the Antarctic. An additional 15 contributed papers were also presented. A workshop was held immediately after the symposium. Discussions held during the symposium focused on 3 broad themes: (1) how best to use seabirds as ecosystem indicators, (2) quantitative considerations for seabirds as indicators, and (3) how to advance the science of seabirds as indicators. In addressing these themes, we asked participants to critically evaluate the role of seabirds as indicators: What are they good at indicating, and what are they not useful for? Are there better, more cost-effective indicators? To what kinds of signals are they most sensitive? Which parameters and species are most useful or practical to measure? Are responses species-specific? How does the role of seabirds compare with other taxa or measurements? What is the role of spatial and temporal scaling in the interpretation of seabird response to change? What new techniques can be applied to facilitate the use of seabirds as indicators? If we predict certain environmental changes in the future, which seabirds and parameters should we be measuring to detect or monitor those changes? The following is a synopsis of major conclusions of the symposium and workshop:

- **There are two types of indicators:** (1) seabirds as ‘sentinels’ or ‘bio-monitors’ of ecosystem change (e.g. contaminant load indicates pollution) and (2) seabirds as quantitative indicators of specific ecosystem components, such as the abundance of a forage fish species. The latter requires detailed knowledge of the functional response of the seabird parameter under investigation to changes in prey density around a colony.

- **In some cases, seabird parameters may be predictive.** This could be important for managing fisheries, where knowledge of seabird responses to ecosystem variability may be used to forecast changes in fish stocks.

- **Seabirds are not needed to indicate atmospheric and ocean climate changes per se** (this can be done directly with satellites and other automated devices such as moorings), but they provide timely and accurate information on the ecological consequences of climate changes that are not as easily or rapidly detected using other organisms. In some cases, biological parameters provide a more reliable indication of ecosystem shifts than physical parameters because they tend to fluctuate less on a year-to-year basis.
• Spatial scale is critical. Variation in seabird response parameters generally reflects meso-scale variability in the environment, e.g. the success of breeding colonies may reflect fluctuations in local prey stocks before, or in addition to, reflecting broad-scale regional variability.

• Different seabird parameters indicate change over a wide range of temporal scales. Population size and trends provide information on ecosystem variability on the scale of years to decades, due to deferred reproduction. In contrast, annual reproductive performance provides information on a monthly scale from the initiation of egg-laying through chick-rearing each year, providing information on shorter term ecosystem variability.

• Multivariate (multi-species, multi-parameter) indices may integrate complex ecological relationships into a single parameter that is easier to evaluate for its ecological significance (and yield concepts that are easier to communicate to the public and managers). However, univariate indices are needed to calculate and interpret multivariate indices and to interpret individual biological functions (e.g. breeding success).

• Relationships between measurable components of seabird biology and prey resources take many forms. Some non-linear functions (e.g. sigmoid curves) indicate where thresholds occur in seabird–prey relationships. Binary (on–off; good or bad foraging) relationships are powerful, especially when considered over large spatial scales. Linear relationships are best for prediction, but rare.

In addition to attending the symposium and workshop, we invited participants to contribute papers to this special Theme Section of Marine Ecology Progress Series. The 10 papers presented here address many of the important questions posed to participants in the symposium. Frederiksen et al. and Montecvecchi advance our knowledge of ways to analyze and interpret complex datasets on reproductive biology and diets, particularly in how to resolve and improve the biological signals resulting from fluctuations in prey abundance. Piatt et al. provide the first explicit test of Cairns’ (1987) seminal predictions about functional relationships between parameters of seabird ecology and prey abundance. Using unique data that they collected and laboratory methods they pioneered for application in marine ecology, Iverson et al. and Kitaysky et al. review their studies of how seabirds respond physiologically to changes in diet composition (as indicated by fatty acids) and prey abundance (as indicated by stress hormones). Robinette et al. focus on how seabird diet may reveal patterns in recruitment of a demersal fish species, while Harding et al. provide an in-depth focus on how a key indicator behavior of a seabird varies in response to prey fluctuations.

Parrish et al. and Springer et al. advance our understanding of the role of ocean climate on the survival and feeding ecology of seabirds in the North Pacific, examining the effects of temporal variability in shelf-edge upwelling and the impact of persistent warming of shelf waters, respectively. Finally, Newman et al. analyze a 35 yr database to assess continent-wide patterns of disease and mortality in marine and aquatic birds; to our knowledge, the first time such a review has ever been conducted.

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LITERATURE CITED


Christensen NL, Bartuska AM, Brown JH, Carpenter S and others (1996) The report of the Ecological Society of America committee on the scientific basis of ecosystem
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INTRODUCTION

There is a clear policy-driven need to develop reliable indicators of the ecological state of marine environments to support ecosystem-based management of living resources (Niemi et al. 2004, Rice & Rochet 2005). While the final choice of indicators will be based on numerous criteria, including cost, practicality, etc., ecologists can play an important role in developing indicators that are both useful to managers and have a sound scientific basis. Seabirds may be useful in this process, as they are sensitive to variations in food supply and relatively easy to observe. However, any individual parameter (e.g. breeding success of a particular species at one site) may also be affected by drivers other than food supply, and selecting a suitable univariate indicator can be difficult, particularly if independent estimates of food availability on the appropriate scale are unavailable. We propose combining several data sets to overcome this limitation: if a given temporal pattern occurs for several parameters measured at one site, or for the same parameter measured at several sites, it is likely to reflect important spatiotemporal environmental variation, probably linked to food supply. Multivariate statistical techniques, such as principal component analysis (PCA), can be used to extract common signals from a number of intercorrelated time series. Examples from seabirds in the North Sea demonstrate that such common signals are correlated with physical and biological environmental variables. We propose a preliminary ‘North Sea seabird index’ and discuss how this index could be used in ecosystem-based management.

KEY WORDS: Ecological indicators · Seabirds · Food availability · Multivariate statistics · Principal component analysis

Seabirds as environmental indicators: the advantages of combining data sets

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ABSTRACT: Breeding performance of seabirds reflects conditions in the marine environment, and seabirds are often considered suitable indicators because they are sensitive to variations in food supply and relatively easy to observe. However, any individual parameter (e.g. breeding success of a particular species at one site) may also be affected by drivers other than food supply, and selecting a suitable univariate indicator can be difficult, particularly if independent estimates of food availability on the appropriate scale are unavailable. We propose combining several data sets to overcome this limitation: if a given temporal pattern occurs for several parameters measured at one site, or for the same parameter measured at several sites, it is likely to reflect important spatiotemporal environmental variation, probably linked to food supply. Multivariate statistical techniques, such as principal component analysis (PCA), can be used to extract common signals from a number of intercorrelated time series. Examples from seabirds in the North Sea demonstrate that such common signals are correlated with physical and biological environmental variables. We propose a preliminary ‘North Sea seabird index’ and discuss how this index could be used in ecosystem-based management.
the critical requirements. However, their sensitivity to stresses is often unknown, and it is not always obvious that they are integrative, i.e. reflect a general response of the ecosystem to natural or anthropogenic stressors. Alternatively, by combining several data sets using, e.g., multivariate statistics, it is possible to develop integrative indicators showing predictable responses to stressors, although data requirements are substantially higher and ease of interpretation may be compromised. This approach is common in freshwater systems (e.g. O’Connor et al. 2000), but has seldom been used in marine contexts to date, with the notable exception of the Combined Standardised Index developed by the British Antarctic Survey based on data from long-term studies of seabirds and pinnipeds on Bird Island, South Georgia (Boyd & Murray 2001, Reid et al. 2005).

Here, we use long-term seabird data sets from the NW North Sea to explore the feasibility and potential advantages of combining data across species and/or sites. First, we validate this approach by testing whether correlations between time series are sufficiently high to make combining them an attractive option and whether such combined indices are as responsive to environmental conditions as are individual time series. Second, we propose a preliminary combined index of the breeding performance of 5 seabird species in this area as a general indicator of the ‘health’ of the marine ecosystem, in terms of providing sufficient food for breeding seabirds to raise their young.

MATERIALS AND METHODS

Combining data. Related ecological time series, e.g. breeding productivity of several seabird species in the same area, are often moderately to highly intercorrelated. This presumably reflects a common dependence on environmental conditions, such as weather or a shared food supply. In addition, each time series may be affected by measurement error as well as idiosyncratic factors, such as varying predation levels at some sites or higher sensitivity of one species to weather. By combining the data sets, it is possible to identify the general response of a species or community to environmental variation, independent of these variable-specific issues. In the rare case when correlations between time series are very low, indicating no general response, there are no gains associated with combining the data sets. The choice of methods for combining several data sets (ecological time series) depends on the nature of the data. If data are roughly normally distributed and all data series are similar in terms of measurement scale and variability, e.g. the breeding productivity of a particular species measured at several sites, then the arithmetic mean provides a simple and useful summary. Appropriate link functions and error distributions can be used to account for non-normal data, if needed. In the case of unbalanced designs with missing data points, least-squares means from a model with year effects only give adjusted means as if the design had been balanced. Some data sets and/or annual values may be considered more reliable than others, e.g. if they are based on larger sample sizes; in this case, appropriate weights can be used when estimating the mean.

When data are more complex, such as when measurement scales and/or variability differ substantially, multivariate techniques must be applied (McGarigal et al. 2000). Several approaches are possible, but here we concentrate on principal component analysis (PCA), which provides an objective method for extracting the strongest possible common signal from a number of intercorrelated time series. Individual principal components are uncorrelated, and thus potentially represent different aspects of seabirds’ responses to the environment. Important diagnostics of PCA include proportions of the total variation explained by each component and correlations between components and original variables (often termed loadings). Standard multivariate techniques, including PCA, do not allow for missing data. In such cases, missing values can be imputed, i.e. replaced by best guesses or specific methods that allow for missing data developed (e.g. Boyd & Murray 2001).

Validating the data combination approach. First, we tested whether the relationship between breeding productivity of black-legged kittiwakes Rissa tridactyla, sea surface temperature (SST) and fishery was consistent between colonies within a region. Breeding productivity (number of fledged chicks per nest built) of kittiwakes on the Isle of May, SE Scotland, is strongly negatively related to late winter SST in the previous year and to the presence of an industrial (fishmeal) fishery for lesser sandeels Ammodytes marinus, the main prey during the breeding season (Frederiksen et al. 2004). Kittiwake breeding productivity has also been monitored under the UK Seabird Monitoring Programme at 6 other colonies in the same region of the NW North Sea (E Scotland and NE England; Fig. 1), as defined by sandeel population structure and correlations between kittiwake breeding productivity time series (Frederiksen et al. 2005, Mavor et al. 2005). We repeated the analysis of Frederiksen et al. (2004) for the Isle of May and these other colonies, as well as for the mean breeding productivity in the region, based on data from 1986 to 2004. The fishery was scored as present in 1991 to 1998, and mean February/March SSTs from this region were obtained from the German Bundesamt für Seeschifffahrt und Hydrographie (www.bsh.de).
Second, we tested whether the relationship between seabird breeding productivity and larval sandeel abundance was consistent between species at one site. Data on annual breeding productivity (number of fledged chicks per nest) of 4 sandeel-dependent seabird species (European shag *Phalacrocorax aristotelis*, black-legged kittiwake, razorbill *Alca torda*, Atlantic puffin *Fratercula arctica*) were collected using standardised methods on the Isle of May from 1986 to 2003 (Harris et al. 2005); there were no missing values in any of these data sets. Although common guillemots also mainly feed their chicks on sandeels, we did not include this species as adults carry single fish back to their offspring, and breeding productivity is consequently more tightly linked to size and quality of prey rather than abundance (Frederiksen et al. 2006). An index of larval sandeel abundance, standardised to 1 May, was estimated from the prevalence, abundance and size of sandeel larvae in Continuous Plankton Recorder samples from the NW North Sea (see Frederiksen et al. 2006 for details). Preliminary analyses showed that the value of the larval sandeel index in the previous year was more closely related to seabird breeding productivity than the same year’s value, indicating a dependence on 1-yr-old (1-group) sandeel (authors’ unpubl. data). We carried out a PCA on the 4 breeding productivity time series, and modelled the first principal component (PC1) as well as the 4 original time series as functions of the lagged sandeel index using linear regression. The PCA was performed on the correlation matrix of the original time series, thus implicitly standardising data to zero mean and unit variance.

A preliminary North Sea seabird index. To develop a general index of seabird breeding performance in the NW North Sea, we combined data from all regularly monitored species on the Isle of May. Data collection at this colony is much more comprehensive than at any other colony in the region, and for black-legged kittiwake the correlation with the regional mean was also highest here (see ‘Results’). Breeding productivity was measured for European shag, black-legged kittiwake, common guillemot, razorbill and Atlantic puffin as described above from 1986 to 2005. For common guillemot and Atlantic puffin, the mean mass of near-fledged chicks was also recorded. Again, there were no missing values in any of the data sets. We carried out a PCA on these 7 response variables using the same approach as above, retaining the first 2 principal components (PC1 and PC2).
RESULTS

Kittiwakes, SST and fishery

Data from each of the 7 colonies in the study region were available for 15 to 19 yr during 1986 to 2004; 13 data points (10%) were missing. Breeding productivities of kittiwakes in the study colonies were highly positively intercorrelated (mean $r = 0.66$, all $r > 0.28$, all $p \leq 0.30, 17$ of $21 \ p < 0.05, n = 13$ to $18$ yr), as also found by Frederiksen et al. (2005) using shorter time series. An ANOVA model weighted by annual sample size with only year effects explained $63\%$ of the total variation; least-squares means estimated from this model were highly positively correlated with raw data from each colony ($r = 0.66$ to $0.96$, all $p < 0.01$), with highest correlation for the Isle of May. Late winter SST lagged by 1 yr together with the presence of a sandeel fishery explained $18$ to $66\%$ of the annual variation in breeding productivity at individual colonies, and model coefficients were similar across colonies, particularly for the SST effect (Table 1, Fig. 1). The same 2 factors were highly significantly related to the regional least-squares mean and explained $61\%$ of the annual variation (Table 1), only slightly lower than the highest value for an individual colony, the Isle of May.

Seabird breeding productivity and larval sandeel abundance

Breeding productivities of the 4 species were mainly positively correlated ($r = -0.16$ to $0.65$, 1 of $6 \ p < 0.05$, $n = 18$ yr). PC1 explained $51\%$ of the total inter-annual variation in breeding productivity, and loadings were high and positive for all original time series (Table 2). Breeding productivity was significantly positively associated with the sandeel larval index for European shag and black-legged kittiwake, but not for razorbill and Atlantic puffin (Table 2, Fig. 2). PC1 was also significantly correlated with the sandeel index, with a slightly lower proportion of variation explained than for shags and kittiwakes (Table 2, Fig. 3).

A preliminary North Sea seabird index

All correlations between the 7 response variables were positive ($r = 0.05$ to $0.84$, $11$ of $21 \ p < 0.05$, $n = 20$ yr). PC1 explained $57\%$ of the total variation, with positive loadings for all original variables, 5 of $7$ above $0.75$ (Table 3). PC2, which explained $19\%$ of the total variation, was mainly positively associated with European shag and black-legged kittiwake breeding productivity (Table 3). PC1 showed a clear declining trend over the study period (Fig. 4; $R^2 = 48\%, p = 0.0007$), whereas PC2 showed an increasing trend after 1990, the trend approaching statistical significance for the whole study period (Fig. 4; $R^2 = 19\%, p = 0.057$).

DISCUSSION

We found that response variables, whether breeding productivity of one species measured at several sites, or breeding performance of several species measured at one site, tended to be well correlated. Data could therefore profitably be combined to identify common signals (regional means or principal components), which in turn were highly positively correlated with the original time series.

The 2 case studies with environmental covariates show that combining data sets resulted in little or no loss in terms of the strength of relationships with relevant environmental parameters (Tables 1 & 2).
There were also substantial gains in terms of general- ity. We conclude that black-legged kittiwake breeding productivity at several colonies in the NW North Sea was negatively correlated with late winter temperatures and the presence of a sandeel fishery, and that breeding productivity of sandeel-dependent seabirds on the Isle of May was positively related to the abundance of sandeel larvae in spring of the previous year. This is an important first step in testing whether multivariate seabird indicators can provide useful information about the marine environment.

Combining data also aids identification of the most relevant univariate indicators, which often can be measured at lower cost and are potentially applicable to large-scale, extensive monitoring programmes. The analysis of black-legged kittiwake breeding productivity at 7 colonies in the NW North Sea showed that data from the Isle of May had the highest correlation with the regional mean ($r = 0.96$), and that the relationships with SST and fishery were strongest for this colony (Table 1). The colony could thus be regarded as the most appropriate location to monitor black-legged kittiwake breeding productivity in this region. Similarly, black-legged kittiwake or European shag would be the most appropriate species to monitor if the aim was to study the relationship between breeding productivity and the abundance of sandeel larvae (Table 2), and mean fledging mass of common guillemot chicks would provide an excellent proxy for the breeding performance of 5 seabird species on the Isle of May (Table 3).

The proposed North Sea seabird index showed some interesting patterns (Fig. 4). PC1, which describes demographic performance of all species with an emphasis on the 3 alcids (Table 3), showed a clear decline over the 20 yr study period, presumably indicating a general deterioration of conditions during the breeding season around the Isle of May. Interpretation of PC2 is more complex, as the 2 variables with the highest loading, European shag and black-legged kittiwake breeding productivity, also load positively on PC1 (Table 3). The positive trend since 1990 (Fig. 4) thus implies that, relative to the alcids, these 2 species have done better in recent years, even though kittiwake breeding productivity has declined over the study period when viewed in isolation (cf. Frederiksen et al. 2004).

The ecological indicators have at least 2 different aims. They may either serve to indicate the general state or ‘health’ of an ecosystem, or they may measure the response of organisms to a specific stressor. The pro-

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Table 3. The first 2 principal components of 7 breeding performance variables of seabirds breeding on the Isle of May, 1986 to 2005. Loadings for each variable and the proportion of the total variance explained by each component are given.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Principal components</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PC1</td>
<td>PC2</td>
<td></td>
</tr>
<tr>
<td>Proportion explained</td>
<td>57%</td>
<td>19%</td>
<td></td>
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</tbody>
</table>

**Breeding productivity**

<table>
<thead>
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<th>PC2</th>
</tr>
</thead>
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<tr>
<td>European shag</td>
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<td>0.69</td>
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<tr>
<td>Black-legged kittiwake</td>
<td>0.53</td>
<td>0.63</td>
</tr>
<tr>
<td>Common guillemot</td>
<td>0.84</td>
<td>-0.42</td>
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<tr>
<td>Razorbill</td>
<td>0.75</td>
<td>-0.41</td>
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<tr>
<td>Atlantic puffin</td>
<td>0.85</td>
<td>0.24</td>
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</table>

**Fledging mass**

<table>
<thead>
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<th>PC2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common guillemot</td>
<td>0.92</td>
<td>-0.13</td>
</tr>
<tr>
<td>Atlantic puffin</td>
<td>0.84</td>
<td>-0.04</td>
</tr>
</tbody>
</table>

---

Fig. 2. Breeding productivity (number of fledged chicks per nest) of 4 seabird species at the Isle of May as related to an index of larval sandeel abundance in the previous spring, 1986 to 2003. Regression lines are shown for significant relationships (see Table 2 for details).

Fig. 3. Breeding productivity (number of fledged chicks per nest) of 4 seabird species at the Isle of May as related to an index of larval sandeel abundance in the previous spring, 1986 to 2003. Regression line indicates a significant relationship (see Table 2 for details). PC1: first principal component.

Fig. 4. The first 2 principal components of 7 breeding performance variables of seabirds breeding on the Isle of May, 1986 to 2005.
posed North Sea seabird index belongs to the first class of indicators. PC1 shows a pronounced decline in conditions for seabirds in this region over the last 20 yr, but we do not know precisely how the decline is expressed. It is very likely that changes in food supply and, specifically, in the availability and nutritional quality of the main prey (lesser sandeels) are related to this decline, but in itself the index does not show this. Seabird-based monitoring has previously shown that lesser sandeels in this region have diminished substantially in size over a 30 yr period (Wanless et al. 2004). Despite the non-specific nature of this index, we argue that it can serve to highlight an aspect of the general health of the local pelagic ecosystem, namely its ability to supply breeding seabirds with sufficient high-quality food to successfully raise their young. Given that direct monitoring of lesser sandeel abundance is both expensive and technically difficult (Greenstreet et al. 2006), using indicators based on the performance of highly visible sandeel-dependent, land-based predators is an attractive option. PCA extracts the strongest possible common signal from a number of correlated ecological time series, and is thus an appropriate method for identifying such a non-specific indicator. On the other hand, if the aim is to develop a more specific indicator, it needs to be validated with relevant environmental data. Alternative multivariate methods, such as canonical correlation analysis (McGarigal et al. 2000) or canonical correspondence analysis (Lepš & Šmilauer 2003), can be used to identify an optimal linear combination of data, maximising the correlation with one or more environmental time series. This combination can then be used as an indicator of this specific aspect of the environment.

One of the most important functions of marine ecological indicators in the near future will be to support the developing concept of ecosystem-based resource management (Brownman & Stergiou 2004, Jennings 2005). To do this, indicators need to provide reliable measures of the health of the ecosystem, so that the consequences of changes in management practice can be monitored and assessed (Niemi & McDonald 2004). An integrative approach is therefore needed. This can be achieved by selecting either a suite of univariate indicators, which together cover the various facets of the ecosystem, or a smaller number of multivariate indicators, each of which summarises the response of a major ecosystem component. In well-studied marine systems, such as the North Sea, the number of potential univariate indicators is huge, and there is substantial scope for simplification by applying suitable multivariate techniques. Multivariate indicators need not be constrained by taxonomical boundaries, but should rather reflect functional categories or guilds. As an example, the seabird index suggested here could be extended to cover all homeothermic land-based marine predators, i.e. including pinnipeds (cf. Boyd & Murray 2001, Reid et al. 2005). Future research should aim at developing robust, integrative indicators of marine systems, and multivariate techniques have an important part to play in this process.

Acknowledgements. We are grateful to everyone who collected kittiwake data as part of the UK Seabird Monitoring Programme, and to M. P. Harris and everyone else who collected seabird data on the Isle of May. Thanks to F. Daunt for producing the map, to J. B. Reid, M. Parsons, S. Hatch and 2 anonymous referees for valuable comments, and to W. J. Sydeman and J. F. Piatt for inviting M.F. to the ‘Seabirds as Indicators’ symposium at the Pacific Seabird Group meeting, Girdwood, Alaska, in February 2006.

LITERATURE CITED


Fig. 4. The first 2 principal components (PC1 and PC2) of 7 seabird breeding performance variables at the Isle of May, 1986 to 2005. Variables included are breeding productivity of 5 species and mean fledging mass of 2 species (see Table 3)


Jennings S (2005) Indicators to support an ecosystem approach to fisheries. Fish Fish 6:212–232


O’Connor RJ, Walls TE, Hughes RM (2000) Using multiple taxonomic groups to index the ecological condition of lakes. Environ Monit Assess 61:207–228


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Binary dietary responses of northern gannets *Sula bassana* indicate changing food web and oceanographic conditions

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ABSTRACT: Interactions between seabirds and their prey are shaped largely by the dynamics of the marine ecosystems in which they are embedded. Physical oceanographic processes can drive the distributions of ectothermic and planktonic prey and hence their availability to marine birds. Owing to the complex nature of these processes and interactions, the signal-to-noise ratios of avian indicators of prey conditions are variable, often low and further degraded (buffered) by seabird behaviour and life-history features. Cairns (1987, Biol Oceanogr 5:261–271) detailed seabird responses operating over a range of temporal scales to variation in food supplies, and suggested that interval relationships might be developed between avian responses and environmental variation. While this may be possible in some instances, it appears unrealistic in most instances to expect interval relationships between seabird responses and prey conditions that are often non-linearly related. The present paper focuses on binary data (e.g. breeding success versus failure) derived from seabirds that can provide robust information about major shifts in prey and oceanographic conditions and that are particularly informative when accumulated over decadal and large ocean scales. Inter-annual and decadal variations in specific and nominally categorized (warm- versus cold-water) prey landings of northern gannets *Sula bassana* at a large oceanic colony in the NW Atlantic reflect shifts in pelagic food webs induced by changes in regional sea surface temperature. Binary patterns emphasize decadal shifts in food webs and yield predictive indication of systemic change.

KEY WORDS: Binary patterns · Bio-indicators · Decadal scales · Seabirds · Ecosystem shift

INTRODUCTION

Considerable research has been directed at the exploitation of information from marine birds and mammals for purposes of assessing the changing states of prey bases and for detecting oceanographic and fisheries effects on top predators (e.g. Boyd et al. 2006, Piatt et al. 2007a, this issue). The physical dynamics of oceans exert considerable influence on interactions between seabird predators and their prey. Driven largely by ocean conditions, the distributions of ectothermic and planktonic prey determine their availability to avian predators (Scott et al. 2006). Owing to the stochastic nature of these processes and interactions, the signal-to-noise ratios of seabird indications of prey conditions are variable, frequently low and are degraded (buffered) by avian behaviour and life-history adaptations (e.g. flexible foraging tactics, deferred reproduction; Burger & Piatt 1990, Montevecchi & Berruti 1991, Daunt et al. 2006). Consequently, it is not simple to effectively derive insight from seabird data about changes in prey and ocean conditions. Yet biological signals complement and can even be more revealing than physical signals in detecting pervasive ocean perturbations, such as regime or ecosystem shifts (McFarlane et al. 2000, Hare & Mantua 2000).

In a seminal paper on bio-indicators, Cairns (1987) proposed patterns of seabird responses operating over a range of temporal (and hence spatial) scales to changes in their prey base. The responses considered
ranged from population through to behavioural levels and included adult survival, breeding success, chick growth, parental attendance and activity (foraging) budgets. Each response, with the exception of foraging budgets, was hypothesized to exhibit relatively sharp nonlinear changes to different levels of prey availability, which was considered on an ordinal scale between low and high. Cairns (1987, p. 267) contended that ‘[a]l[l] present seabird data can yield information on marine food supply on ordinal scales, but assigning food availability to interval or ratio scales must await rigorous testing of the relationships...’. Over the 20 yr since Cairns’ paper appeared, there have been numerous attempts to assess seabirds as indicators of prey conditions. The most recent of these sought to directly assess the predictions of Cairns’ (1987) models, and found support for some of the predictions and not for others (Piatt et al. 2007b, this issue).

However, in most instances it is unrealistic to derive interval scaling between seabird responses and prey conditions that are often nonlinearly related. Yet this circumstance in no way precludes the derivation of information about marine ecosystems from seabird research. Associations of nominal patterns of seabird biology and prey and oceanographic conditions have proven highly informative in many instances (e.g. Schreiber & Schreiber 1984). Binary relationships between avian predators, prey and oceanography gain considerable power and robustness as they are cumulated over time, space and species (Hatch 1996). For example, in an ocean-basin study of black-legged kittiwakes *Rissa tridactyla*, Hatch et al. (1993) demonstrated striking inter-annual patterns in the concordances and dis-concordances of reproductive success versus failure among colonies in the Bering Sea and Gulf of Alaska from 1978 through 1989 (Fig. 1). In 1978, colonies in the Bering Sea failed, while those in the Gulf of Alaska were productive. In 1984, this pattern reversed, whereas in 1988 all colonies throughout the study area were successful and in 1989 virtually all colonies failed. The information derived from these signals captured systemic patterns that occurred over scales that were larger than those of fishery activities and oceanographic research in the region.

The present paper builds on the potential of most studies of seabird ecology to detect binary changes in reproductive and behavioural parameters in response to environmental change. In this respect, I compare inter-annual and decadal associations in the species compositions of prey landings by northern gannets *Sula bassana* at a large oceanic colony with sea surface temperature (SST) patterns and anomalies in the NW Atlantic. Prey landings are assessed on a single-species basis and in nominal multi-species ecological classifications of prey from temperate/subtropical and from low Arctic Ocean regions, hereafter referred to as warm- and cold-water prey. Emphasis is directed at the cumulative information that can be derived for

![Fig. 1. Rissa tridactyla. Inter-annual ocean-basin patterns of breeding success (●) and failure (○) of black-legged kittiwakes at colonies in the North Pacific (after Hatch et al. 1993)](image-url)
these types of responses when combined over decades and longer and over large oceanographic scales to indicate shifts in food webs and ecosystem conditions.

**MATERIALS AND METHODS**

**Study site.** Research was conducted in Funk Island Ecological Reserve (49°45’N, 53°11’W), a small (800 × 400 m) flat granite rock in the northwest Atlantic (Montevecchi & Tuck 1987), about 50 km off the northeast Newfoundland coast (Fig. 2), Canada. About 10,000 pairs of northern gannets *Sula bassana* nest in the colony (Chardine 2000), which is the third largest and most oceanic of the 6 gannet colonies in North America.

**Prey load sampling.** Food samples were obtained by approaching roosting gannets that often regurgitated as they moved away from researchers (Montevecchi & Myers 1995). Some samples were also obtained when gannets had GPS and other data loggers attached and removed and from discarded regurgitations and scraps in the colony. While there are likely differences between samples collected in roosts and in the colony, samples from all sources were comparable, so most regurgitations were collected at roosts well outside the colony to minimize disturbance to nesting areas. Regurgitated prey were identified to species, sex and condition (gravid, spent/immature) whenever possible. Prey landings are presented as percentages of the total estimated mass of prey landed during each year. A total of 8239 prey samples were obtained during late July and early to mid-August from 1977 to 2006, with the exception of 1981, when it was not possible to land on the island (Table 1).

**Sea surface temperatures.** SSTs (0 to 20 m), corresponding with the maximum dive depths of northern gannets (Garthe et al. 2000), were obtained from Hydrographic Stn 27 (48°32.8’N, 52°35.2’W) located 250 km S and downstream of Funk Island in the Labrador Current. The station has been checked regularly since its establishment in 1946. Measurements from Stn 27 provide robust ocean climate signals for the entire Newfoundland–Labrador Shelf (Petrie et al. 1988, Myers et al. 1990). Annual averages of SST during June, July and August were used.

---

**Table 1. Sula bassana. Dates of collection and number of prey samples from gannets in the colony on Funk Island, 1977 to 2005**

<table>
<thead>
<tr>
<th>Year</th>
<th>Date</th>
<th>With 1 species</th>
<th>With &gt;1 species</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1977</td>
<td>12 Jul</td>
<td>105</td>
<td>0</td>
<td>105</td>
</tr>
<tr>
<td>1978</td>
<td>11–20 Aug</td>
<td>496</td>
<td>12</td>
<td>508</td>
</tr>
<tr>
<td>1979</td>
<td>31 Jul–6 Aug</td>
<td>162</td>
<td>4</td>
<td>166</td>
</tr>
<tr>
<td>1980</td>
<td>1–9 Aug</td>
<td>217</td>
<td>7</td>
<td>224</td>
</tr>
<tr>
<td>1982</td>
<td>9–13 Aug</td>
<td>191</td>
<td>25</td>
<td>216</td>
</tr>
<tr>
<td>1983</td>
<td>5–13 Aug</td>
<td>488</td>
<td>2</td>
<td>490</td>
</tr>
<tr>
<td>1984</td>
<td>9–19 Aug</td>
<td>225</td>
<td>8</td>
<td>233</td>
</tr>
<tr>
<td>1985</td>
<td>4–10 Sep</td>
<td>184</td>
<td>16</td>
<td>200</td>
</tr>
<tr>
<td>1986</td>
<td>7–15 Aug</td>
<td>493</td>
<td>22</td>
<td>515</td>
</tr>
<tr>
<td>1987</td>
<td>22–26 Aug</td>
<td>144</td>
<td>8</td>
<td>152</td>
</tr>
<tr>
<td>1988</td>
<td>12–20 Aug</td>
<td>525</td>
<td>36</td>
<td>561</td>
</tr>
<tr>
<td>1990</td>
<td>18 Jul–11 Aug</td>
<td>340</td>
<td>38</td>
<td>378</td>
</tr>
<tr>
<td>1991</td>
<td>13 Jul–16 Aug</td>
<td>411</td>
<td>21</td>
<td>432</td>
</tr>
<tr>
<td>1992</td>
<td>5–10 Aug</td>
<td>293</td>
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<td>301</td>
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<tr>
<td>1993</td>
<td>5–12 Aug</td>
<td>258</td>
<td>18</td>
<td>276</td>
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<tr>
<td>1994</td>
<td>11–14 Aug</td>
<td>50</td>
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</tr>
<tr>
<td>1995</td>
<td>4–11 Aug</td>
<td>279</td>
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<td>281</td>
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<tr>
<td>1996</td>
<td>5–8 Aug</td>
<td>348</td>
<td>3</td>
<td>351</td>
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<td>1997</td>
<td>1–8 Aug</td>
<td>244</td>
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<td>246</td>
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<td>1998</td>
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<td>14</td>
<td>460</td>
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<td>6–12 Aug</td>
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<td>2006</td>
<td>6–14 Aug</td>
<td>216</td>
<td>7</td>
<td>223</td>
</tr>
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<td>Totals 1977–2006</td>
<td>7932</td>
<td>307</td>
<td>8239</td>
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</table>
Data analyses. One-way ANOVAs and Tukey post hoc tests were used to compare decadal differences in the prey landings of gannets; chi-squared and binomial tests were used to assess decadal binary patterns in the gannets’ landings of warm- and cold-water prey (Siegel 1957). Pearson correlations were run between individual prey species and between amalgamations of warm- and cold-water prey landings and SST. Level of significance is taken as p < 0.05.

RESULTS

Inter-annual variation in prey landings

As evident in their prey landings at Funk Island since 1977, gannets are generalist predators that exploit a diverse array of pelagic fish and squid with considerable inter-annual variation (chi-squared = 10 801.6, df = 130, p < 0.0001; Fig. 3). From 1977 to 1980, 77 ± 11% of the prey landed was Atlantic mackerel *Scomber scombrus*. In 1982, mackerel made up only 13% of the estimated prey landed and was replaced by Atlantic herring *Clupea harengus*, which represented 60% of the prey landed and which is second to mackerel in energy density among the gannets’ prey spectrum (Montevecchi et al. 1984). In 1983, the relationship between the landings of these pelagic fishes was reversed, with mackerel comprising 13% of the landings and herring 12%; this relationship of greater landings of mackerel compared to herring continued until 1989. From 1989 onward, mackerel was landed very irregularly by the gannets, with no landings from 1996 through 2001 and with contrasting large landings in 2005 and 2006. Her- ring were landed in large proportions in 1993 and 1994 (35 and 37% of total mass, respectively; Fig. 3).

From 1977 to 1982, short-finned squid *Illex illecebrosus* made up from 7 to 21% of the prey landed, averaging 11 ± 6% per yr. In contrast, squid were only landed in 7 of the years between 1983 and 2006 (1989 to 1992, 1996, 1997, 2004), comprising 5% or usually less of the prey.

From 1977 to 1983, Atlantic saury *Scomberesox saurus* were either not landed (1977) or were a very minor component of the landings, ranging from 1 to 10%. Then, in the mid- to late 1980s, saury was a major component of the gannets’ prey every year except 1986 (percent of total mass of prey landed = 54% [1984], 39% [1985], 4% [1986], 19% [1987], 44% [1988], 63% [1989]). From 1990 to 2004, no saury were landed in most years, in 5 of the years <1 to 3% were landed, and saury comprised 12 and 13% of the prey landed in 1994 and 1998, respectively. In 2005 and 2006, 33 and 80% of the prey landed by the gannets were Atlantic saury (Fig. 3). The mean percentages of saury landed during the 1970s/1980s (20.85 ± 22.95), 1990s (2.65 ± 4.78) and 2000s (16.66 ± 30.44), though differing by an order of magnitude, are not significantly different owing to the high inter-annual variability associated with the means ($F = 2.15$, df = 2, 26, p = 0.136).

Landings of Atlantic salmon *Salmo salar* during the 1970s/1980s, 1990s and 2000s differed significantly ($F = 3.87$, df = 2, 26, p = 0.034). From 1977 to 1989, Atlantic salmon was landed in minute amounts, ranging from 0 to 1.4% of the estimated total landings, averaging 0.31% of the prey landed per yr. Circumstances changed in 1990, and from 1990 to 1996 salmon comprised from 3 to 7% of gannets’ annual prey landings. During the 1990s, Atlantic salmon averaged 3.4% of the total prey landed per yr. The largest harvests of salmon occurred in 2001 and 2002 (27 and 32% of the total mass of prey landed, respectively). Seven percent of the landings in 2003 were salmon, and none were landed thereafter (Fig. 4). Landings from 2000 to 2006 averaged 9.3% of the annual prey landings.

From 1977 to 1989, capelin *Mallotus villosus*, a small forage fish, comprised <5% of the mass of gannets’ prey landings in all years except in 1978 (9%) and 1982 (12%), when small amounts were also landed (Fig. 3). From 1989 until 2004, capelin was a common prey of gannets, ranging from 26 to 100% of prey landed each year. Significantly less capelin was landed by gannets...
Montevecchi: Binary responses of seabirds

in the 1970s/1980s than in the 1990s and 2000s ($F = 23.68$, $df = 2, 26$, $p < 0.001$ and Tukey post hoc test).

Small amounts of cod *Gadus morhua* (discards) and sandlance *Ammodytes* sp. were also landed in 1 or 2 of the years.

**Decadal variation in prey landings**

When these highly variable prey landings of the gannets are collapsed into the binary categories of warm-water migratory prey (*mackerel, squid, saury*) from temperate and cool subtropical ocean regions and cold-water low arctic prey (*herring, capelin, salmon, sandlance, cod*), striking decadal patterns emerge (Fig. 5). Migratory warm-water species comprised most of the gannets’ prey landings in the late 1970s and throughout the 1980s (binomial test of equal proportions of warm- and cold-water prey, $p = 0.003$). In a marked reversal of this pattern, from 1990 through 2004 cold-water prey comprised almost all of the gannets’ prey landings (binomial test of equal proportions of warm- and cold-water prey, $p < 0.001$). A comparison of the landings of warm-water migratory prey landed before and after the 1991 cold-water perturbation (Fig. 6) proves to be highly significant ($F = 43.57$, $df = 1, 27$, $p < 0.001$). In 2005 and 2006, for the first time since 1989, migratory warm-water pelagic fishes comprised 81 and 93%, respectively, of the estimated prey landed by gannets.

**Annual and decadal associations between prey landings and SST**

Following the lowest SST on record in 1991, values returned to positive thermal anomalies by the mid- to late 1990s (Fig. 6). Still, warm-water migratory prey did not regain their dominance in the gannets’ prey landings until 2005, lagging about a decade after the reoccurrence of positive SST signals (Fig. 4). Sixteen years passed (from 1989 to 2005) before warm-water prey again dominated landings. 2005 was a warm-water year in the region (but not the warmest in recent years). There were no significant associations between the annual landings of any prey or combined landings of warm- or cold-water prey and average annual SST from 1977 to 2006. The prevalence of migratory warm-water pelagic species in the gannets’ prey landings continued in 2006.
DISCUSSION

A highly flexible foraging strategy directed at a wide breadth of pelagic prey is a striking feature of the northern gannets’ *Sula bassana* feeding ecology (e.g. Garthe et al. 2007). The generalist pattern of their changing dietary diversity is evident in their prey landings on Funk Island from 1977 through 2006. Inter-annual variation in the gannets’ landings of mackerel and squid exhibited significant correlations with commercial landings and independent research indices of these species over multiple spatial and temporal scales beyond the gannets’ foraging range around the colony (Montevecchi & Myers 1995). These associations are driven by prey availability, largely by negative events when birds and humans catch little or none of a particular pelagic species.

Physical forcing and lagging biological responses

The 1991 cold-water perturbation in the NW Atlantic—a centennially significant event (Drinkwater 1996)—acted as a physical forcer that influenced and inhibited warm-water pelagic species such as mackerel, saury and squid from migrating into the region (Montevecchi & Myers 1995). This cold-water incursion induced an extensive regime-type shift in the pelagic food web (Montevecchi & Myers 1996). By the mid-1990s, SSTs had returned to pre-perturbation levels, yet a return to prior warm-water prey landings by both birds and commercial fishers lagged by about another 10 yr (see also Davoren & Montevecchi 2003). It is this type of on/off response that is responsible for the lack of inter-annual associations (correlations) between the prey landings of birds and average annual SSTs. These decadal patterns and their coincidence with oceanographic perturbation are clarified when the variation in inter-annual prey landings are lumped into the binary categories of warm- and cold-water prey.

Binary responses and systemic shifts

Binary classification, amalgamation and analysis can provide robust signals from apex marine predators (see Hatch 1996 for analyses of binary patterns). In 2005, the prominence of migratory warm-water mackerel and saury in the gannets’ landings returned for the first time in 16 yr. This avian signal of warm-water prey also coincided with the largest mackerel fishery landings in the Newfoundland region since 1989 (NAFO Division 3K and 3L reports; M. Koen-Alonso pers. comm.).

The changes in prey landings by the gannets signalled a shift in the pelagic food web driven by oceanographic changes, leading to greater representation of migratory warm-water pelagic species in regional seasonal assemblages and food webs. These signals from seabirds can also be used to anticipate predator–prey and wider food web and oceanographic patterns. As predicted (Montevecchi 2005), ocean temperatures were warm and the mackerel fishery flourished in 2006. The prey landings of gannets in 2006 were again dominated by migratory warm-water prey from temperate and subtropical ocean regions, and ocean temperatures in the NW Atlantic were among the warmest on record (E. Colbourne pers. comm.). In the NW Atlantic in 2006, auks laid their eggs about 2 wk earlier than in previous years, spawning capelin and humpback whales *Megaptera novaenaemigia* moved inshore early, lumpfish *Cyclopterus lumpus* were egg-laden in May, well before their usual time during summer and large squid were abundant in inshore waters (W.A.M., D. Fifield, A. Hedd, J. Lavers, T. and K. Power pers. obs.). So at least during 2005 and 2006, a shift back to warm-water ecosystem conditions was evident. Continuation of this warm-water condition occurred in 2007 and is expected to continue further.

Seabird indicators

Seabird studies of biophysical environmental conditions have proven highly informative in other contexts. For instance, broad-scale biological shifts are driven at times by radical state changes (abundance versus scarcity) exhibited by focal forage species that fuel large vertebrate food webs (Chavez et al. 2003). Seabird studies are particularly useful in documenting condition changes in these forage species (e.g. Österblom et al. 2001, Davoren & Montevecchi 2003, Miller & Sydeman 2004, Wanless et al. 2004, 2005) that often reflect food resource states. Importantly, seabirds also target prey that are not commercially exploited (and hence excluded from most fishery research programs) or are not accessible to standard survey methods (Barrett et al. 1990, Montevecchi 1993). Recent studies use data-logging devices to interrogate free-ranging seabirds and mammals about environmental information (Wilson et al. 2002, Daunt et al. 2003, 2006, Garthe et al. 2007). When carried out in conjunction with vessel surveys of prey densities and distributions, these studies hold the further potential of detailing the behaviour and decision-making of individual foragers (Garthe et al. 2000, Ollason et al. 2006, Staniland et al. 2006) and directly assessing functional responses, the mechanisms of higher level population patterns.
LITERATURE CITED


MacFarlane GA, King JR, Beamish RJ (2000) Have there been recent changes in climate? Ask the fish. Prog Oceanogr 47:147–169


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Seabirds as indicators of marine food supplies: Cairns revisited

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ABSTRACT: In his seminal paper about using seabirds as indicators of marine food supplies, Cairns (1987, Biol Oceanogr 5:261–271) predicted that (1) parameters of seabird biology and behavior would vary in curvilinear fashion with changes in food supply, (2) the threshold of prey density over which birds responded would be different for each parameter, and (3) different seabird species would respond differently to variation in food availability depending on foraging behavior and ability to adjust time budgets. We tested these predictions using data collected at colonies of common murre Uria aalge and black-legged kittiwake Rissa tridactyla in Cook Inlet, Alaska. (1) Of 22 seabird responses fitted with linear and non-linear functions, 16 responses exhibited significant curvilinear shapes, and Akaike’s information criterion (AIC) analysis indicated that curvilinear functions provided the best-fitting model for 12 of those. (2) However, there were few differences among parameters in their threshold to prey density, presumably because most responses ultimately depend upon a single threshold for prey acquisition at sea. (3) There were similarities and some differences in how species responded to variability in prey density. Both murres and kittiwakes minimized variability (CV < 15%) in their own body condition and growth of chicks in the face of high annual variability (CV = 69%) in local prey density. Whereas kittiwake breeding success (CV = 63%, r² = 0.89) reflected prey variability, murre breeding success did not (CV = 29%, r² < 0.00). It appears that murres were able to buffer breeding success by reallocating discretionary 'loafing' time to foraging effort in response (r² = 0.64) to declining prey density. Kittiwakes had little or no discretionary time, so fledging success was a more direct function of local prey density. Implications of these results for using ‘seabirds as indicators’ are discussed.

KEY WORDS: Ecological indicators · Seabirds · Food availability · Threshold · Functional response · Predator–prey dynamics

INTRODUCTION

Annual global fisheries landings are currently 80 million t, and seabirds worldwide consume similar quantities of fish (Brooke 2004). With such strong dependence on shared resources, it is not surprising that we look to seabirds for additional insights into the status of fish stocks and the health of marine ecosystems (Cairns 1987, Montevecchi 1993, Furness & Camphuysen 1997). For this purpose, seabirds offer many advantages. They are highly visible at sea, and large numbers gather annually to reproduce at colonies where it is often possible to study the biology of several species in great detail every year.

However, care must be taken when interpreting seabird data as a proxy for fish abundance (Furness & Camphuysen 1997) because different components of seabird biology may respond differently to prey fluctuations, and responses also vary among species. Twenty years ago, Cairns (1987) published a seminal paper in

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which he sought to clarify relationships between seabirds and their food supplies. He predicted that many responses of seabirds to fluctuations in prey abundance would be non-linear, and further, that different parameters such as growth rates, breeding success or survival would respond over different ranges of prey density (around thresholds, Fig. 1). Finally, he predicted that different seabird species would respond differently depending on their diet and ability to adjust time budgets. Cairns had 2 main objectives in his analysis: (1) to ‘develop an integrated system of parameter measurement that indicates food availability over the full spectrum of feeding conditions’ and (2) ‘to stimulate rigorous tests of the proposed relationships’ (p. 262).

Since Cairns’ paper was published, there have been a few coordinated studies of seabird biology in relation to prey abundance (e.g. Monaghan et al. 1989, 1994, Hamer et al. 1991, 1993, Uttley et al. 1994, Reid et al. 2005, Frederiksen et al. 2006), but none were designed to explicitly test Cairns’ predictions. In order to flesh out functional response curves, one needs data collected over a wide range of prey densities (Piatt 1990). For most seabirds and parameters, this has simply not been done (Furness & Camphuysen 1997), owing largely to the cost and technical difficulties of measuring forage fish abundance over the times and spaces relevant to seabird colonies.

Following the 1989 ‘Exxon Valdez’ oil spill in Alaska, understanding how seabirds had responded to concurrent large-scale fluctuations in prey abundance was paramount to understanding the effects of the spill itself (Anderson & Piatt 1999). We therefore used Cairns’ hypotheses as a framework for examining relationships between seabirds and their prey in the Gulf of Alaska (Piatt & Harding 2007). Our study constituted a natural experiment to resolve predator–prey functional relationships by studying 3 closely situated colonies with markedly different prey fields over a 5 yr period. These colonies differed in other respects besides local prey density (e.g., prey distribution, colony size), but the signal from spatio-temporal variability in prey abundance overwhelmed other sources of variability, permitting us to resolve many functional predator–prey relationships (Speckman 2004, Piatt & Harding 2007, Harding et al. 2007).

In the present paper, we use results of our natural experiment to test Cairns’ (1987) 3 predictions about the form and variation of seabird responses to changes in local prey density. We plot data collected on a dozen different parameters of breeding and behavior from common murres *Uria aalge* and black-legged kittiwakes *Rissa tridactyla* against prey density estimated from hydro-acoustic surveys. We analyze the fit of parameter responses to various linear and non-linear models using regression and AIC analyses, compare thresholds among parameters, and then compare responses and thresholds between murres and kittiwakes. Implications of these results for using seabirds as indicators are discussed within the framework of Cairns’ original hypothesis.
MATERIALS AND METHODS

Study sites and rationale. This study was conducted during 5 yr (1995 to 1999) at 3 seabird colonies in Lower Cook Inlet, Alaska (Fig. 2), providing us with 15 colony-years of data for many parameters that we investigated (less for some parameters when it was impossible to collect data, e.g. feeding or growth rates when no chicks were produced). The colonies are separated from each other by about 100 km and are in oceanographically distinct habitats (Abookire & Piatt 2005, Speckman et al. 2005). We confirmed that there were order-of-magnitude differences in forage fish densities among the 3 areas by sampling near shore with beach seines (Robards et al. 1999) and by sampling offshore with mid-water trawls and hydroacoustic surveys (Abookire & Piatt 2005, Speckman et al. 2005). Four species comprised 99% of the catches in all areas: sand lance *Ammodytes hexapterus* (71%), herring *Clupea harengus* (17.7%), juvenile walleye pollock *Theragra chalcogramma* (8.8%), and capelin *Mallotus villosus* (1.7%), and these fish were also the overwhelming choice of prey consumed by seabirds at all colonies (Kitaysky et al. 1999, Harding et al. 2002, Jodice et al. 2006, J. F. Piatt unpubl. data).

Local prey density. We measured local fish densities around each of 3 seabird colonies by conducting hydro-acoustic surveys on a grid of transects arranged in most years as shown in Fig. 2, within a 50 km radius of each site (Speckman et al. 2005, Harding et al. 2007). Transects around the Barren Islands were concentrated in the NE quadrant, known as foraging grounds for the majority of murres *Uria aalge* and kittiwakes *Rissa tridactyla* from the Barrens (J. F. Piatt unpubl. data). About 1100 linear km were surveyed in all areas combined each year (except 820 km in 1995) (Speckman 2004). Hydro-acoustic surveys were conducted during a 3 wk period in each year (1995, 10 to 23 August; 1996, 14 to 31 July; 1997, 19 July to 8 August; 1998, 21 July to 12 August; 1999, 25 July to 16 August), usually encompassing periods of late incubation and early chick rearing for common murres (overall colony/year mean date of hatch was 10 August; J. F. Piatt & A. B. Kettle unpubl. data).

Hydro-acoustic data were collected with a single beam 120 kHz BioSonics DT4000 system with a 6° beam angle. Before each cruise the acoustic system was calibrated using a tungsten carbide sphere. To identify acoustic signals and measure the size of individual fish, we conducted 163 mid-water trawls (Abookire & Piatt 2005). Acoustic data were analyzed using SonarData Echoview software (Ver. 2.1) and integrated with a minimum threshold of –70 dB to obtain relative measures of acoustic biomass ($S_A$). These were converted to absolute estimates of fish density (fish m$^{-3}$) by dividing $S_A$ by $\sigma$ (backscattering cross-sectional area of single prey) for species with the following known target strengths (TS): walleye pollock TS = 21.1Log(L) – 70.5, herring TS = 202.0Log(L) – 67.6, capelin TS = 28.4Log(L) – 81.8, sand lance TS = 20.0Log(L) – 80, and cod TS = 20.0Log(L) – 65; which accounted for 99.2% of all fish caught (see Speckman et al. 2005 for TS sources). The proportion of catch, expressed as catch per unit effort, standardized to the number captured per km trawled, was used to convert acoustic backscatter to species-specific fish density (g m$^{-3}$). Geometric mean acoustic densities were calculated from transformed data as the mean (logx + 1) values, and then transformed back to original density units.

Seabird parameters. Density of seabirds at sea was determined from strip transects conducted simultaneously with hydro-acoustic surveys (above). All species of seabirds observed within 150 m on either side of the vessel were counted using protocols described by Gould & Forsell (1989). Average densities on transects were calculated for each species in each area (Fig. 2) and year (except 1995, Speckman 2004).
Behavioral activity budgets were determined from all-day observations of 8 to 12 nest-sites of adult murres and kittiwakes at each colony during the incubation and chick-rearing period in each of the 15 colony-years (see Harding et al. 2007 for more details). During observations, the time was recorded for each adult arrival, delivery of prey to chicks (chick-rearing period), exchange of incubation or brooding duty, and adult departure. On Gull (1996 to 1997) and Barren (1997 to 1999) islands, murre observations were recorded by video from first to last light and analyzed later (Zador & Piatt 1999). In most instances, we observed murres and kittiwakes on 3 or more observation-days during incubation and chick-rearing of each year.

From these observations, we calculated average annual rates of nest-site attendance by 1 and 2 adults, chick-feeding rates, and foraging-trip durations. Nest attendance was measured in bird-minutes per nest per h (e.g. a nest with 1 bird attending for a full hour and its mate attending for half of the hour has 90 bird-minutes that hour). Adult provisioning frequency was measured in feedings per nest per h. The mass and species composition of kittiwake chick meals was measured and used to estimate total energy delivered to chicks daily (see Jodice et al. 2006). Analysis of variance indicated that neither nest-site nor observation-day contributed significantly to variability in behavioral parameters in a given year, and we therefore used nest-site as the sample unit. Sample sizes ranged from 20 to 35 nest-site-days watched per island-year (except at Chisik, where kittiwakes failed in all years but 2).

Measures of murre and kittiwake breeding biology were derived from data recorded during regular (3 d average) observations of 20 to 30 nest-sites on 7 to 10 plots scattered around the colony (e.g. Utley et al. 1994, Suryan & Irons 2001). For kittiwakes, we estimated laying success, clutch size, hatching success, fledging success, brood size at fledging, chick age, and reproductive success. Chicks were considered fledged at 32 d of age. For murres, we estimated hatching success, fledging success, chick age, and reproductive success. Chicks were considered to have fledged if they disappeared from the nest-site >15 d after hatching (minimum fledging age, Gaston & Jones 1998).

We captured or collected both adult and chick murres and kittiwakes at their colonies to measure body size and body mass and to calculate growth rates and fledging condition of chicks. Adult body mass of both murres and kittiwakes was obtained from 2 sources: (1) adults captured at the colony throughout breeding to assess body condition (1997 to 1999) and (2) adults shot near colonies for diet studies (1995 and 1996). Only birds measured during late incubation through early chick-rearing were used to calculate an annual index of body condition, and a minimum of 10 to 35 birds was included in each colony-year estimate. For murres, there was no difference in mean size of birds among colonies (ANOVA, $F_{2,12} = 0.522$, $p = 0.61$), so here we simply present data on body mass. Because kittiwakes are sexually dimorphic and samples were unevenly composed of both sexes, we used the ratio of body mass to wing length as an index of body condition (Benson et al. 2003).

Kittiwake chick growth rates were calculated from a plot of mass versus age during the linear phase of growth, defined as falling between 6 and 22 d of age or between 60 and 300 g of mass (Benson et al. 2003). We tried to measure a total of 30 to 45 kittiwake chicks for growth in each colony and year, but in 6 of 15 possible colony-years fewer chicks were available for measuring and sample sizes ranged from 2 to 16 birds. It was not possible to repeatedly capture and weigh murre chicks without major disturbance, so murre chicks were captured only once immediately after fledging from nests at dusk. Samples were obtained throughout the fledging period (average of 65 chicks per colony during 10 colony-years). An index of fledging body mass was calculated by dividing mass by wing length, and this serves as a proxy for chick growth rate.

**Analysis.** Parameters of murre and kittiwake biology were plotted against forage fish biomass to examine the form of each response. Because we were testing Cairns’ hypothesis that responses should be non-linear and thresholds should differ among parameters and species, we used least-squares estimation to fit linear and several non-linear models (Reid et al. 2005). Thresholds were estimated from the inflection mid-points of sigmoidal and step functions and as the 50% mid-point of exponential curves (Fig. 1). The potential strength of relationships between forage fish abundance and response parameters was assessed from the $r^2$ of each regression, and statistical significance was determined from the corresponding $F$-statistic (Reid et al. 2005). We assumed statistical significance at the $p < 0.05$ level.

Data were fit to 1 linear and 4 different non-linear models, including hyperbolic, sigmoidal (logistic), step, and exponential decay functions. These were the forms predicted by Cairns (1987) and might be reasonably expected from foraging seabirds (Piatt 1990). They also correspond to the Type I (linear), Type II (hyperbolic), and Type III (sigmoid/step) predator–prey functional relationships described by Holling (1959) and commonly observed in vertebrate predators (Murdoch & Oaten 1975).

The following 2-parameter function was used to fit hyperbolic curves:

$$ f = \frac{a \times x}{b + x} $$

where $a$ is the maximum value, $b$ is the dissociation constant, and $f$ starts at zero and rises to $a$. 
The following 4-parameter logistic function was used to fit sigmoidal curves:

\[ f = \frac{(a - d)}{1 + (x/c)^b} + d \]

where \( a \) is the asymptotic maximum, \( b \) is the slope parameter (\( b < 0 \) gives slope \( > 0 \)), \( c \) is the value at inflexion point and \( d \) is the asymptotic minimum.

The step function represents a simplification of the sigmoidal curve. A simple box model (Piatt & Methven 1992) of a step function was used to locate thresholds in response plots and estimate goodness of fit \((r^2)\). The model used was:

\[ f = k_1D \text{ if } D > D_T \]
\[ f = k_2D \text{ if } D < D_T \]

where \( f \) is the bird parameter value, \( D \) is the forage fish density, \( D_T \) is the test threshold for forage fish density, and \( k_1 \) and \( k_2 \) are mean parameter values above and below the test threshold \( D_T \). The best-fit (highest \( r^2 \)) to the step function occurs at the inflexion point (Piatt 1990).

A non-linear exponential decay function was used to model negative, declining responses to prey density using the following:

\[ f = a \times \exp(-bx + x) \]

where \( a \) is amplitude and \( b \) is the rate constant.

Whereas regression is useful for determining the strength of possible functional relationships and for identifying thresholds, it was more appropriate to use AIC, adjusted for finite sample size (\( \text{AIC}_c \); Burnham & Anderson 2002) to identify the best-fitting model among several possible alternatives. For positive relationships between seabirds and prey, we compared 5 possible functional models: (1) null—no relationship whatsoever between seabird parameters and food density (slope equals zero), (2) linear (positive slope), (3) hyperbolic, (4) sigmoidal, and (5) a step function. For negative relationships, we compared 3 likely or possible models: (1) null (as above), (2) linear (negative slope), and (3) a negative exponential function.

Each model was statistically represented with a least-squares regression model in which the error sums of squares, sample size, and number of estimated parameters all influenced the \( \text{AIC}_c \) calculation (Burnham & Anderson 2002). The model with the lowest \( \text{AIC}_c \) was assumed to best represent the data. Models in which the difference in \( \text{AIC}_c \) from the minimum value \((\Delta \text{AIC}_c)\) is \(< 2\) are considered plausible alternative models. For each model, we also calculated an \( \text{AIC}_c \) weight \((w)\) that reflects the relative likelihood of that model being the best-fitting model among those considered, and in which all \( \text{AIC}_c \) weights within an analysis sum to 1 (Burnham & Anderson 2002).

**RESULTS**

**Form of responses**

For common murres *Uria aalge*, no linear relationships were observed among the 10 parameters investigated (Fig. 3, Table 1). Most (8/10) responses to prey density could be fit significantly with sigmoidal or step functions, 1 response was fit significantly with an exponential decay function, and 2 responses exhibited no significant relationship with prey density. \( \text{AIC}_c \) analysis confirmed that non-linear models were best among the choices we examined (Table 2) and suggested that 6 of 10 responses were best fit by step, hyperbolic, or exponential functions. \( \text{AIC}_c \) analysis penalizes models with more equation parameters and small sample sizes, and so \( \Delta \text{AIC}_c \) values and likelihood weights (Table 2) should be considered for alternate models (Burnham & Anderson 2002). The weight of evidence strongly supports null models for body condition, fledging success, and breeding success, and non-linear models for fledgling body condition and attendance during incubation and chick-rearing. Other responses were more ambiguous and could be fit reasonably well by 2 or 3 competing models (Table 2).

These results indicate that for murres, relations between reproductive parameters (hatching, fledging, and breeding success) and food supply were marginal at best. Adult body condition was most independent of food supply, while chick condition at fledging exhibited a strong non-linear relation to food and growth was restricted at low levels of prey density. Foraging trip duration increased in an exponential fashion with decreasing prey density. While the chick-feeding rate was weakly related to prey density, other measures of foraging activity such as density at sea (aggregative response) and discretionary attendance at the nest site during incubation and chick-rearing (time that can be allocated instead to foraging) were strong non-linear functions of prey density.

As for murres, no linear relationships were observed among 12 parameters investigated for black-legged kittiwakes *Rissa tridactyla* (Fig. 4, Table 1). Most (8/12) responses to prey density could be fit significantly with sigmoidal or step functions, 1 response was fit significantly with an exponential decay function, and 4 responses exhibited no significant relationship with prey density. \( \text{AIC}_c \) analysis confirmed that non-linear models were best among the choices we examined (Table 2), and suggested that 6 of 12 responses were best fit by step, hyperbolic, or exponential functions. The weight of evidence (1) strongly supports null models for attendance, body condition, and clutch size and (2) strongly supports non-linear models for chick growth rate, fledging success, and breeding success.
Other parameter responses were more ambiguous, and could be fit reasonably well by 2 or 3 competing models (Table 2), but tended towards either null or linear fits (laying and hatching success, chick feeding rate), or non-linear fits (density at sea, foraging trip duration, brood size).

These results indicate that, in contrast with murres, reproductive parameters for kittiwakes such as fledging and breeding success were strongly related to fluctuations in prey density. Other reproductive parameters such as clutch size, laying success, and hatching success were essentially independent of food supply. Also, in contrast to murres, the discretionary attendance of paired adults at the nest site during chick-rearing did not vary with food supply. As for murres, kittiwake chick condition was markedly reduced at low prey densities and adult body condition remained remarkably constant over a wide range of prey densities.

The average prey density threshold for all parameters in murres that exhibited significant relationships with prey density (n = 8; Table 1) was $0.022 \pm 0.00033 \text{ g m}^{-3}$ and in kittiwakes (n = 8) was $0.021 \pm 0.00028 \text{ g m}^{-3}$. A 2-way ANOVA indicated no significant difference in thresholds among species ($F = 3.06$, $p = 0.11$, df = 1,15), but a significant difference in thresholds among different types of parameters (see Table 1; $F = 44.6$, $p < 0.001$, df = 4,15). This was entirely due to the higher threshold values estimated for foraging trip durations, which differed significantly from all other types of parameters (Tukey test; Act $>$ Gro, Att, Br, and For, $p < 0.05$; see Table 1).
In addition to assessing the form of functional relations (above), we examined the range in variability of seabird responses (Table 1), as measured by the coefficient of variation (CV).

Forage fish biomass varied about 12-fold among colony-years, with a CV of 79% (Table 1, Fig. 5). In some respects, murres and kittiwakes responded in the same way to this variation in prey density. Both species exhibited similar levels of variability in density of foraging aggregations at sea (up to 20-fold, CV = 72% for both species), which also reflected the variability in forage fish biomass. Despite this large variability in prey biomass, both species exhibited minimal variability in adult body condition or chick growth (<2-fold, CV < 15%) and only moderate variability in foraging-trip duration (ca. 2-fold, CV = 20 to 25%).

Murres and kittiwakes differed dramatically in other respects. Whereas murres maintained low variability in chick-feeding rates (<2-fold, CV = 15%) and moderate levels of variability in hatching, fledging, and breeding success (up to 5-fold, CV = 21 to 29%), kittiwakes exhibited much higher levels of variation in chick-feeding rate (up to 5-fold, CV = 42%) and in hatching, fledging, and breeding success (up to 36-fold, CV = 37 to 87%). Also in contrast, kittiwakes exhibited little variation in discretionary attendance of adults at nest-sites (<2-fold, CV < 10%), whereas this was the most variable parameter in murres (up to 30-fold, CV = 65 to 69%).

**DISCUSSION**

**Non-linearity of response**

Cairns’ (1987) first prediction was upheld: where there was a significant functional relationship with prey density, it was non-linear for parameters such as aggregation at sea, colony attendance, foraging trip duration, chick growth brood size, fledging success, and breeding success. A few studies have demonstrated similar results, albeit with fewer parameters. For example, breeding success in several seabird species has been shown to be a curvilinear function of food
Table 2. *Rissa tridactyla, Uria aalge*. Identification of best-fit models using Akaike’s information criterion, adjusted for finite sample size. Possible models included linear, hyperbolic (hyper), sigmoidal (sigm), step and negative exponential (exp) functions. The best-fitting model is indicated by ΔAICc = 0, but all models with ΔAICc < 2 (in bold) and high AICc weights relative to other models have substantial support and offer plausible alternative models of functional relationships.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>n</th>
<th>Null</th>
<th>Linear</th>
<th>Hyper</th>
<th>Sigm</th>
<th>Step</th>
<th>Exp</th>
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<tbody>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td>0.00</td>
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<td>-</td>
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Density (i.e. Arctic skua Stercorarius parasiticus, Furness & Camphuysen 1997; Arctic tern Sterna paradisaea, Suddaby & Ratcliffe 1997; and black-browed albatross Thalassarche melanophris, Reid et al. 2005), and the aggregative response of common murres *Uria aalge* and Atlantic puffins Fratercula arctica to prey schools at sea is sigmoidal (Piatt 1990).

We did not exhaust the list of possible seabird parameters that could be examined (e.g. survival), and we might not have been able to resolve relationships in some parameters, owing in part to small sample sizes and inter-colony sources of variability that were not accounted for in our study (Harding et al. 2007). It is also noteworthy that some parameters were independent of prey density over a wide range of poor to excellent feeding conditions, and this is discussed in more detail below (see ‘Poor indicators’).

The fact that many of these functional relationships were non-linear demonstrates that, like other vertebrate predators (Murdoch & Oaten 1975), seabirds are constrained by basic physical (e.g. prey dispersion) and biological (e.g. prey quality, assimilation) factors in how efficiently they can exploit local prey resources (Piatt 1990). Constraints may operate at each end of the prey-density spectrum, leading to suppression of a response at low prey densities or a plateau in response at high prey densities (Holling 1959). Whatever the ecological explanation, non-linearity has practical implications for using seabirds as indicators of prey stocks. Indicators are most useful if they have sensitive and predictable relationships with the environmental feature we wish to monitor over the full, continuous range of environmental variation likely to be encountered (Dale & Beyeler 2001). Unfortunately, our study suggests that few seabird parameters are correlated in a continuous fashion to changes in prey or, at best, they are linearly related over a small range of prey densities.

### Different parameter thresholds

Therefore, we are often left with interpreting non-linear seabird responses, which tend to fluctuate rapidly between low and high values over relatively small ranges of prey density. This is still useful, but obviously more limiting. It is also why Cairns proposed using a suite of concurrently measured parameters to assess changes in prey stocks. In order for this to work, however, Cairns’ second prediction would need to be true: that different seabird parameters would have differing thresholds to prey density (Fig. 1).
Our results did not provide strong support for this prediction. Mid-point thresholds (inflection points) in our sigmoidal and step response curves (Table 1) were very similar, occupying a narrow range of prey densities (0.018 to 0.021 g m\(^{-3}\)) within the range (0.008 to 0.090 g m\(^{-3}\)) observed during 15 colony-years of acoustic surveys. However, we did observe higher mid-points (e.g. 0.028 g m\(^{-3}\)) in foraging-trip durations of murres *Uria aalge* and kittiwakes *Rissa tridactyla*. This is consistent with Cairns’ prediction that activity budgets would change at higher prey densities in order to buffer foraging success. This was the only parameter type with significantly higher thresholds, but also the only parameter with a threshold measured as the 50% mid-point (in contrast to inflection point).

Aside from this possible exception, why should prey density thresholds for other foraging activities, attendance, chick growth, and breeding success all be the

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**Fig. 4. Rissa tridactyla.** Response of different parameters of kittiwake biology or behavior to variation in prey density. Graphs include predicted form (solid line) of relationship from the best-fitting model function (null, linear, hyperbolic, sigmoidal, step, or exponential decay) as determined by using Akaike’s information criterion adjusted for sample size (AIC\(_c\)) analysis.
same? Perhaps because there is only one true physical threshold, and that is the fish school density above which seabirds can successfully acquire food energy at a rate that is sufficient to support daily metabolic demands (Piatt 1990). Tracking of prey at sea (aggregative response) sets the baseline variability for all other parameters, because success in prey acquisition (which dictates foraging-trip duration and time-activity budget) depends on success in tracking the prey, and, in turn, all other parameters (chick-feeding rate, chick growth, reproductive success) vary with the rate of prey acquisition and subsequent rate of energy delivery (e.g. Jodice et al. 2006). In contrast to Cairns’ prediction, then, we conclude that most response parameters should have the same threshold, rather than a wide range of thresholds, to prey density.

On the other hand, murres can buffer breeding success against declining prey densities by re-directing discretionary colony attendance time towards foraging (Burger & Piatt 1990, Zador & Piatt 1999). Consequently, we observed little or no response in murre breeding success, while attendance time-budgets varied with prey density in non-linear fashion (Harding et al. 2007). In this case, Cairns’ prediction was probably correct: a failure in murre breeding success would indicate much lower food supplies than a failure or decline in any other parameter we measured, or at least point to some unusual changes in the environment. For example, recent unusual breeding failures of murres in the North Sea were attributed not to scarcity of prey, but to unusually low (and unexplained) energy value of prey (Wanless et al. 2005).

Fig. 5. Rissa tridactyla, Uria aalge. A comparison of variability among colony-years in different parameters of kittiwake and murre biology and behavior, with respect to variability in the food supply (darker bar)
Differential species responses

We found strong support for Cairns’ prediction that different species would respond differently to fluctuations in food supply. In the most extreme example, kittiwake breeding success was strongly influenced by food supply (Table 1) and slightly more variable (Fig. 5), whereas murre breeding success was independent of food supply in our study and less than half as variable. One explanation for this difference is that murres have little difficulty meeting their nutritional needs over a wide range of prey availabilities, and when they do, they simply reallocate some discretionary time to foraging effort in order to buffer their reproductive success (Harding et al. 2007). In contrast, kittiwakes are near their maximum performance limits most of the time and have little or no discretionary time to buffer against a reduction in prey availability.

Consider the differences in morphology, life history, and foraging behavior that account for this differential response. Murres must acquire more food than kittiwakes to sustain themselves each day because of differences in body size (1040 vs. 405 g, respectively, in Cook Inlet), costs of flight (wing loading: 1.86 vs. 0.39 g cm$^{-2}$; Gabrielsen 1994), and foraging (diving vs. surface-feeding). We calculate from measures of field metabolic rates (FMR; Gabrielsen 1994) and assimilation efficiency (87%; Romano et al. 2006) that murres (2.14 kJ d$^{-1}$ g$^{-1}$ FMR) and kittiwakes (2.03 kJ d$^{-1}$ g$^{-1}$ FMR) feeding on sand lance (5.0 kJ g$^{-1}$ wet; Van Pelt et al. 1997) would need to capture and eat 512 and 189 g, respectively, of fish per day. This is actually a similar burden for each species because it represents about half their respective body masses.

From this point forward, however, additional daily needs may diverge markedly between species, owing to costs of rearing and feeding chicks (Gabrielsen 1994). The cost of rearing 1 chick increases demand from 49 to 53% of body mass in adult murres (an 8% increase), but from 46 to 67% of body mass in adult kittiwakes (a 46% increase). Adult kittiwakes raising 2 chicks need to acquire 381 g of sand lance daily, or 94% of their body mass (a 104% increase in demand). Since murres lay only 1 egg, and raise chicks to only one-quarter adult mass before fledging, they never incur the same obligation as kittiwakes that often try (and more often fail) to raise 2 chicks in Alaska (Hatch et al. 1993).

Furthermore, even though murres need to acquire 1.5 to 2.7 times more prey biomass daily than kittiwakes, they typically acquire what they need in about half the time. On average, kittiwake foraging trips were about 1.4 h longer than those of murres (typically 2 h) in Cook Inlet, a difference also observed elsewhere (Hamer et al. 1993, Monaghan et al. 1994). Because murre and kittiwake chicks need about 4 meals per day, the cumulative result is an enormous difference in foraging time-budgets between species. It explains why murres have several hours of extra discretionary time to reallocate to foraging when prey are scarce, while kittiwakes have almost none. The difference may arise from the fact that kittiwakes are restricted to feeding only on organisms found at the sea surface (<0.5 m), whereas murres can dive deep enough to exploit the entire water column of lower Cook Inlet. If most of the exploitable fish biomass is above 50 m (Speckman 2004), murres would have access to 100 times more prey biomass than kittiwakes at any given distance from a colony.

In summary, every species of seabird has a different set of biological and behavioral adaptations for responding to changes in food supply, so we do not expect all species to react the same way. A further point made by Cairns (1987) and corroborated in our study is that if we wish to use multiple seabird species as indicators of marine food supplies, we had better first characterize the similarities and differences in their response to variability in food supply. Additionally, it may be useful to combine response data from different species using a multivariate index that captures the essence of the response and allows us to use a selection of species as multivariate indicators of food supplies (Reid et al. 2005, Fredericksen et al. 2006, Piatt & Harding 2007).

Poor indicators

It is equally important and biologically interesting to consider which parameters are not useful indicators of marine food supplies. The list of parameters that we studied is by no means exhaustive, but did include some that are often listed among useful indicators (Cairns 1987, Weimerskirch et al. 2001, Reid et al. 2005). In particular, this includes body condition and clutch size.

We found no relationship between adult body condition and food density for either murres or kittiwakes. These results were not expected. It was reasonable to assume that body condition would be sensitive to variations in food supply (Monaghan et al. 1989, Hamer et al. 1991). Experimental studies have shown that adult body condition can be affected negatively by increasing workload (Golet & Irons 1999). In field studies where seasonal variability in body mass was accounted for in the analysis, however, variability in adult body condition among years was exceedingly low (CV = 0.6 to 6.6%) for skua, terns, albatross, murres, and kittiwakes (Harris & Wanless 1988, Hamer et al. 1991, Suddaby & Ratcliffe 1997, Weimerskirch et al. 2001).

2001). Reid et al. (2005) examined annual variability in 32 parameters of seabird and mammal biology in the Antarctic, and found that the 7 least variable parameters involved measures of body mass (e.g. birth mass, fledging mass, adult arrival mass, etc.) and all had CVs < 10%.

This suggests that both murres and kittiwakes minimize variability in their own body condition. This is consistent with the idea of a trade-off between investment in the current year’s reproductive effort and subsequent adult survival (Stearns 1992). The importance of maintaining adult body condition is implied from the strong linkage between body condition and survival in seabirds (Erikstad et al. 1998, Golet et al. 1998, Weimerskirch et al. 2001). After taking care of themselves, it follows that adults would try to minimize variation in chick growth and condition, which is linked with survival to breeding age (Sagar & Horning 1998, Weimerskirch et al. 2000).

Black-legged kittiwakes lay up to 3 eggs per clutch, but clutch size and laying success in kittiwakes were independent of food supply in Cook Inlet. On average, 69% of pairs that attempted to breed eventually laid eggs. For those that laid, the average clutch size was 1.49 ± 0.18 SD eggs per nest. Laying success (CV = 29%) was more variable than clutch size (CV = 12%). These observations may be explained in at least 2 ways. First, there was a gap in time between measurements: clutch size and laying success were measured in June, while food supply was measured in late July to early August. Alternatively, kittiwakes may have a programmed approach to egg-laying that is largely independent of food supply except under extreme conditions, i.e. when food supplies and nutrient reserves are so low as to preclude egg formation. Evidence from a variety of seabirds suggests that clutch size is usually maximized and regulation of breeding effort occurs later, by brood reduction or nest desertion (e.g. Mannonagh et al. 1989, Sydeman et al. 1991, Hamer et al. 1993, Suddaby & Ratcliffe 1997).

Conclusions and future considerations

We join the ranks of those who promote the cautious use of seabirds as indicators of marine food supplies and call for more studies to elucidate the form of functional relationships and sources of variability (Cairns 1987, Montevucchi 1993, Furness & Camphuysen 1997, Reid et al. 2005). However, it is now clear that we ought not to expect many linear relationships between parameters of seabird biology and food supply (Reid et al. 2005). Seabirds are in most circumstances unlikely to gauge subtle or continuous changes, but they may perform well as binary indicators (Montevucchi 2007, this Theme Section) that signal changes from good to bad, and vice versa. On the other hand, foraging-trip duration was one parameter that varied continuously (if not linearly) with prey density, and is perhaps deserving of more attention.

While other factors such as weather and predation can influence kittiwake breeding success (Hamer et al. 1993, Hatch et al. 1993), the species appears to be very sensitive to fluctuations in food supply. This parameter should, therefore, prove to be a reliable long-term indicator of variability in the marine environment (e.g. Aebischer et al. 1990, Piatt & Harding 2007). In contrast, murre breeding success may tell us little about food supplies, except under extreme circumstances, whereas murre time-budgets are sensitive to prey fluctuations. Given that murre species are widely being monitored in the Northern Hemisphere (Gaston & Jones 1998), it is perhaps time to add attendance time-budgets to the repertoire of parameters we routinely measure at murre colonies.

It is useful to know the form of a seabird’s response to changing prey density, but the variability of its response is equally important in assessing its ability to deal with change. We find it intriguing that independent studies of seabirds in Alaska (Fig. 5) and the Antarctic (penguin and albatross; Reid et al. 2005), with similar sampling effort, found that (1) the highest CV of any parameter was <90% in both studies and (2) that some parameters in both studies fell into similar groupings of those with low CVs (e.g. body condition), moderate CVs (e.g. foraging), and high CVs (e.g. breeding success). This leads us to wonder: are there limits in variability, and do these differ much among species and ecosystems? To what extremes of variation can seabirds be pushed by climate change and regime shifts (e.g. Sydeman et al. 1991, Anderson & Piatt 1999) before they collapse? If there are differences among species, can we predict which species will be the best indicators of unusual variability in their environments?

Finally, we note that despite many advances in knowledge since Cairns’ predictions were made, much uncertainty remains about using seabirds as indicators of marine food supplies (Frederickson et al. 2006). More research is needed on a wider variety of seabird species and their functional relationships with prey. Also, we think that for some parameters, responses may not be evident except under the most extreme conditions of prey scarcity. It may be that experimental situations (e.g. with captive birds in aquaria, manipulative experiments in the wild) are needed to address this gap. In general, some of the best indicators in our study (and Reid et al. 2005) were those which had both high annual variability and a strong functional relationship with prey density. Paradoxically, highly variable parameters are not recommended for use as eco-
logical indicators (Dale & Beyeler 2001). Less variable parameters might be just as sensitive, but less practical if they have a weaker signal-to-noise ratio. Owing to these many uncertainties, and until we better understand the responses of individual species, it may be most prudent to combine data from multiple parameters and species to generate robust multivariate indicators of prey stocks (Frederiksen et al. 2006, Piatt & Harding 2007). In any case, we find it encouraging that increasing evidence points to bottom-up control of seabird populations (Aebischer et al. 1990, Speckman et al. 1995, Frederiksen et al. 2006), which further suggests that seabirds are likely to track spatial and temporal variation in prey abundance.

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Seabirds as indicators of food web structure and ecosystem variability: qualitative and quantitative diet analyses using fatty acids

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ABSTRACT: The dynamics of predator–prey relationships, the structure of food webs, and the foraging behavior of individuals are critical to understanding animal ecology, interactions of predators with their prey, and effects of environmental variability on ecosystems. Like many other predators, seabirds are effective samplers of prey populations, and their diets can provide information about lower trophic levels over a range of spatial and temporal scales. Recognizing limitations of traditional methods of diet analysis, we validated the use of fatty acid (FA) signatures of subcutaneous adipose tissue biopsies for estimating diets of free-ranging seabirds. Calibration coefficients (CCs) for individual FAs were determined from captive common murres (n = 13) fed a long-term, single-species diet. Quantitative FA signature analysis (QFASA), using these CCs, was then validated in murres (n = 26) and red-legged kittiwakes (n = 13) fed controlled mixed-species diets. FAs were analyzed from 426 free-ranging red-legged Rissa brevirostris and black-legged kittiwakes R. tridactyla, and common Uria aalge and thick-billed murres U. lomvia from the Bering Sea, 284 of which were also sampled for stomach contents analysis. Qualitatively, FA signatures revealed distinct separation of diets among all 4 species, and further separation by location and year. QFASA diet estimates were similar to those based on stomach contents, with diets of kittiwakes dominated by myctophids, while those of murres comprised a mixture of other forage species. QFASA estimates were indicative of regional habitat differences, and were consistent with other aspects of seabird ecology at our study sites. We conclude that seabird FAs provide important information about ecosystems, but this will likely depend on each species’ foraging behavior and the complexities of the ecosystem it occupies.

KEY WORDS: Seabirds · Fatty acids · Diet · Food webs · Black-legged kittiwakes Rissa tridactyla · Red-legged kittiwakes Rissa brevirostris · Common murres Uria aalge · Thick-billed murres Uria lomvia

INTRODUCTION

Describing complex interactions among species in ecosystems, how interactions are shaped by abiotic factors, and how they change over time and space can represent a tremendous challenge (Steele 1974). The concept of using information from upper trophic level predators to indicate ecosystem state, including information about lower trophic levels, has been acknowledged for several decades. For instance, species of marine mammals, as well as seabirds and predatory fish, have been used to indicate marine prey stocks and distribution, and to study habitats and food webs in relation to prey populations, oceanographic domains, and environmental variability (e.g. Springer et al. 1984, 1986, 1996, Montvecchi 1993, Sinclair et al. 1994, Roseneau & Byrd 1996, Boyd & Murray 2001, Iverson et al. 2006). However, the nature and extent of what higher predator diets can tell us will likely depend on the foraging behavior of a given predator and the complexities of its ecosystem (e.g. McCafferty et al. 1999, Croxall 2006).
If seabirds are to be useful as indicators and sentinels of marine ecosystem structure and variability, then we must find appropriate factors that are readily measured, sensitive to stresses or change, and are integrative. Among these, diet is an obvious choice. Studies of diets can provide information about food web differentiation and the importance and likely abundance of various prey across spatial and temporal scales. This information, in conjunction with other types of data, is important to understanding seabird distributions and population dynamics, and ecosystem structure and change over time.

Traditional approaches to studying seabird diets have well-known shortcomings and biases. For instance, analysis of stomach contents obtained from killed birds eliminates both the bird and the opportunity for longitudinal studies of individuals, and often, stomachs are empty. Additionally, information is obtained only on the most recent meal, which may not be reflective of longer-term diet, and prey with hard parts resistant to digestion, such as squid beaks, are overrepresented, while soft-bodied prey that are easily digested, such as euphausiids, are under-represented. Although stable isotopes can provide useful information (e.g. Hobson et al. 1994, Votier et al. 2003), they can generally only be used to estimate trophic level of consumption (e.g. Hobson et al. 1994, Votier et al. 2003), they can generally only be used to estimate trophic level of feeding, not specific composition of diets. Visually identifying or intercepting prey carried in the beaks of adults when they return to the nest site to feed chicks (e.g. Hatch & Sanger 1992), or identifying the contents of gular pouches of auklets Aethia spp. (Bedard 1969), can be used only in some species and only during the relatively short annual period of chick rearing, and diets of chicks may differ significantly from those of adults (Furness et al. 1984, Hobson et al. 1994).

An alternative, or complementary, method for determining predator diets is to use fatty acid (FA) profiles, or signatures, in their adipose tissue (Iverson 1993). FAs are the largest constituent of lipids and their great diversity, biochemical restrictions, and, in some cases, unique origin among plants and animals has led to their use as trophic tracers in a wide variety of predators (reviewed in Budge et al. 2006). Alone, FA signatures can be used to examine differences or changes in foraging patterns or diets, both within and between populations of predator species, without specifying what species are eaten. However, used in conjunction with a detailed prey FA database and a recently developed statistical model, it is possible to quantitatively estimate the species composition of diets of individual predators at time scales relevant to the ecological processes affecting survival, as has been demonstrated in several marine and aquatic mammals (Iverson et al. 2004, 2006). Furthermore, adipose tissue samples for the analysis of FAs can be obtained from live predators by biopsy with minimal invasiveness. Although FA techniques have been used to infer foraging in a few seabird species (Raclot et al. 1998, Käkelä et al. 2005), to date, quantitative analysis has not been performed or validated. Therefore, our aim was to validate quantitative FA signature analysis (QFASA) as a method to estimate seabird diets, using both captive and field studies of 4 species in the Bering Sea, black-legged kittiwakes Rissa tridactyla (BLKI), red-legged kittiwakes R. brevirostris (RLKI), common murres Uria aalge (COMU), and thick-billed murres U. lomvia (TBMU).

**MATERIALS AND METHODS**

**Sampling site and live biopsy technique.** To first examine variability of FA composition within individuals, adipose tissue was sampled postmortem at 3 different locations in the body (mesenteric, breast, and subcutaneous at the synsacrum) in each of 18 birds, sacrificed in the wild, representing all 4 study species. The FA composition of all adipose tissue depots within individuals was indistinguishable (note: data available from the authors). Thus, since synsachral adipose tissue (on the lower back, anterior to the tail and avoiding the uropigial gland) can be obtained easily by biopsy from live birds, we sampled this adipose tissue depot in all remaining live and dead birds.

A live biopsy technique (Enderson & Berger 1968) was used to obtain synsacral adipose tissue samples from captive birds and from live, free-ranging birds captured at nest sites. The bird was held cradled breast down, and ethanol (70%) was swabbed on the feathers and skin covering the synsacrum to moisten the feathers and disinfect the area. The feathers were parted, and an incision of approximately 0.5 cm in length was made just through the skin. Between 0.05 and 0.30 g (depending on species and fat condition) of adipose tissue was excised using forceps and a scalpel blade, and placed in aluminum foil. The incision was then closed with surgical glue, and the bird was released. Samples were placed in chloroform containing 0.01% BHT (an antioxidant) in glass vials with Teflon-lined caps as soon as possible and stored frozen until analysis.

**Captive feeding trials.** Partially incubated eggs of COMU (n = 26) and RLKI (n = 13) were collected in Cook Inlet and on the Pribilof Islands, Alaska, respectively, transported to captive facilities, and incubated until hatching (see Kitaysky et al. 2001, Benowitz-Fredericks & Kitaysky 2005). Chicks were raised in individual nests and hand-fed controlled diets, half at 100% and half at 60 to 70% rations on each diet. COMU chicks were fed only silverside Menidia menidia from hatching until Day 10. From Days 11 to 45, half of the COMU chicks were continued only on sil-
verside and the other half were fed only rainbow smelt Osmerus mordax. On Day 45, synsacral adipose tissue was obtained by biopsy from all individuals. RLKI chicks were fed a mixture of 8 parts herring Clupea harengus to 2 parts silverside from hatching until Day 15. From Days 16 to 20, half of the RLKI chicks were fed only silverside and the other half were fed only rainbow smelt, and all were biopsied on Day 42. Biopsies were stored frozen in air-tight vials. Silverside (n = 15), rainbow smelt (n = 15), and herring (n = 10) were collected from the lots being fed, placed in air-tight plastic bags, and stored frozen.

Field studies: free-ranging birds and prey. Synsacral adipose tissue samples were collected and analyzed from 426 free-ranging seabirds in 1999 and 2000 from St. Paul and St. George Islands (Pribilof Islands) and Bogoslof Island (Aleutian archipelago), Alaska: COMU (n = 68), TBMU (n = 136), RLKI (n = 88), and BLKI (n = 134). Birds were either captured alive (n = 142), sampled by biopsy (as described above) and released, or sacrificed in the field (n = 284) for other studies and used to compare diets derived from FAs with those from traditional stomach contents analyses. In the same years, a total of 161 individuals of 15 forage species believed to represent the potential prey was collected from the same areas as the birds—around the Pribilofs and Bogoslof—as opportunity provided, by ourselves, the National Marine Fisheries Service, and the U.S. Fish and Wildlife Service. Prey species collected included arrowtooth Atheresthes stomias and several other flounders Pleuronectidae spp., capelin Mallotus villosus, kelp greenling and other greenlings Hexagrammos spp., herring, walleye pollock Theragra chalcogramma, sandlance Ammodytes hexapterus, northern smooth-tongue Leuroglossus schmidti, myctophids (northern lampfish Stenobrachius leucopsarus), euphausids Thysanoessa spp., and squids Gonatidae spp. All prey were placed in air-tight plastic bags and stored frozen until analysis.

Sample analyses. Lipid was quantitatively extracted from seabird fat samples and homogenates of each individual prey according to Iverson et al. (2001). FA methyl esters were prepared using acidic transesterification, analyzed in duplicate by gas chromatography using a polar capillary column coated with 50% cyanopropyl polysiloxane (0.25 µm film thickness; J&W DB-23), and identified using a suite of techniques, according to all methods outlined in Iverson et al. (1997, 2002). Stomachs of all birds collected in the field were removed soon after death, and the contents were preserved frozen or in 70% ethanol until they were identified and enumerated. Prey remains were sorted and identified to the lowest taxonomic level practical, which was generally to species for fishes and to genera or families for invertebrates. Wet mass of prey was estimated using morphometric relationships between fish mass and otolith length and between squid mass and beak size, or by estimating lengths of prey lacking otoliths (e.g. fish without heads, other invertebrates) and using relationships relating estimated length to mass (e.g. Springer et al. 1996, Harvey et al. 2000).

Statistical analyses and QFASA. Differences among seabird species, location, and year were evaluated using a combination of univariate and multivariate techniques. Discriminant analysis (SPSS) was performed using the log-transformed percentage ratios of 17 FAs that had the largest overall variance and an overall mean of ≥0.4% of total FAs (Iverson et al. 2002). The diets of both captive and free-ranging birds were estimated using the QFASA model developed by Iverson et al. (2004) and the prey database we developed above, according to the ‘Field Studies’ section (see Iverson & Springer 2002 for presentation of prey FA data). Basically, QFASA estimates the diet by weighting the mixture of FA signatures of prey species that most closely resemble that of the predator’s adipose tissue stores and then after accounting for the relative fat content of each prey species, translates the signature mix into a diet estimate. An integral part of the QFASA model is the use of calibration coefficients (CCs) to account for predator lipid metabolism by weighting individual FAs according to their tissue deposition relative to diet (Iverson et al. 2004, 2006, Cooper et al. 2005). We calculated seabird CCs from the captive COMUs that had only been fed a constant diet of silverside since hatching.

RESULTS

Captive validation studies

The prey used in captive feeding trials differed somewhat in total lipid concentration, with herring averaging 5.2 ± 0.28%, silverside averaging 6.0 ± 0.30%, and rainbow smelt averaging 3.4 ± 0.20% fat. However, the FA signatures of the 3 species differed markedly (Fig. 1a). For instance, of the 2 primary diet items, smelt was extremely high in 18:2n-6 and 18:3n-3, components that are usually relatively rare in marine systems and thus low in free-ranging seabirds; in contrast to smelt, silverside was extremely high in 22:5n-3 and 22:6n-3. Both of the main diets (silverside and smelt) contained extremely low levels of the long-chain monounsaturated isomers of 20:1 and 22:1 in contrast to herring. Consistent with large differences in the FA signatures of prey, there were large differences between the birds fed different diets (Fig. 1b). In large part, the FA signatures of COMU and RLKI fed similar diets (i.e. primarily silverside or primarily smelt)
closely resembled one another, especially in the long-chain polyunsaturated FAs (≥18:2n-6), while within each species, individuals fed different diets differed substantially. Absolute, although minor, differences in levels of FAs between COMU and RLKI fed the same predominant diet presumably reflected the fact that the 2 groups were fed different diets for the first 10 to 15 d.

The 13 COMU chicks that were fed a constant diet of silverside from hatching until 45 d could be used to calculate CCs for individual FAs, since they were never fed anything else. In general, CCs were close to 1.0 for many of the FAs measured and, overall, were similar in nature to CCs previously calculated for phocid seals and mink Mustela vison fed marine diets (Fig. 2a: numerical values for CCs available from authors). Significant deviations were apparent in CCs for several FAs, especially several minor or trace components that are heavily influenced by biosynthesis. These and other FAs that arise solely from biosynthesis were not used in diet estimations. However, given the very tight response among individuals for almost all other FAs (in most cases SEs were too small to see), these CCs can be used to weight individual FAs in the QFASA model. These CCs were then applied to all captive birds in modeling diets. We ran the QFASA model using several different sets of FAs as outlined in Iverson et al. (2004), but since there were no significant differences in diet estimates by FA set, we used the ‘extended dietary’ set, which utilized the maximum number of
relevant FAs. QFASA estimates of diets of captive seabirds corresponded very well to the experimental diets (Fig. 2b). There was no significant difference between the groups fed 100% or 60 to 70% rations in the QFASA diet estimates (hence, apparent turnover of FAs); thus, both are averaged together. COMU fed only silverside were estimated to have only silverside in their diet, with no herring and only a trace of smelt incorrectly identified. In contrast, COMU fattened primarily on smelt were estimated to have fed primarily on smelt with some silverside, likely residual from the first 10 d of feeding; again no herring was detected. Likewise, the diets of RLKI estimated from QFASA corresponded to the known diets of primarily silverside or smelt, with some residual herring and silverside identified from the first 15 d of feeding; a minor amount of smelt was misidentified in the silverside-fed birds.

Free-ranging seabirds

The FA composition of adipose tissue varied substantially across the 4 study species. Although differences were apparent in many of the minor components, differences among species were best illustrated by the most abundant and variable FAs (Fig. 3a). The largest differences, regardless of location or year sampled, were apparent between kittiwakes and murres. That is, FA patterns in COMU and TBMU were similar to one another and notably different from those observed...
in BLKI and RLKI. For instance, among FAs that arise solely or mostly from diet, kittiwakes had extremely high levels of 20:1n-11 and 22:1n-11 and very low levels of 18:4n-3, 20:5n-3, 22:5n-3, and 22:6n-3 in comparison to murres. Nevertheless, FA signatures also varied among individual species and differed considerably from those of the birds fed captive diets (Figs. 1b & 3a). Results of discriminant analyses confirmed the significance of these overall species differences (Fig. 3b), but also demonstrated the broad overlap in FA signatures (and thus diet) of COMU with TBMU and of RLKI with BLKI.

Fig. 3. (a) Selected FAs (17 of 67 identified) with the largest overall variance and an overall mean of ≥0.4% of total FAs that illustrate characteristic differences in patterns among free-ranging common and thick-billed murres (COMU and TBMU, respectively) and red-legged and black-legged kittiwakes (RLKI and BLKI, respectively). Bars are means, and vertical lines are 1 SE. FAs differed significantly among species (p < 0.001, MANOVA). (b) Plot of the group centroids (within-group mean for the first and second discriminant functions) from discriminant analysis performed on all individuals from (a). Ellipses represent 95% of the data point clouds for each species. The first 3 discriminant functions were significant (p < 0.001); the first function accounted for 98.5% of the variance: 71.7% of all original grouped cases and 68.8% of cross-validated grouped cases were correctly classified to species (Wilk’s λ < 0.001). Virtually all misclassifications were within the murres and kittiwakes, i.e. when separation of species groups (murres versus kittiwakes) was considered, individuals were accurately classified to species group with >99% success. (c) Plot of the group centroids from discriminant analysis on RLKI (n = 88) and BLKI (n = 134) by major region and year. The first 5 discriminant functions were significant (p < 0.001); the first 2 functions accounted for 74.2% of the variance: 68.1% of all original grouped cases and 61.7% of cross-validated grouped cases were correctly classified to species (Wilk’s λ < 0.001). Most misclassifications were within species, i.e. when all kittiwakes were grouped, individuals were accurately classified to major region and year with 83.4% success.
In addition to large overall differences between species, there was also significant within-species variability. For instance, there was clear evidence of differences by location and year in both kittiwakes and murres. When each species was considered separately, 96, 80, and 80% of RLKI, BLKI, and TBMU, respectively, were correctly classified by location and year (small group sample size prevented this analysis for COMU). Considering RLKI and BLKI together, a plot of the group centroids illustrates annual and geographical differences in FA signatures between 1999 and 2000 at both Bogoslof and the Pribilofs, indicating differences in diets (Fig. 3c).

Of the 284 birds that were sacrificed, 49 had empty stomachs. The remaining 235 birds were used to qualitatively compare diet estimates from QFASA modeling of adipose tissue FAs and from prey remains in stomachs. The QFASA and stomach contents analyses produced similar diet estimates within each of the 4 species (Fig. 4a, b). The principal difference was that QFASA indicated a greater proportion of some prey that occurred infrequently in stomachs and a lower proportion of squids. Both methods estimated that the diets of the 2 kittiwakes were dominated by myctophids, which appeared in only trace amounts in the murres. Although RLKI had the least diverse diet using either method, feeding primarily on myctophids, QFASA revealed that capelin, sand lance, and euphausiids each contributed about 10% to their diets. In contrast, murre diets were generally more diverse, composed primarily of fishes, such as capelin, pollock, sand lance, and northern smooth-tongue, and euphausiids. Squids, which were estimated to be of some importance to TBMU based on stomach contents

![Fig. 4. (a) QFASA estimates of diets of free-ranging murres and kittiwakes (n = 235) in comparison to (b) diet estimates from stomach contents analysis in the same individuals. Prey species present in the database, but not detected in diets by either method are not illustrated. ‘Other fish’ were identified in stomach contents merely as other fish. Using QFASA, these were individually identified and included species such as arrowtooth flounder, other flatfish, and greenlings, but are combined for presentation in order to compare with stomachs. Bars are means of each species estimated in diets, and vertical lines are 1 SE. For abbreviations see Fig. 3](image-url)
analyses, were found to be much less important when estimated by QFASA, and of little or no importance to COMU or kittiwakes.

QFASA results from the complete set of 426 birds were consistent with qualitative analyses of foraging (e.g. Fig. 3b,c) and revealed significant differences in diets with location (e.g. between the Pribilofs and Bogoslof overall, but also between St. Paul and St. George Islands) and with year in all 4 species (p < 0.05, MANOVA). Information obtained from QFASA could also be used to calculate average fat (and thus a proxy of energy) content of diets. On average, the fat contents of RLKI and BLKI diets (11.9 ± 0.22% and 10.2 ± 0.32%, respectively) were almost double those of COMU and TBMU diets (4.8 ± 0.19% and 5.9 ± 0.15%, respectively) (p < 0.001). RLKI diets across both major regions were higher in fat content in 2000 (12.3 ± 0.20%) than in 1999 (10.3 ± 0.50%) (p < 0.001), and were consistent with higher indices of productivity, e.g. clutch size, laying success, hatching success, fledging success, and chick growth (V. Byrd & D. Kildaw unpubl. data) and lower levels of circulating corticosterone, an index of stress, in 2000 compared to 1999 (A. Kitaysky unpubl. data). However, it is not known whether this was related to dietary energy content or absolute intake of prey, as BLKI exhibited similar patterns in productivity, but diets did not differ significantly in fat content between the 2 yr. Fat content of murre diets varied only by about 10% between years, and murres exhibited no differences in productivity.

**DISCUSSION**

The results from our captive feeding studies clearly demonstrated that the greatest influence on the FA composition of adipose tissue is diet (Fig. 1). Hence, FAs can be used to qualitatively infer foraging and diet differences in free-ranging seabirds, among individuals, populations, and species, as well as over temporal and spatial scales. Patterns of adipose tissue FAs alone allowed us to discriminate diet differences between all 4 seabird species (black-legged kittiwakes *Rissa tridactyla*, red-legged kittiwakes *R. brevirostris*, common murres *Uria aalge*, and thick-billed murres *U. lomvia*), between the 2 yr, and between the Pribilofs and Bogoslof (e.g. Fig. 3). Differences we detected among species were consistent with results of other studies of murres and kittiwakes, which have shown varying degrees of dietary distinction among them in the Bering Sea (Hunt et al. 1981, Springer et al. 1996). The interannual differences we detected were also associated with differences between 1999 and 2000 in productivity and physiological condition of adults. Geographic variability in diets likely reflected food web structure that is, in turn, related to habitat characteristics across the region: Bogoslof is the most oceanic of the islands, lying in deep water just off the Aleutian Arc, whereas the Pribilofs lie in shallow water in the middle domain of the continental shelf, but near the ecotone between shelf and basin habitats. Species assemblages, including potential prey, in the basin are much different than on the shelf (Mecklenburg et al. 2002).

The results from the captive feeding studies further demonstrated that the response of adipose tissue FAs in seabirds to dietary FA intake is highly predictable (Fig. 2a) and that diet can be quantitatively and quite accurately characterized using QFASA in a simple system of 3 prey types (Fig. 2b). We then used the QFASA model to estimate diets of free-ranging seabirds in the Bering Sea using a much more complex prey database and compared these estimates to those derived from stomach contents in the same individuals. We would not expect results from the 2 analyses to be identical, as they are associated with different time scales of inference and the biases inherent in stomach content analyses preclude using them as a standard. Thus, we did not statistically test their similarity, but rather used the comparison as a framework for interpretation of QFASA. Both methods estimated the same dominant prey (Fig. 4a, b) and characterized well-established differences in typical diets of murres and kittiwakes across this region (e.g. Springer et al. 1996).

Differences between results of the QFASA and stomach contents analyses were consistent with expectations. For example, QFASA indicated a greater contribution of soft-bodied prey recorded infrequently in stomach contents and a lesser contribution of squids (the beaks of which are known to be selectively retained in stomachs). Likewise, QFASA estimated less pollock (relatively robust otoliths) and more capelin and sand lance (relatively small otoliths) than stomach contents did. QFASA was also able to quantify soft-bodied invertebrates, which were identified in stomachs in the present study, but commonly disintegrate quickly after being consumed (Furness et al. 1984, Hobson et al. 1994). Differences also likely arise from the fact that stomach contents generally represent diet consumed during the most recent feeding bout, whereas QFASA represents diets integrated over weeks.

We have demonstrated that QFASA can be a powerful technique for determining diets of free-ranging seabirds, providing opportunities for obtaining greater information than possible using other methods. Moreover, investigating such trophic relationships with traditional methods of diet analysis would require sacrificing great numbers of birds over an extended period each summer at each location. Many of the issues required for using QFASA and assembling a prey FA
database have previously been reviewed (Iverson et al. 2004, Budge et al. 2006). Nevertheless, there remain several areas for further investigation with seabirds. The estimation of predator CCs is an integral component of QFASA. In our captive study, we assumed that after a long-term, single-species diet (in fact the only diet ever consumed), a bird’s FA signature would look as much like the diet as it ever would, and used this as a basis for weighting FAs. Although there was a high degree of correspondence between seabirds and seal and mink data sets (Fig. 2a), and we are confident we have good estimates of the CCs for the seabirds used in our experiment given the success of our QFASA modeling, clearly more studies are needed to confirm patterns of FA deposition with additional species and with adults versus chicks. For instance, while variation was clearly apparent, the only important dietary FA with a CC in birds quite different than that of both seals and mink, on average, was 22:1n-11, which was also quite low in the silverside fed to the CC birds (Fig. 1a). Thus, it would be useful to evaluate this in future studies. Interestingly, unlike previous studies, the choice of the FA set used for modeling, including removal of FAs with large CCs, had no significant effect on diet estimates. In addition to the above issues, a better understanding of the time scales over which changes in diet are reflected, and the effects of ration size are also important.

QFASA estimates of diet meet several important requirements for ecological indicators: FA are easily measured, sensitive to change and responsive to change in a predictable manner, and are integrative. A particular advantage of QFASA is that fat samples can be obtained humanely, with minimal invasiveness, allowing greater sample sizes as well as longitudinal studies of individuals. Coupled with information on the physiological status of individuals and on the outcome of individual and colony-wide nesting attempts, we have tools that will help us to greatly improve our understanding of the nature and consequences of fluctuations in food web productivity critical to the maintenance of seabird populations. Such detailed information will be especially useful in furthering our understanding of how ecosystems vary spatially and temporally in response to climate change and other perturbations.

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Stress hormones link food availability and population processes in seabirds

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ABSTRACT: Catastrophic population declines in marine top predators in the northern Pacific have been hypothesized to result from nutritional stress affecting reproduction and survival of individuals. However, empirical evidence for food-related stress in wild animals is frequently lacking or inconclusive. We used a field endocrinology approach to measure stress, identify its causes, and examine a link between stress and population processes in the common murre Uria aalge. We tested the empirical relationship between variations in the stress hormone corticosterone (CORT) and food abundance, reproduction, and persistence of individuals at declining and increasing colonies in Cook Inlet, Alaska, from 1996 to 2001. We found that CORT secretion in murres is independent of colony, reproductive stage effects, and gender of individuals, but is directly negatively correlated with abundance of their food. Baseline CORT reflected current food abundance, whereas acute stress-induced CORT reflected food abundance in the previous month. As food supply diminished, increased CORT secretion predicted a decrease in reproductive performance. At a declining colony, increased baseline levels of CORT during reproduction predicted disappearance of individuals from the population. Persistence of individuals in a growing colony was independent of CORT during reproduction. The obtained results support the hypothesis that nutritional stress during reproduction affects reproduction and survival in seabirds. This study provides the first unequivocal evidence for CORT secretion as a mechanistic link between fluctuations in food abundance and population processes in seabirds.

KEY WORDS: Corticosterone · Food availability · Stress · Seabirds · Population processes

INTRODUCTION

The identification of causes and consequences of stress in populations of wild animals is a fundamental ecological problem. Food limitations have long been suggested to control seabird population dynamics by altering the survival and reproductive performance of individuals (Lack 1966). During the past 3 decades, catastrophic population declines have occurred among some seabirds in the northern Pacific (Hunt & Byrd 1999). It has been hypothesized that deterioration of food resources during reproduction resulted in food-related stress, which in turn reduced fitness of marine top predators (Merrick et al. 1987, Hunt et al. 1996, Piatt & Anderson 1996). However, an empirical relationship between food availability and stress has not been previously quantified in free-living seabirds, and the direct effect of food-related stress on reproduction and survival of individuals has yet to be elucidated. The present paper provides the first unequivocal evidence for food-related stress as a mechanistic link between fluctuations in food abundance during reproduction and population processes in seabirds.

Traditional methods for measuring food-related stress in free-living seabirds are not always effective. In this context, food-related stress can be defined as changes in the physiological condition of individuals that experience a shortage of food that impairs their ability to reproduce successfully. Alternatively, less severe food shortages may allow reproduction to proceed, but low post-fledging survival of young raised on low quality/quantity diets may precipitate reproduc-
tive failure (Kitaysky et al. 2006) and/or affect their recruitment to breeding populations (Thompson & Ollason 2001). More importantly, breeding during suboptimal foraging conditions may be detrimental to post-reproductive survival of adults (e.g. Kitaysky et al. 2001b, Golet et al. 2004). In long-lived animals, food-related stress is most likely to affect reproductive success (e.g. Kitaysky & Golubova 2000) or the survival of young rather than that of adults (Williams 1966). Yet, in some species, young may tolerate large fluctuations in food supply and fledge successfully despite severe food shortages (e.g. Kitaysky 1999, Wanless et al. 2005, Benowitz-Fredericks et al. 2006, Kitaysky et al. 2006), and survival of chicks may be affected by factors independent of food supplies, such as predation and inclement weather (e.g. Lloyd 1979, Regehr & Monttevecchi 1997). In others, parents buffer their young from variations in food availability by increasing their effort in foraging during food shortages (Shea & Ricklefs 1995, 1996, Zador & Piatt 1999, Kitaysky et al. 2000, 2001b). Furthermore, long-lived seabirds do not recruit to breeding colonies until they are several years old and frequently forego reproductive attempts (e.g. Mougin et al. 1997); therefore, a time series of several decades is required to assess the consequences of current environmental conditions on future population dynamics (Thompson & Ollason 2001). Thus, empirical evidence for the direct effects of food-related stress on seabird reproduction and survival is difficult to obtain while using traditional methods. In this study, we used a field endocrinology approach to measure stress, identify its causes, and to examine the hypothesized link between food-related stress and population processes in the common murre Uria aalge—one of the most abundant seabirds in the North Pacific.

Birds respond to food stress by increasing secretion of the steroid hormone corticosterone (CORT, the primary avian glucocorticoid). Results of controlled experiments suggested a direct relationship between food availability and secretion of stress hormones in birds (Kitaysky et al. 1999a, 2001a, Pravosudov et al. 2001, Lynn et al. 2003, Clinchy et al. 2004, Pravosudov & Kitaysky 2006). Specifically, baseline CORT was found to be proportional to the severity of experimentally induced nutritional deficits in the young of several species of seabirds (reviewed in Kitaysky et al. 2003). In adult free-living birds, experimental food supplementation also reduced CORT secretion (Lancot et al. 2003, Clinchy et al. 2004). However, effects of food supplementation on CORT in adults were not consistent across the reproductive season (e.g. Lancot et al. 2003), probably reflecting temporal changes in the natural food availability and/or physiological transitions of birds between different stages of reproduction (Kitaysky et al. 1999b, Wingfield & Kitaysky 2002). Also, there is a possibility of synergistic effects of food-related stress with other ecological factors, such as predator and parasite pressures (e.g. Clinchy et al. 2004, Roauf et al. 2006), inclement weather (Wingfield et al. 1997), and changes in parental effort at different stages of a bird’s reproductive cycle (Kitaysky et al. 1999b).

The field endocrinology approach potentially offers an opportunity to discriminate between short-term and chronic effects of food stress on free-living individuals. Baseline CORT concentrations (measured in the blood of undisturbed birds immediately after capture) increase quickly (within hours or days) in response to a food shortage (Lynn et al. 2003, Edwards 2004). During prolonged food shortages, when animals are exposed to chronically elevated baseline CORT secretion, their adrenal function is enhanced (Akana et al. 1992, Dallman et al. 2004), which results in higher maximum CORT production in response to a standardized stressor (capture, handling, and restraint, sensu Wingfield 1994, hereafter called ‘acute stress’). Thus, acute stress-induced CORT levels may provide an integrative measure of an individual’s nutritional history over longer time periods (wk) than baseline CORT (d) (Kitaysky et al. 2001a, 2005). In seabirds, acute stress-induced CORT is expected to correspond to food availability and baseline CORT measures taken several weeks earlier (Kitaysky et al. 2001a).

The goals of the present study were (1) to measure physiological stress and to identify its causes in breeding seabirds and (2) to establish a link between stress during reproduction and the patterns of fecundity and persistence of individuals in a population. The specific objectives were (a) to assess variability in CORT secretion between colonies (with declining versus increasing numerical trajectories during the past 2 decades) within a single population, among years (1996 to 2001) and reproductive stages (egg-laying, incubation, and chick-rearing), and in relation to gender of individuals; (b) to directly measure intra-seasonal and inter-annual changes of food abundance in the vicinities of colonies (1996 to 1999); and (c) to determine colony-wide reproductive performances at the various stages of reproduction (1996 to 2001) and persistence of individuals in a colony (1997 to 2001).

**MATERIALS AND METHODS**

We conducted the present study at 2 major seabird colonies in Cook Inlet, Gulf of Alaska, from May to September in 1996 to 2001. The colonies are about 100 km apart and are situated in oceanographically distinct habitats (Robards et al. 1999, 2002). Duck Island (west side of Cook Inlet; 60° 09’ N, 152° 34’ W) is
surrounded by weakly stratified, relatively warm estuarine waters, whereas Gull Island (east side of Cook Inlet, 59°35’N, 151°19’W) is surrounded by colder, oceanic waters with warm surface layers that result from runoff (Robards et al. 1999). Common murres Uria aalge breeding on these colonies are morphologically and genetically indistinguishable (J. F. Piatt & V. Friesen unpubl. data; S. V. Drovetski, A. S. Kitaysky, J. F. Piatt unpubl.). Currently, common murres are much more numerous on Gull Island (4000 breeding pairs) compared to Duck Island (1200 breeding pairs). However, the numbers of birds breeding on these islands changed drastically over the past 3 decades—they steadily declined at Duck Island (−8.9% yr⁻¹) and increased at Gull Island (+9.1% yr⁻¹) (Piatt 2002). From 1998 to 2001, the survival estimates of adult murres were consistently lower at Duck Island (90.8%) than at Gull Island (94.0%) (Piatt 2004).

**Blood sample collection and CORT assays.** Birds were captured from their nesting sites using noose poles. In each year, birds were sampled during daylight hours every 2 wk from June to September (except that in 1996 birds were sampled only once on Gull Island at the incubation stage). Reproductive stages (egg-laying, incubation, and chick-rearing) and breeding status of birds were verified by the presence of a brood patch, egg, or chick at the capture site. For all birds (n = 523), initial blood samples were taken within 5 min of capture. It takes at least 3 min for levels of CORT to begin to rise in the blood in response to a stressor (Romero & Reed 2005) so this first sample provides a baseline measure of circulating CORT and does not reflect the stress induced by capture. Some birds (n = 276) were then held in breathable mesh bags, and additional blood samples were taken at 10, 30, and 50 min post-capture. Because the rate at which CORT levels rise can differ among individuals (e.g., Cockrem & Silverin 2002, Cockrem 2004), for each bird we chose the sampling point that yielded the highest levels of CORT; in all cases this was the 30 or 50 min sample. This parameter (maximum CORT level attained in response to a standardized capture, handling, and restraint stressor) reflects the birds’ ability to produce CORT. Approximately half of all birds were released after collection of the baseline sample; therefore, sample sizes are smaller for maximum CORT. All bleeds were taken from the brachial vein; blood samples were kept on ice until centrifugation to separate the plasma from the red blood cells. Plasma was drawn off red blood cells and kept frozen until assayed for corticosterone. While being held, all birds were banded with metal US Fish and Wildlife bands and a combination of colored plastic bands, which ensured that no individual was sampled twice and allowed us to monitor individual birds.

**Hormone assay.** Total corticosterone was measured using a radioimmunoassay. For each sample, 20 µl of plasma were equilibrated with 2000 cpm of tritiated corticosterone prior to extraction with 4.5 ml distilled dichloromethane. After extraction, percent tritiated hormone recovered from each individual sample (average hormone recovery was 95%) was used to correct final values. Samples were reconstituted in PBS-G-buffer (PBS supplemented with gelatin) and combined with antibody and radiolabel in a radioimmunoassay. Dextran-coated charcoal was used to separate antibody-bound hormone from unbound hormone. Inter- and intra-assay variations were <4% and 2%, respectively.

**Beach seines.** We conducted the concurrent measurements of food abundance and CORT on a regular schedule (approximately every 2 wk), which allowed us to examine the relationship between CORT levels and food abundances during 3 different time intervals: within the current 2 wk, within the current month, and during the previous month (i.e. CORT measurements lagged behind food measurement with a period of 1 mo). We used beach seines to measure forage fish abundance in waters adjacent to breeding colonies where birds foraged. Beach seines effectively and non-selectively sample shallow, inshore waters with smooth bottoms (Cailliet et al. 1986). Samples were collected about every 2 wk during May through September, 1996 to 1999 (detailed methods are described in Robards et al. 1999 and Abookire et al. 2000). Nets were deployed from a small boat and set parallel to shore, about 25 m from the beach. Seine catch per unit effort (CPUE) mirrored patterns of fish abundance offshore in mid-water trawls and hydro-acoustic surveys (Robards et al. 1999, Abookire et al. 2000, Piatt 2002). CPUE was calculated as the total catch of all fish per seine averaged by site and day. Catches consisted of sand lance Ammodytes hexapterus Pallas, Pacific herring Clupea harengus pallasii, Salmonidae, Osmeridae, and Gadidae. The body length of forage fishes sampled in beach seines in general matched those of fishes captured by birds (Piatt 2002). These fish species comprised >90% of the seabirds’ diets during this study (Kitaysky et al. 1999a, Piatt 2002). CPUE data were log(x + 1) transformed to meet assumptions required for parametric statistical procedures.

**Reproductive performance.** We examined relationships between CORT levels and estimates of reproductive performance. Timing of breeding and reproductive performance were measured at all colonies from 1996 to 2001. Reproductive parameters were assessed using study plots and standardized methods (Birkhead & Nettleship 1982). Breeding parameters were calculated as the mean of plot means. We monitored 5 and 9 plots containing an average of 20 and 13 nest sites (sites with eggs, range 8 to 40) at Gull and Duck
Islands, respectively. Plots were checked every 1 to 2 d at Gull and every 3 d at Duck Island. We observed the status of nests from observation points on each island using binoculars at close range from hides. We quantified timing of breeding as the mean of plot medians for lay date. We calculated hatching success as the number of eggs laid that hatched, fledging success as the number of chicks fledged per egg laid, and reproductive success as the number of chicks fledged per nest. Chicks were considered to have fledged successfully if they disappeared from the nest site ≥15 d after hatching because 15 d is the minimum nest departure age for common murre chicks and we never observed mortality in older chicks.

**Survival study.** We examined the relationship between baseline CORT levels in individuals during a given reproductive season and the presence of those individuals at the colony during subsequent reproductive seasons. We distinguished ‘persistence of individuals in a colony’ (hereafter called ‘persistence’) from survival, because we did not survey all colonies in the region and thus were not able to distinguish between mortality and emigration if a bird was subsequently absent from the colony at which it was banded. Furthermore, at least 1 individual banded as a breeder at Duck Island was observed on Gull Island during subsequent years, confirming the possibility for movement of breeding birds between the focal colonies. To measure persistence of birds in a colony, we employed traditional methods. Specifically, we captured adult breeding birds (actively attending a nest site, egg, or chick) and marked them using a numbered stainless steel band and a unique combination of colored plastic leg bands. We collected blood from captured individuals for CORT and genetic analysis of gender, and took measurements of their body mass and skeletal elements. In subsequent years, we conducted re-sighting by intense daily searches throughout the colony for about 6 wk yr⁻¹, starting before egg-laying and continuing until re-sighting curves reached a plateau, indicating that all marked birds had been encountered (Hatch et al. 1993). Several years of re-sighting effort are recommended to ensure re-sighting of individuals that have been present in a colony but may be missed if re-sighting effort is limited to only 1 or 2 subsequent years (Lebrerton et al. 1992). With 5 yr of effort (including 4 yr of banding followed by 4 yr of re-sighting), and using only individuals with complete re-sighting histories, we were able to distinguish among 3 scenarios of a bird’s persistence in a colony in relation to its baseline CORT during that current reproductive season. Specifically, individuals were either: (1) re-sighted at the colony in the following year (hereafter ‘re-sighted’); (2) skipped the following year, but were re-sighted during 2 subsequent years (‘skipped’); or (3) were not re-sighted during the following season or during 2 subsequent years (‘disappeared’).

**Sex determination.** To identify bird gender, we extracted genomic DNA from blood samples following the salt-extraction protocol described in Medrano et al. (1990) and modified as in Sonsthagen et al. (2004). We amplified the DNA of 271 individuals using standard polymerase chain reaction (PCR) conditions with the P8/P2 primer set to determine the gender of each bird based on the chromo-helicase-binding domain (CHD) gene. Sex was assigned based on the absence (male: ZZ) or presence (female: ZW) of the band for the W chromosome. For quality control purposes, approximately 20% of samples was re-extracted and re-processed.

**Data analysis.** All analyses were conducted using the SYSTAT and STATISTICA statistical packages. Data were log-transformed to meet assumptions for normal distribution and homogeneity of variance. Statistical analyses consisted of the following steps.

**Measuring stress and identifying its causes:** First, to examine whether differences in stress are intrinsic to a colony (Duck vs. Gull Island) and/or to the reproductive stage (egg-laying, incubating, and/or chick-rearing), we used univariate conventional ANOVA, where CORT was a dependent variable, and colony, reproductive stage, and year with interaction terms were factors. Second, we used ANCOVA with factors identified as significant in the previous step, and food abundances during current 2 wk (F2W), current mo (FCM), and previous mo (FPM) as covariates. Separate models were run for baseline and maximum CORT levels, and the Bonferroni adjustment of probabilities for multiple comparisons was used. Third, we used the information-theoretic approach to identify suitable models for predicting stress (CORT) in adult murres (Burnham & Anderson 1998, Anderson et al. 2000). Specifically, we examined a relative contribution of colony, reproductive stage, year, gender, body mass, and F2W, FCM and FPM, based on ANOVA, multiple regression, and ANCOVA approximating models. We had not planned to use the information-theoretic approach when we initiated the data collection; thus, we had no a priori reasons to focus on any particular sets/combinations of parameters and included all combinations of factors in our approximating models. We tested 83 approximating models in these analyses (we did not test models that included combinations of all interactions among different factors). We calculated the Akaike information criterion (AIC) for each approximating model using the formula $AIC = N \ln (\sigma^2) + 2K$, where $N$ is sample size, $\sigma^2$ is residual sum of squares from a model divided by $N$, and $K$ is the number of parameters estimated in each...
model. We converted AIC to AICc values, which is recommended when sample sizes are small relative to the number of parameters being estimated (N/K ≤ 40; Burnham & Anderson 1998). The model with the lowest AICc was considered the best. Then we calculated the Akaike weights (Wi) for each model using the formula: \[ W_i = \frac{[\exp(-0.5 \times \Delta_i)/\sum_r[\exp(-0.5 \times \Delta_r)]]}{\Sigma_{r=1}^{R} \exp(-0.5 \times \Delta_r)} \]. These values indicate the approximate probabilities that model \( i \) is the best model in the set of models considered, and the relative likelihood that model \( i \) is better than model \( j \) is \( W_i/W_j \). We used multi-model inference and determined the set that includes the best model in 95% of all samples (Burnham & Anderson 1998).

Finally, to elucidate the importance of food abundance in determining CORT levels, we used linear regression analyses of means of the colony-specific CORT measured within the current 2 wk against mean food abundances measured either during the current 2 wk, current mo, or during a previous mo, whichever was included in the best fitting model according to the information-theoretic analyses, had a highest beta-weight within the best model, and was also identified as the best predicting variable in univariate analyses.

**Testing the relationships between CORT and reproductive performance:** We relied on estimates of reproductive performance derived on a colony-wide basis. Concurrent sampling of birds for determination of CORT and reproductive performance has always been done on different groups of birds to avoid the possible effects of capture on estimates of reproductive performance. Relationships between CORT levels and measures of the reproductive performance were not different between the colonies (parallelism of slope tests with p-values > 0.1). We used Spearman correlation analyses to examine relationships between means of colony/yr/stage-specific CORT and reproductive performance values for egg-laying, early incubation, late incubation, and chick-rearing stages. Because CORT levels at earlier stages could affect reproductive performance at later stages (i.e. CORT during incubation may affect fledging success, etc.), we tested all possible combinations of these parameters.

**Testing the relationships between CORT and persistence of birds in a colony:** A detailed comparison of adult murres’ survival between the Duck and Gull colonies has previously been conducted (Piatt 2004). The specific goal of this current study was to determine persistence of individuals in relation to the food-related stress they have experienced, and thus we used a sub-set of all available data that included only complete re-sighting histories for individuals that were sampled for CORT and were not otherwise manipulated (n = 372). We used a 2-way ANOVA with baseline CORT as a dependent variable and colony, fate of birds (re-sighted, skipped, and disappeared as defined above), and interaction between colony and fate as factors. For pair-wise comparisons of the means, we used Tukey honestly significant difference (HSD) post hoc tests.

**RESULTS**

**Baseline CORT levels**

**Univariate analysis**

There was a significant difference in baseline CORT among years (Fig. 1, see Table 1 for statistical analysis). There were no consistent differences between colonies and stages, rather seasonal dynamics differed among years, colonies, and stages (Table 1).

Overall, baseline CORT levels changed in opposite ways between colonies (significant Year × Colony interaction term); specifically, CORT decreased at Duck Island and increased at Gull Island during the study period (Fig. 1). Significant interaction terms between year, colony, and reproductive stage (Table 1) suggest that fluctuations in baseline CORT could not be attributed to the effects of colony and reproductive stage per se; rather, they reflected changes in ecological factors. ANCOVA with year as a factor and measurements of food abundance as covariates confirmed this. Specifically, the year effect became non-significant when controlled for variations in abundance of food (Table 1), whereas measurements of food abundance had highly significant effects on baseline CORT.

**Information-theoretic modeling**

The information-theoretic approach identified a model with food abundance as the best approximating model for baseline CORT (Table 2). Specifically, the model that included F2W (beta weight = −0.75), FCM (beta weight = 0.47), and FPM (beta weight = −0.28) was the top model. Other models including year, colony, stage, and sex of birds should probably not be discounted; however, Akaike weight for the top model was so much higher than that in the next best models (17 and 57 times better for Models 2 and 3, respectively), indicating that Model 1 was much better than Models 2 and 3. Overall, compared to other factors, F2W was by far the most important factor explaining variability in baseline CORT, as it was included as a factor in each of the top 10 models (Table 2). F2W alone explained 56% of the variability in baseline CORT (Fig. 2).
Maximum acute stress-induced CORT levels

Univariate analysis

There was a significant difference in maximum CORT among years and stages (Fig. 1, see Table 1 for statistical analysis). However, year and stage effects were not consistent between colonies. During the study period, inter-annual changes in maximum CORT levels differed between colonies—they remained relatively constant at Duck Island and increased at Gull Island (Fig. 1). Significant interaction terms between year, colony, and reproductive stage (Table 1) suggest that fluctuations in the adrenocortical stress response could not be attributed to the colony and reproductive stage effects per se.
rather, maximum CORT levels reflected changes in ecological factors. ANCOVA with year and stage as factors, and measurements of food abundance as covariates confirmed this suggestion. Specifically, the effect of stage disappeared and the effect of year diminished when those factors were controlled for variations in food abundance, whereas FPM had a highly significant effect on maximum CORT (Table 1).

Information-theoretic modeling

The information-theoretic approach identified a model with FPM (beta weight = −0.85), year (beta weight = 0.20), colony (beta weight = 0.54), and stage (beta weight = −0.44) as the best approximating model for maximum CORT (Table 2). The second best model also included sex (beta weight = −0.10) of the birds. Year and FPM were the most important among the top 10 models. FPM alone explained 31% of the variability in maximum CORT (Fig. 2).

Table 1. Uria aalge. Effects of year, colony, reproductive stage, and food abundance on baseline and maximum corticosterone (CORT) in common murres breeding on Duck Island and Gull Island from 1997 to 2001

<table>
<thead>
<tr>
<th>Factor</th>
<th>df effect</th>
<th>MS effect</th>
<th>df error</th>
<th>MS error</th>
<th>F</th>
<th>p</th>
<th>Bonferroni significance</th>
</tr>
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<tbody>
<tr>
<td><strong>Baseline CORT (ANOVA)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year</td>
<td>4</td>
<td>1.638</td>
<td>493</td>
<td>17.39</td>
<td>&lt;0.00001 Yes</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Colony</td>
<td>1</td>
<td>0.240</td>
<td>493</td>
<td>2.65</td>
<td>0.10428 No</td>
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<td></td>
</tr>
<tr>
<td>Stage</td>
<td>2</td>
<td>0.275</td>
<td>493</td>
<td>2.93</td>
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<td></td>
</tr>
<tr>
<td>Year × Colony</td>
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<td>1.831</td>
<td>493</td>
<td>19.45</td>
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<tr>
<td>Year × Stage</td>
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<td>493</td>
<td>4.43</td>
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<td></td>
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<tr>
<td>Colony × Stage</td>
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<td>493</td>
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<td>Colony × Year × Stage</td>
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<td>0.145</td>
<td>493</td>
<td>1.54</td>
<td>0.13903 No</td>
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<tr>
<td><strong>Baseline CORT—effect of food abundance (ANCOVA)</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Food (current 2 wk)</td>
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<td>5.064</td>
<td>295</td>
<td>53.15</td>
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<tr>
<td>Food (current mo)</td>
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<td>1.099</td>
<td>295</td>
<td>11.53</td>
<td>0.00077 Yes</td>
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<td></td>
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<tr>
<td>Food (previous mo)</td>
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<td>1.115</td>
<td>295</td>
<td>11.70</td>
<td>0.00071 Yes</td>
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<tr>
<td><strong>Maximum CORT (ANOVA)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year</td>
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<td>0.505</td>
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<td>13.60</td>
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<tr>
<td>Colony</td>
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<td>1.11</td>
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<tr>
<td>Stage</td>
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<td>24.07</td>
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<td>Year × Stage</td>
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<tr>
<td>Colony × Year × Stage</td>
<td>6</td>
<td>0.061</td>
<td>200</td>
<td>2.09</td>
<td>0.05658 No</td>
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<tr>
<td><strong>Maximum CORT—effect of food abundance (ANCOVA)</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Food (current 2 wk)</td>
<td>1</td>
<td>0.002</td>
<td>115</td>
<td>0.06</td>
<td>0.81509 No</td>
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<tr>
<td>Food (current mo)</td>
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<td>115</td>
<td>0.99</td>
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<tr>
<td>Food (previous mo)</td>
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<td>115</td>
<td>20.02</td>
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</table>

CORT and reproductive performance

Baseline CORT at the egg-laying and incubation stages was negatively correlated with hatching, fledging success, and overall productivity (Table 3). Baseline CORT at incubation was also positively correlated with phenology of egg-laying—in other words, baseline CORT was higher during years with relatively late egg-laying (Table 3). Baseline CORT at chick-rearing was not correlated with indices of reproductive performance. Maximum CORT levels at early and late incubation were negatively correlated with hatching and fledging success, and maximum CORT at late incubation was negatively correlated with overall productivity (Table 3). Maximum CORT values at egg-laying and chick-rearing were not correlated with indices of reproductive performance (Table 3). Maximum CORT was not correlated with phenology of egg-laying (Table 3).

Table 2. Uria aalge. Models of baseline and maximum levels of corticosterone (CORT) in common murres breeding on Duck and Gull Island colonies from 1997 to 1999, using theoretic-information criterion. Food abundance during: current 2 wk (F2W); current mo (FCM); previous mo (FPM). Ev. ratio: evidence ratio

<table>
<thead>
<tr>
<th>Variables</th>
<th>K*</th>
<th>ΔAICc*</th>
<th>SSE</th>
<th>W*</th>
<th>Ev. ratio</th>
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</thead>
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<td><strong>Baseline CORT (n = 271)</strong></td>
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<td></td>
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<td></td>
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<tr>
<td>F2W, FCM, FPM</td>
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<td>0.00</td>
<td>0.097</td>
<td>0.879</td>
<td>1.0</td>
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<tr>
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<td>0.052</td>
<td>17.0</td>
</tr>
<tr>
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<td>0.100</td>
<td>0.016</td>
<td>56.5</td>
</tr>
<tr>
<td>F2W, stage, sex</td>
<td>5</td>
<td>8.71</td>
<td>0.101</td>
<td>0.011</td>
<td>78.0</td>
</tr>
<tr>
<td>F2W, colony, stage</td>
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<td>8.75</td>
<td>0.101</td>
<td>0.011</td>
<td>79.3</td>
</tr>
<tr>
<td>F2W, FCM</td>
<td>4</td>
<td>9.61</td>
<td>0.102</td>
<td>0.007</td>
<td>122.2</td>
</tr>
<tr>
<td>F2W</td>
<td>3</td>
<td>10.10</td>
<td>0.103</td>
<td>0.006</td>
<td>156.4</td>
</tr>
<tr>
<td>F2W, FPM</td>
<td>4</td>
<td>10.75</td>
<td>0.102</td>
<td>0.004</td>
<td>216.3</td>
</tr>
<tr>
<td>F2W, year, colony, stage</td>
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<td>11.08</td>
<td>0.101</td>
<td>0.003</td>
<td>254.7</td>
</tr>
<tr>
<td>F2W, year, stage, sex</td>
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<td>11.17</td>
<td>0.101</td>
<td>0.003</td>
<td>266.3</td>
</tr>
<tr>
<td><strong>Maximum CORT (n = 110)</strong></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>FPM, year, colony, stage</td>
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<td>0.00</td>
<td>0.035</td>
<td>0.601</td>
<td>1.0</td>
</tr>
<tr>
<td>FPM, year, colony, stage, sex</td>
<td>7</td>
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<td>0.034</td>
<td>0.391</td>
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<td>FPM, year</td>
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<td>Year</td>
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<tr>
<td>Body mass, year</td>
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<td>19.41</td>
<td>0.043</td>
<td>0.000</td>
<td>16365.1</td>
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</table>

*Defined in ‘Data analysis’
The relationship between baseline levels of CORT and re-sighting of murres at the colonies was different between Duck and Gull colonies (colony × re-sighting interaction term \( F_{2, 366} = 5.53859, p = 0.004; \) Fig. 3). At Duck Island colony, baseline levels were significantly higher among birds that were not re-sighted during 3 consecutive reproductive seasons (disappeared) compared to birds that were re-sighted during a following reproductive season (Tukey post hoc \( p = 0.005 \)). CORT levels in birds that skipped the next season but were re-sighted during the following 2 seasons were not different from those in disappeared (\( p = 0.960 \)) or were re-sighted (\( p = 0.066 \)) at the declining Duck Island colony. There were no differences in baseline CORT among re-sighted, skipped, and disappeared birds at the increasing Gull Island colony (\( p > 0.267; \) Fig. 3).

**DISCUSSION**

Fluctuations in availability of food have long been hypothesized to play a major role in regulating seabird populations. In the present study we used a field endocrinology approach to measure stress, identify its causes, and to examine the hypothesized
link between food-related stress and population processes in the common murre *Uria aalge*. A long-term series of measurement of stress and food abundance allowed us to establish: (1) a direct link between changes in food abundance and stress status of individuals, (2) negative effects of food-related stress on fecundity, and (3) negative effects of food-related stress on persistence of individuals in a declining colony.

**CORT as a measure of food-related stress**

CORT is an important regulator of carbohydrate, lipid, and protein metabolism and thus is expected to play a role during nutritional limitations (reviewed in Sapolsky et al. 2000, Romero 2004). Consequently, several studies suggested that CORT may provide information on the stress status of individuals in relation to the abundance of their food (Kitaysky et al. 1999a, Romero & Wikelski 2000, Lacntot et al. 2003, Clinchy et al. 2004). However, the idea of using CORT as a direct measure of food availability in free-living animals was controversial (e.g. Lanctot et al. 2003). First, CORT production in birds may reflect population-specific parameters and/or endogenous changes in the physiology of individuals at different stages of their life cycle (i.e. Wingfield 1994, Romero et al. 1997, Kitaysky et al. 1999b, Romero 2002). Second, CORT may be released in response to a wide range of adverse environmental conditions (Wingfield 1994, Wingfield et al. 1997). It was also not well known whether elevated levels of CORT would only be associated with catastrophic events, such as famine (i.e. Romero & Wikelski 2000); CORT may also reflect moderate changes in food supplies.

In the current study we have addressed at least some of these concerns and present the first empirical evidence for CORT secretion as a quantitative link between changes in food abundance and stress status in free-living seabirds. Contrary to the first argument, a long-term series of data in our study revealed that secretion of CORT reflects changes in ecological conditions rather than changes that are specific for a particular colony or reproductive stage. We did not find a consistent effect of the colony across years (Fig. 1). Our results show clearly that baseline and acute stress-induced levels of CORT may change in all possible ways among stages (see Fig. 1). We conclude that studies of seasonal changes in the adrenocortical function might yield equivocal results if they are based on short time series that do not cover a full range of environmental conditions. This study calls for a revision of the conclusion regarding the intrinsic contribution of the reproductive stage as a driving force for changes in adrenal activity.

In contrast to the second argument, our results show that in breeding common murres the variability in CORT levels is largely explained by the variations in food supply (Fig. 2). Specifically, 2 different analytical approaches used in this study confirmed this: univariate analyses showed that colony and reproductive stage had no effect on CORT levels when these factors (with a potentially inherent effect on CORT secretion) were controlled for changes in food availability. The information-theoretic analyses also identified models that included measures of food abundance as the best approximating models for CORT. We are not arguing that other factors do not contribute to changes in CORT in seabirds. It might well be that sickness, parasite infestations, and agonistic social interactions contribute greatly to variation in CORT secretion in seabirds. However, in our study, we sampled only actively breeding individuals; in other words, our sampling was ‘biased’ toward healthy individuals because all others that were sick, heavily parasitized, or had not accumulated sufficient resources to participate in reproduction were not sampled. Furthermore, our sampling was limited to ‘socially established’ individuals that have succeeded in securing a nest site, mate, egg, or chick, and others that had failed at those stages were also not sampled. Our selective sampling may explain why the variations in food were by far the most important factors determining CORT secretion in common murres in this study. We would argue that the selection criteria used in our study are not only appropriate, but are strictly required to examine a functional link between food-related stress and population processes in seabirds. We would also argue that, although changes in food abundance explained a large portion of variability in CORT, our assessment of food availability was probably far from the ideal. Specifically, although it is arguably the best practical way to measure temporal and spatial changes in food resources in marine environments, beach seine trawling has provided us with the information on food abundance only. Yet, food availability is the only true measure of foraging conditions in animals, and it may vary depending on distribution and density of patches, distance from a breeding colony, energetic density of prey, etc. Thus, food abundance as we measured it was still only a proxy for food availability, and a significant effect of year on CORT levels (at least in case of the maximum CORT) may easily reflect this imperfection in our measurements of food resources. If food availability rather than food abundance could be measured in marine environments, we expect an even higher proportion of variability in CORT would have been explained by variations in food resources.

The field endocrinology approach offers the possibility to discriminate between short- and long-term changes in food resources, and provides a measure of recovery from food-related stress in free-living indi-
individuals. Baseline CORT increases quickly (within hours or days) in response to experimentally induced food shortages (Kitaysky et al. 2001a, Lynn et al. 2003, Edwards 2004). Supporting this, concurrent measurements of CORT and food abundance in this study identified that baseline CORT is directly correlated with changes in current food abundance. On the other hand, the adrenocortical stress response integrates changes in food abundance over longer time periods. During prolonged food shortages, when animals are exposed to chronically elevated baseline CORT secretion, their adrenal function is enhanced (Akana et al. 1992, Dallman et al. 2004), which results in higher maximum CORT production in response to a standardized stressor (Kitaysky et al. 2001a). Accordingly, acute stress-induced CORT levels of common murres in the present study were best explained by changes in food abundance during the previous month. Thus, acute stress-induced CORT levels provide an integrative measure of an individual’s nutritional history over longer time periods (wk) than baseline CORT (d). In a parallel study of free-living adult black-legged kittiwakes, we found that baseline CORT was also directly related to changes in food abundance during the current 2 wk, whereas their adrenocortical stress response was best correlated with changes in baseline CORT or food abundance during the current month (A. S. Kitaysky, J. F. Piatt unpubl. data). Similar results were also obtained for juvenile kittiwakes and common murres—their adrenocortical stress response reflected experimentally controlled nutritional history during a 3 to 4 wk period (Kitaysky et al. 1999a, 2001a). Whether the adrenocortical stress response is related to the severity of food shortages or the recovery from nutritional stress is allometrically related to body size of animals is not currently known. Thus, although it is clear that recent past nutritional history of birds at large defines the magnitude of the adrenocortical response to acute stressors, at least in the species of seabirds we have examined, future controlled experiments should examine the possibility that the time required to recover from food shortages depends on an animal’s body size.

To conclude, multiple controlled experiments and observations of adrenal function in wild birds suggested that CORT secretion may be used to assess food stress in seabirds. Results obtained in this current study provide unequivocal evidence for a direct quantitative relationship between natural variability in food and the adrenocortical function in wild seabirds. We conclude that with careful sampling criteria, CORT can be used as a reliable measure of food-related stress and to gauge relative food availability in free-living seabirds. CORT can be used as an ecological indicator, as it is relatively easy to measure, not invasive, and responsive to food shortages in a predictable manner.

It is also very important that we can measure CORT as frequently as desired, unlike other ‘remote’ processes like food availability.

**Food-related stress affects fecundity**

Although corticosterone production may reflect the intensity of a stressor, the question remained whether naturally occurring levels of CORT are relevant to reproduction of wild animals (i.e. Lanctot et al. 2003, Lormee et al. 2003). We found a persistent negative relationship between increased CORT secretion and fecundity. Because we were able to identify the changes in food abundance as a major factor affecting CORT, this current study provides direct support for the hypothesis that food-related stress during reproduction can contribute to decreased fecundity of seabirds. Specifically, we consistently found negative relationships between CORT and reproductive performance at various stages of reproduction, both within and between colonies. This relationship may be causal. CORT is involved in the regulation of body maintenance processes, in part by modifying the behavior of individuals in accordance with ecological and life-history events (Wingfield & Kitaysky 2002). In particular, an increase in baseline CORT in parent seabirds changes the allocation of resources away from reproductive processes (by decreasing parental care) and towards body maintenance (by increasing foraging; Kitaysky et al. 2001b). Accordingly, in this study, baseline CORT was a reliable predictor of performance at the current stage (except at chick-rearing). Baseline CORT was a better predictor of reproductive performance compared to maximum CORT. According to correlation analyses, relationships between baseline CORT and reproductive performance were significant in 11 out of 16 possible combinations, while maximum CORT was significant only in 5 out of 16 possible combinations (Table 3). It is not surprising, however, because the effects of CORT on fecundity are expressed via behavioral modifications; and increases in baseline CORT have been shown to induce behavioral changes, whereas maximum CORT represents only the bird’s capacity for stronger physiological and behavioral responses to environmental perturbations. Whether this potential would be realized or not depends on current environmental conditions.

**Food-related stress affects persistence of individuals in a colony**

It is not well understood whether or not food is a major cause of changes in adult seabird survival...
(Aebischer & Coulson 1990, Sandvik et al. 2005). Furthermore, to establish an effect of food-related stress during reproduction on persistence of adults in a population, one should be able to determine the relative contribution of factors affecting survival of adults during different stages of their life (i.e. during reproductive or post-reproductive stages), which is difficult (Fredericksen et al. 2004). This is of critical importance, however, as effects of stress during reproduction may not manifest for a prolonged period after a stressful event has already passed (Hunt & Byrd 1999, Kitaysky et al. 2001b, Golet et al. 2004).

Several studies have shown a negative relationship between endogenous CORT and survival of individuals (Romero & Wikelski 2000, Brown et al. 2005). During El Niño events, increased adrenocortical function in marine iguanas was negatively correlated with their subsequent survival (Romero & Wikelski 2000). In this case, an El Niño-induced famine was most likely a causal factor inducing increased CORT secretion and survival. However, El Niño may be characterized as a catastrophic event, and whether a relationship between CORT and survival would be observed under less drastic declines in foraging conditions remains to be shown. In another well-studied system, the cliff swallow, higher CORT secretion was related to higher mortality of individuals (Brown et al. 2005). At least in some cases, increased CORT secretion in swallows could be attributed to a decrease in food availability and/or to metabolic challenges induced by heavy parasite loads in individuals (Raouf et al. 2006). However, because food abundance was not quantified in this system, the relative contribution of various factors (i.e. food-related stress and parasite infestation) to survival of adult swallows has not been established.

We found that persistence of individuals in a declining colony is driven by food-related stress during the reproductive period (Fig. 3). Specifically, individuals that disappeared from this colony had higher levels of CORT compared to individuals that were re-sighted (Fig. 3). This result supports the hypothesis that population processes and the main factor contributing to population dynamics in seabirds—adult persistence in a colony—are constrained by food resources. The results of re-sighting at a declining colony may be interpreted in 2 ways: (1) food stress and/or elevated CORT is detrimental to the survival of affected individuals and murres that disappeared from the colony; (2) food stress and/or elevated CORT induced birds to skip reproduction or relocate. In this second case, CORT may be functioning as an anti-stress mechanism, allowing long-lived birds to avoid being stressed by skipping reproduction or permanently leaving the food-poor colony (Wingfield & Kitaysky 2002). Either way, the disappearance of breeders from the colony was associated with nutritional stress during reproduction.

We also found that persistence of individuals in an increasing colony (Gull Island) is independent of foraging conditions during the reproductive season. These contrasting results for colonies with opposite numerical trends might be explained by several mutually non-exclusive mechanisms. First of all, it is possible that common murres from the focal colonies over-winter in different regions and are exposed to different environmental conditions. Although we cannot rule out this possibility, it is highly unlikely because of a close physical proximity of the colonies and the absence of population differentiation between them. Second, there is a possibility that murres breeding at a declining colony are older individuals compared to those breeding at an increasing colony. Specifically, analyses of survival and recruitment of common murres in Cook Inlet indicate that during the last 2 decades there was virtually no recruitment of young into the colony at Duck Island, in contrast to high recruitment and immigration into the Gull Island colony (Piatt 2004, S. V. Drovettski, A. S. Kitaysky, J. F. Piatt unpubl.). A senescent decline in survival of common murres has been previously demonstrated (Crespin et al. 2006) and, in combination with the results of this current study, it may suggest that nutritional stress during reproduction has a stronger effect on senescent individuals (breeding at Duck Island) compared to on young individuals (breeding at Gull Island). However, existing evidence argues against this hypothesis. Crespin et al. (2006) showed that senescence affects both survival and reproduction in the common murre. Thus, survival and breeding success of ageing birds at Duck Island are expected to be lower than at Gull Island. However, although survival probabilities were consistently lower at Duck Island, the declining colony (Piatt 2004), reproductive performance of murres did not differ between Gull and Duck colonies (Piatt 2002). Furthermore, because food abundance was lower in the vicinity of Duck Island compared to Gull Island (at least from 1996 to 1999; Piatt 2002), murres breeding there have performed better than expected compared to birds breeding at the food-rich Gull Island colony (Piatt 2002). This conflicting evidence for a possible differential effect of food limitations on senescent versus young individuals requires further examination. Finally, common murres breeding at Duck Island could be higher quality and/or more experienced individuals than those breeding at Gull Island. Recent studies of seabirds suggest substantial heterogeneity in quality of individuals breeding at the same colonies (e.g. Cam et al. 1998, 2002). Considering the almost exponential increase in numbers of common murres at Gull Island and the steady decline at Duck Island, it is plausible that het-
erogeneity in quality of individuals is higher at Gull Island compared to Duck Island. Factors affecting adult survival probably consist of predictable/unavoidable (e.g. climate-driven changes in food resources) and unpredictable/random (e.g. collision with a rock) elements. Thus, the persistence of high-quality experienced breeders at Duck Island is mostly a result of unavoidable factors (food limitations), whereas random effects prevail in determining the persistence of low-quality inexperienced breeders at the Gull Island colony. It is extremely important to be able to distinguish among the scenarios described above, as it would allow us to predict responses of colonies with differential numerical trajectories to future environmental perturbations. For instance, a colony of murres at Gull Island has increased from a few to 1000s of individuals during the last 3 decades, probably due to the sudden appearance of relatively unlimited food supplies resulting from climate-driven changes in the ecosystems of the Gulf of Alaska (Anderson & Piatt 1999).

Because of food-rich environments, birds of varying quality were able to reproduce successfully at this colony. If environmental conditions return to a prior state of the ecosystem, an unprecedented decline in numbers of breeding murres would be observed at this colony due to an increased proportion of inferior phenotypes. Whether individuals that would not be able to sustain breeding at the Gull Island colony would move somewhere else or die is not clear.

From 1996 to 1999, directly measured food abundance was higher in the vicinity of Gull Island compared to Duck Island (Piatt 2002). However, during the last 2 yr of observations (2000 and 2001), both measures of CORT tended to be higher in murres on Gull Island than on Duck Island (Fig. 1). This suggests that during our study we probably witnessed the beginning of a regime shift in the ecosystem of Cook Inlet. Thirty years ago, breeding murres were much more numerous on Duck Island as compared to Gull Island, probably reflecting former abundances of food in the vicinities of those colonies (Piatt & Anderson 1996). Based on changes in food availability (as gauged by CORT), we predict that again Gull Island is becoming a food-poor colony, whereas Duck Island is becoming a food-rich colony.

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Spatial patterns of recruitment in a demersal fish as revealed by seabird diet

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ABSTRACT: Understanding recruitment in demersal fish requires determination of larval survival and delivery to appropriate settling habitats. Sanddabs *Citharichthys* sp. are an abundant neritic fish of Central California, an area of persistent upwelling. ‘Upwelling shadows’ develop in the lee of coastal promontories, retain surface waters, and may promote spatial variation in fish settlement. To test this hypothesis, we studied the diet and foraging dimensions of a seabird (*Cepphus columba*) specializing in sanddab consumption at windward and leeward sites over a 6 yr period. We integrated the bird’s take of sanddab with information on upwelling intensity and variability and sanddab larval abundance based on net sampling. Seabird diet at both sub-colonies was variable, but dominated by Age 1 sanddabs. Sanddabs were more prevalent in the diet of guillemots at the leeward site, and diet was more variable at the windward site. Persistent upwelling led to regional increases in sanddab larval abundance which, in turn, resulted in enhanced recruitment to leeward waters, as reflected in seabird diet. Pulsed upwelling was related to apparent increased recruitment in windward waters. This study is one of the first to suggest that seabird diet can be used as an indicator of spatial variability in recruitment and settlement of demersal forage fish.

KEY WORDS: Pigeon guillemot · Sanddab · Diet · Larval abundance · Coastal promontory · Upwelling shadow · Relaxation · Demersal fish settlement

INTRODUCTION

Recruitment in open marine fish populations is dependent on larval survival and settlement (Caley et al. 1996, Levin 1996). For neritic species, settlement may be affected by spatial variability in oceanographic processes that affect the distribution of larvae as they reach settlement age (Jenkins & Black 1994, Wing et al. 1998). In eastern boundary current systems, upwelling promotes ocean productivity, but strong, persistent upwelling may advect ichthyoplankton away from suitable coastal habitats (Cury & Roy 1989). Recent research has shown that the effect of upwelling on advective processes depends, in part, on coastal topography; in particular, ‘upwelling shadows’ on the leeward sides of coastal promontories can act as retention areas even when upwelling is strong and persistent (Wing et al. 1995, 1998). Moreover, nutrients entrained within upwelling shadows facilitate primary and secondary productivity for weeks longer than in areas outside shadows (Graham & Largier 1997).

We tested the hypothesis that recruitment of a demersal fish in an upwelling system varies spatially, with recruitment greater in either windward or leeward habitats depending on the interplay of upwelling effects and coastal topography. While increased upwelling (i.e. more intense and/or more persistent) should increase regional productivity and hence survival of larvae in general, Ekman transport of these larvae could differ on the 2 sides of a coastal promontory (Fig. 1). In windward habitats, increased upwelling may lead to increased offshore advection, reduced recruitment and a reduced Age 1 population the following year. In leeward habitats, increased upwelling may result in an upwelling shadow that will retain larvae and their food. This, in turn, may lead to increased larval recruitment and an increased Age 1 population. Conversely, the Age 1 population should...
be increased at windward sites and reduced at leeward sites when prior-year upwelling weak and/or variable. Variable upwelling should result in more relaxation events, and thus, a reduction in net offshore transport at windward sites.

We tested this hypothesis by integrating regional upwelling indices with net samples of sanddab *Citharichthys* sp., larval abundance and diet of a nearshore seabird, the pigeon guillemot *Cepphus columba*, collected upstream and downstream from a coastal promontory. Traditional methods for estimating demersal fish recruitment involve trawl samples to estimate age-specific abundance (Caley et al. 1996). We used a similar approach, but substituted trawl samples with seabird diet, which provides a proxy to abundance of Age 1 individuals. This approach is based on research showing that seabirds can be used as reliable indicators of change in prey populations (Sunada et al. 1981, Cairns 1992, Hatch & Sanger 1992, Montevecchi & Myers 1995, 1996, Miller & Sydeman 2004, Abraham & Sydeman 2006). However, our approach is novel because we integrate the seabird data with net samples and use seabird diet to test hypotheses of fish settlement to local neritic habitats, a new application.

**MATERIALS AND METHODS**

**Study area, diet and foraging observations.** We studied sanddabs *Citharichthys* sp., birds *Cepphus columba* and upwelling at the Point Arguello Promontory, north of Point Conception, Central California (Fig. 2). We defined the promontory as extending from Point Michelle in the north to Sudden Ranch in the south. The coastal habitat here supports ~500 pairs of breeding pigeon guillemots (D. P. Robinette unpubl. data), with the birds nesting in rock crevices. Though guillemots typically take a diverse array of prey (Follett & Ainley 1976, Ewins 1993, Litzow et al. 2000), prey specialization has been observed at both the individual and colony level (Golet et al. 2000, Litzow et al. 2000). Specialization is an ideal trait for an indicator species if the predator does not switch to a single alternate prey in the absence of the dominant prey (Anderson & Gress 1984, Monaghan 1996). This is the case for guillemots at Point Arguello.

We obtained information on diet composition and foraging dimensions of guillemots at 2 sub-colonies,
1 windward and 1 leeward of the Point Arguello Promontory. Point Pedernales, our windward site, is located approximately 3 km northeast of Point Arguello (Fig. 2). Our leeward site was on the south side of Point Arguello. We made observations during the chick-rearing seasons at Point Pedernales from 2000 to 2002 and again from 2004 to 2005 (n = 132 h total) and at Point Arguello from 2001 to 2005 (n = 206 h total). During chick-rearing, adults return to breeding crevices with whole prey items in their bills. Adults typically land on the rocks outside crevices, allowing identification of prey type. We located 18 crevices at Point Pedernales and 34 at Point Arguello. Because not all crevices are active during a given year, the annual number of crevices used in our analyses ranged from 7 to 9 at Point Pedernales and from 10 to 25 at Point Arguello. We made observations with binoculars and a spotting scope from approximately 30 m. We identified prey to the lowest taxonomic level possible (usually family) and estimated prey size as a multiple of guillemot bill length. Over all years, we identified a total of 684 prey items at Point Pedernales (windward) and 1201 at Point Arguello (leeward). We used percent sanddab as our basic index of sanddab take by the birds. We calculated percent sanddab as the percent of total identified prey items that were sanddabs. To examine if guillemots take an alternate dominant prey in some years, we also calculated diet diversity using the Shannon-Wiener diversity index given in Brower et al. (1998):

\[
H' = -\sum p_i \log_{10} p_i
\]

where \( p_i \) is the proportion of total identified prey items from prey group \( i \). This index has a range of values from zero to \( \log(S) \), where \( S \) is the total number of species in the sample.

**Pigeon guillemot foraging directions.** Beginning in 2004, we recorded the directions foraging guillemots were leaving in and returning to Point Arguello; in 2005, we extended this effort to Point Pedernales. We made flight observations concurrently with diet observations. At each point, we divided our field of view into north, northwest, west, southwest and south. When birds left the colony, we recorded the direction the bird was last observed flying. For returning birds, we recorded the direction from which they came into view. We recorded a total of 149 departing and 183 returning flights in 2004 and 175 departing and 201 returning flights in 2005 at Point Arguello. We recorded a total of 378 departing and 229 returning flights at Point Pedernales in 2005.

**Sanddab larval abundance.** We estimated regional sanddab larval abundance using data from the California Cooperative Oceanic Fisheries Investigations (CalCOFI). CalCOFI surveys are conducted on a quarterly basis (winter, spring, summer and fall). We used data from bongo tows conducted at nearshore stations along CalCOFI Lines 77 and 80 (Fig. 2). Ohman & Smith (1995) have described the methods. Data were standardized by soaking time and provided as number of larvae \( m^{-2} \). Occasionally, 1 or 2 stations were missed during a particular quarterly survey. Additionally, differences among stations can differ by orders of magnitude. We therefore calculated the geometric mean of larval abundance across stations. We calculated geometric means by transect in order to control for transect effects during statistical analyses. Additionally, because sanddab spawning is triggered by temperature changes associated with upwelling and can continue past the upwelling season (Rackowski & Pikitch 1989), we calculated geometric means of larval abundance for 3 time periods based on CalCOFI surveys: (1) spring and summer, (2) fall and (3) spring, summer and fall.

**Upwelling indices.** The peak upwelling season along the Central California coast occurs from April through August (Hickey 1979). We estimated the intensity and variability of upwelling using monthly upwelling indices calculated for 36°N, 122°W by the Pacific Fisheries Environmental Laboratory (www.pfeg.noaa.gov). We calculated indices using the same time periods used for larval abundance. We used data from April through August for spring to summer larval abundance, September through November for fall, and April through November for spring, summer and fall. We estimated annual upwelling intensity by summing monthly values to create cumulative upwelling indices (CUI) for each time period. We also calculated period-specific estimates of upwelling variability by calculating the standard deviations of upwelling within a period.

**Statistical analyses.** We used tests of homogeneity based on the Pearson goodness-of-fit chi-squared statistic to determine if foraging directions varied by subcolony and year. We compared 2004 and 2005 at Point Arguello, as well as Point Arguello and Point Pedernales in 2005. To determine which upwelling variables influenced regional larval abundance and at which temporal scales these processes were working, we created predictive linear models with larval abundance measured at the 3 time periods as dependent variables and upwelling intensity and variability at the 3 time periods as independent variables. We used Mallows’ \( C_p \) criterion to determine the best model for each dependent variable (Mallow 1973). We put 2 limitations on model selection. First, the maximum number of independent variables used was 3 — the CalCOFI transect plus 2 upwelling variables. Second, we did not use upwelling variables containing fall values to predict the previous spring to summer larval abundance. The dependent variable (larval abundance for the respec-
tive time period) was log transformed in these analyses to meet assumptions of linear models (Nur et al. 1999). We present standardized regression coefficients (Kutner et al. 2005) to compare among models. Finally, we used the upwelling and larval abundance variables with the strongest association (as indicated by the standardized regression coefficient) in linear models relating these variables to proportion of sanddab in guillemot diet. Based on the mean guillemot bill length reported by Ewins (1993) and the age-class lengths of sanddabs reported by Rackowski & Pikitch (1989), we determined that guillemots in our study were taking Age 1 sanddabs. We therefore used a lagged approach in our models, relating upwelling and larval abundance in yr\(^2\) to diet in yr\(^{1+1}\). When modeling the effects of upwelling on guillemot diet, we controlled for larval abundance; when modeling the effects of larval abundance, we controlled for upwelling. Both models used logit-transformed percent sanddab and controlled for COFI transect impacts. We estimated separate slopes for windward and leeward sites for the respective variable of interest (larval abundance or upwelling) in a single model when a statistically significant difference between the slopes was detected. We used STATA 8.2 statistical software (STATA 2005) for all statistical analyses except for tests of homo-geneity, which were done by hand.

**RESULTS**

**Sanddab consumption by guillemots**

A total of 23 prey species and groups were taken (Tables 1 & 2). Sanddabs were the dominant prey at both sites in all years. Percent sanddab Citharichthys sp. was strongly negatively correlated with diet diversity at both sites, indicating guillemots Cepphus columba did not switch to a single alternate prey species in years when sanddabs were less available (windward: \(r = -0.900, p = 0.019\); leeward: \(r = -0.900, p = 0.019\)). Sanddab consumption at the leeward site was more consistent than at the windward site. Annual percent sanddab ranged from ~41 to 64% of the diet at the leeward site (Table 2) and from ~24 to 60% of the diet at the windward site (Table 1). The coefficient of variation (CV) for the windward site (38.24) was more than twice that of the leeward site (17.36). Overall, mean (±SE) annual percent sanddab was greater at the leeward site (50.28 ± 3.90, n = 5) than at the windward site (42.94 ± 3.74); the take of sanddab between the sites among years was not significantly correlated (\(r = -0.400, p = 0.300\)).

**Foraging directions**

There were among-year differences in the directions guillemots left and returned to Point Arguello (leaving: \(\chi^2 = 26.93, df = 4, p < 0.005\); returning: \(\chi^2 = 26.07, df = 4, p < 0.005\)). However, the majority of guillemots left and returned from the south and southwest in both years (Fig. 3). The most pronounced differences were that guillemots foraged more to the south in 2004 and more to the southwest in 2005. Guillemots from Point Pedernales mainly foraged to the north and northwest (Fig. 4). There were differences in foraging directions between Point Pedernales and Point Arguello (leaving: \(\chi^2 = 221.46, df = 4, p < 0.005\); returning: \(\chi^2 = 246.40, df = 4, p < 0.005\)). Together, these data suggest that guillemots from Arguello forage leeward, while guillemots from Pedernales forage windward of the promontory.

### Table 1. Cepphus columba. Diet composition (% total observations yr\(^{-1}\)) and diet diversity (\(H^\prime\), Shannon-Wiener index) of pigeon guillemots breeding at the Point Pedernales (windward) sub-colony in 2000 to 2002 and 2004 to 2005

<table>
<thead>
<tr>
<th>Prey taxon</th>
<th>2000</th>
<th>2001</th>
<th>2002</th>
<th>2004</th>
<th>2005</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sanddab (Citharichthys sp.)</td>
<td>23.73</td>
<td>57.50</td>
<td>29.11</td>
<td>60.42</td>
<td>43.95</td>
</tr>
<tr>
<td>Anchovy (Engraulis mordax)</td>
<td>0.00</td>
<td>1.25</td>
<td>0.00</td>
<td>2.08</td>
<td>3.24</td>
</tr>
<tr>
<td>Smelt (Family Osmeridae)</td>
<td>0.00</td>
<td>0.00</td>
<td>6.33</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Squid (Loligo sp.)</td>
<td>0.00</td>
<td>1.25</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Rockfish (Sebastes sp.)</td>
<td>1.69</td>
<td>0.00</td>
<td>5.70</td>
<td>0.00</td>
<td>4.42</td>
</tr>
<tr>
<td>Saury (Cololabis saira)</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>1.18</td>
</tr>
<tr>
<td>Octopus (Octopus sp.)</td>
<td>6.78</td>
<td>5.00</td>
<td>9.49</td>
<td>0.00</td>
<td>1.18</td>
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<tr>
<td>Sculpin (Family Cottidae)</td>
<td>15.25</td>
<td>7.50</td>
<td>17.09</td>
<td>14.58</td>
<td>2.95</td>
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<tr>
<td>Cuskel (Family Ophidiidae)</td>
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<td>0.00</td>
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<td>1.47</td>
</tr>
<tr>
<td>Kelpfish (Family Clinidae)</td>
<td>1.69</td>
<td>0.00</td>
<td>0.00</td>
<td>2.08</td>
<td>2.95</td>
</tr>
<tr>
<td>Greenling (Hexagrammos sp.)</td>
<td>0.00</td>
<td>1.25</td>
<td>1.27</td>
<td>0.00</td>
<td>3.24</td>
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<tr>
<td>Shrimp (Crangon sp.)</td>
<td>0.00</td>
<td>3.16</td>
<td>6.25</td>
<td>12.68</td>
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<tr>
<td>Blinky (Hypsoblennius sp.)</td>
<td>0.00</td>
<td>0.00</td>
<td>0.63</td>
<td>2.08</td>
<td>1.18</td>
</tr>
<tr>
<td>Lingcod (Ophidon elongatus)</td>
<td>1.69</td>
<td>2.50</td>
<td>6.33</td>
<td>0.00</td>
<td>0.29</td>
</tr>
<tr>
<td>Sardine (Sardinops sagax)</td>
<td>0.00</td>
<td>0.00</td>
<td>2.08</td>
<td>0.00</td>
<td>0.00</td>
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<tr>
<td>Midshipman (Porichthys sp.)</td>
<td>20.34</td>
<td>18.75</td>
<td>11.39</td>
<td>4.17</td>
<td>10.62</td>
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<tr>
<td>Surfperch (Family Embiotocidae)</td>
<td>0.00</td>
<td>1.25</td>
<td>1.27</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Gunnel (Family Pholididae)</td>
<td>3.39</td>
<td>1.25</td>
<td>1.27</td>
<td>4.17</td>
<td>2.65</td>
</tr>
<tr>
<td>Prickleback (Family Stichaeidae)</td>
<td>15.25</td>
<td>0.00</td>
<td>6.96</td>
<td>0.00</td>
<td>4.13</td>
</tr>
<tr>
<td>Sandcrab (Blepharipoda occidentalis)</td>
<td>5.08</td>
<td>1.25</td>
<td>0.00</td>
<td>0.00</td>
<td>2.06</td>
</tr>
<tr>
<td>Poacher (Family Agonidae)</td>
<td>1.69</td>
<td>1.25</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Combfish (Zaniolepis sp.)</td>
<td>3.39</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>1.47</td>
</tr>
</tbody>
</table>

| Diversity (\(H^\prime\)) | 0.90   | 0.63   | 0.93   | 0.62   | 0.89   |

| n     | 59     | 80     | 158    | 48     | 338    |

Overall, mean (±SE) percentage of sanddab was greater at the leeward site (50.28 ± 3.90, n = 5) than at the windward site (42.94 ± 3.74); the take of sanddab between the sites among years was not significantly correlated (\(r = -0.400, p = 0.300\)).
Spring to summer upwelling variability was the best predictor of regional larval abundance for all 3 time periods (Table 3). Fall upwelling variability was also a good predictor of fall larval abundance, and fall upwelling intensity predicted spring to fall larval abundance. Overall, the strongest relationship was between spring to summer upwelling variability and spring to fall larval abundance. Thus, upwelling variability during the spring to summer period appears to be driving regional larval abundance, and the effects of this variability last through fall. The relationship is negative, illustrating that fewer larvae are present when upwelling variability is greatest (Fig. 5).

There was a strong, significant relationship between the proportion of sanddab in the guillemot diet and the spring to summer upwelling variability when controlling for location and larval abundance (Table 4). Furthermore, the effects of upwelling differed between windward and leeward sites, with the tightest relationship and steepest slope occurring with windward diet (Fig. 6).
There was also a strong, significant relationship between guillemot diet and spring to fall larval abundance when controlling for location and upwelling variability (Table 5). The effects of larval abundance also differed between sites. Though the slopes for windward and leeward sites were similar, the strongest relationship by far was with leeward diet (Fig. 7). Thus, it appears that windward diet is most affected by variability in Ekman transport during the spring to summer of the previous year, while leeward diet is most affected by larval abundance in the spring to fall of the previous year.

**DISCUSSION**

Our results suggest that persistent upwelling is more important than upwelling intensity in determining regional sanddab *Citharichthys* sp. larval abundance. If upwelling, regardless of intensity, is short-lived, regional nutrient and phytoplankton concentrations will diminish quickly. Persistent upwelling, however, will have a prolonged impact on regional productivity and thus increase larval survival. Our results support this hypothesis in that more persistent (i.e. less variable) upwelling in our study led to increased regional larval abundance.

The benefits of an upwelling shadow are similar to those of persistent upwelling in that nutrient enrichment and primary productivity are prolonged. In essence, an upwelling shadow is a circulating body of water driven by upwelling-favorable winds (Graham & Largier 1997). The nutrients retained in this circulation provide for prolonged algal blooms, and thus, prolonged food availability for zooplankton. Though we
Table 4. *Citharichthys* sp. Effects of spring to summer upwelling variability on logit-transformed percent sanddab controlling for spring to fall larval abundance. Site-specific effects (differing between windward and leeward sites) are included. Note slopes for upwelling variability differ significantly between sites ($F_{1,5} = 48.67$, $p < 0.001$). Linear model: $F_{4,5} = 36.83$, $p < 0.001$, $R^2 = 0.967$

<table>
<thead>
<tr>
<th>Factor</th>
<th>Coefficient</th>
<th>SE</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>$-3.072$</td>
<td>0.434</td>
<td>$-7.08$</td>
<td>$0.001$</td>
</tr>
<tr>
<td>Larval abundance</td>
<td>0.144</td>
<td>0.017</td>
<td>8.28</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>Upwelling variability</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Windward site</td>
<td>0.069</td>
<td>0.006</td>
<td>11.27</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>Leeward site</td>
<td>0.031</td>
<td>0.006</td>
<td>5.13</td>
<td>0.004</td>
</tr>
</tbody>
</table>

Table 5. *Citharichthys* sp. Effects of spring to fall larval abundance on logit-transformed percent sanddab controlling for spring to summer upwelling variability. Site-specific effects (differing between windward and leeward sites) are included. Note slopes for larval abundance differ significantly between sites ($F_{1,5} = 12.22$, $p = 0.017$). Linear model: $F_{4,5} = 10.97$, $p = 0.011$, $R^2 = 0.898$

<table>
<thead>
<tr>
<th>Factor</th>
<th>Coefficient</th>
<th>SE</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>0.496</td>
<td>0.233</td>
<td>2.13</td>
<td>0.087</td>
</tr>
<tr>
<td>Upwelling variability</td>
<td>0.066</td>
<td>0.010</td>
<td>5.76</td>
<td>0.002</td>
</tr>
<tr>
<td>Larval abundance</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Windward site</td>
<td>0.112</td>
<td>0.032</td>
<td>3.47</td>
<td>0.018</td>
</tr>
<tr>
<td>Leeward site</td>
<td>0.224</td>
<td>0.037</td>
<td>6.00</td>
<td>0.002</td>
</tr>
</tbody>
</table>

Fig. 6. *Citharichthys* sp. Scatter plots of logit-transformed percent sanddab in the guillemot *Cepphus columba* diet versus spring to summer upwelling at the: (A) windward and (B) leeward sub-colonies. Values plotted are residuals from the linear model presented in Table 4.

Fig. 7. *Citharichthys* sp. Scatter plots of logit-transformed percent sanddab in the guillemot *Cepphus columba* diet versus spring to fall larval abundance at the: (A) windward and (B) leeward sub-colonies. Values plotted are residuals from the linear model presented in Table 5.
In conclusion, this is one of the first studies to use seabird diet as a proxy for recruitment in a demersal fish. We were successful in relating some aspects of diet to the oceanographic factors that likely have a mechanistic influence on sanddab populations on leeward and windward sides of coastal promontories in the lee of Point Arguello. Leeward diet during the following year. We expected an upwelling shadow in the lee of Point Arguello, to our knowledge one has never been documented. Trainer et al. (2000) observed a diatom bloom in the lee of Point Arguello that lasted for over 3 wk, suggesting the presence of a small, nearshore shadow.

Our results further support the idea of an upwelling shadow in the lee of Point Arguello. Leeward diet had the strongest relationship with prior-year larval abundance, suggesting larvae are not being transported offshore from leeward habitats. Though the relationship between leeward diet and prior-year upwelling variability was significant, it was weak. Thus, variable upwelling may contribute to increased sanddab in the leeward diet during the following year. We expected this relationship to be opposite, since upwelling shadows should be prolonged and more effective during persistent upwelling. However, our results suggest that the upwelling shadow is simply acting as a buffer, minimizing the direct effects of upwelling by maintaining nutrient levels (and thus larval survival) in the leeward area during periods of high variability. This would explain the lower variability in diet at the leeward site. Overall, it appears that the number of larvae fed into the shadow is more important in determining leeward sanddab recruitment than the upwelling event that created the shadow.

Conversely, upwelling variability was very important in determining windward diet, with increased upwelling variability leading to increased sanddab in the windward diet. When upwelling is variable, there are more relaxation events. Relaxation decreases the net offshore transport of larvae by allowing displaced larvae to drift back to nearshore habitats. This has been documented for larvae of other marine species (see Graham & Largier 1997). Sanddabs have a long (approximately 270 to 320 d) 5-stage larval cycle, with the earliest stages acting as passive drifters and the later stages capable of remaining nearshore (Sakuma & Larson 1995). Thus, hydrodynamics during the early larval stages are important in determining the alongshore distribution of settlement-age sanddabs. This is likely why spring to summer upwelling variability had the most impact on windward diet the following year. Sakuma & Larson (1995) and Sakuma & Ralston (1995) suggest that early-stage sanddab larvae reside on the offshore side of upwelling fronts. During upwelling events, the larval pool is pushed offshore over the mid-shelf region, where they are subject to further displacement—mid-shelf transport during the upwelling season is offshore and equatorward (Dever 2004, Ohashi & Wang 2004, Dong & Oey 2005).

Conversely, inner shelf transport appears to be very different from mid-shelf transport (Cudaback et al. 2005). In the absence of upwelling-favorable winds, transport over the inner shelf has an onshore tendency. Additionally, the inner shelf experiences much more poleward transport during relaxation than the midshelf, and transport is often poleward, even during upwelling. Thus, larvae that were displaced offshore and equatorward during upwelling can potentially be replaced through poleward transport during periods of relaxation. Cudaback et al. (2005) also noted that transport over the inner shelf responds much more consistently to relaxation than upwelling. We therefore suggest that pulses of relaxation (i.e. variable upwelling) are likely important for recruitment to windward areas and perhaps non-shadow areas in general.

Future research should verify the existence of an upwelling shadow in the lee of the Point Arguello Promontory through the use of advanced very high resolution radiometer (AVHRR) satellite imagery and the fine-scale mapping of surface currents. Additionally, more guillemot Cepphus columba sub-colonies should be studied in order to (1) create replicates of leeward and windward sites and (2) investigate how proximity to the apex of the promontory (i.e. Point Arguello) affects the relationships between sub-colony diet composition and larval abundance and upwelling dynamics. While guillemots at the Point Pedernales sub-colony had a strong tendency toward windward foraging, with very few trips in the leeward direction, foraging directions at the south Point Arguello sub-colony were more variable. Though the majority of the trips were in the leeward direction, there was a moderate number toward the west in 2005. Birds departing to the west can potentially forage on either side of the promontory. It is therefore possible that diet at Point Arguello is weakly influenced by windward recruitment. This may have distorted the potential correlation between diet at Arguello and upwelling variability. Preliminary data from a sub-colony on the immediate north side of Point Arguello also showed variable foraging directions, but with a tendency toward windward foraging. We propose adding this sub-colony as our windward replicate, in addition to a sub-colony located at Rocky Point (Fig. 2) as our leeward replicate. This will allow us to investigate whether sub-colonies further away from the apex show stronger correlations in support of our hypotheses. If a given sub-colony is highly dependent on a particular foraging habitat (e.g. windward versus leeward), it will be a better indicator of recruitment to that habitat than if it were influenced by recruitment patterns in both habitats.
this upwelling system. While our basic premise and methodology (using seabird diet to assess demersal fish availability) is not novel (Mills et al. 2007), relating diet composition to habitat associations and potential mechanistic determinants of recruitment is new. We suggest that the concept of seabirds as indicators of forage fish can be expanded to include spatial as well as temporal components.

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Seabird behavior as an indicator of food supplies: sensitivity across the breeding season

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ABSTRACT: We used empirical data on the time allocation of common murres Uria aalge in relation to measures of local prey density to examine whether adults provisioning chicks are more sensitive to changes in prey density than birds that are incubating eggs. We hypothesized that seasonal differences in food requirements of incubating and chick-rearing parents would affect the form of the relationship between time spent at the colony and local food density. We found that the relationship did differ between the incubation and chick-rearing period in 3 important ways: (1) there was a strong non-linear relationship between food density and colony attendance during chick-rearing and a weaker relationship during incubation; (2) incubating birds were able to maintain relatively constant rates of attendance over a wider range of food densities than chick-rearing birds and only reduced colony attendance under extremely poor feeding conditions, if at all; and (3) incubating birds spent more time attending nest sites at the colony than provisioning birds. These differences confirmed that chick-rearing parents are more sensitive to changes in food density than incubating parents, and that measurements of time allocation during the incubation period would have limited value as an indicator of ecosystem change.

KEY WORDS: Colony attendance · Prey density · Seabird · Uria aalge · Hydroacoustic surveys · Incubation · Provisioning · Chick-rearing

INTRODUCTION

Seabirds may be useful indicators of change in marine ecosystems when aspects of their biology or behavior respond in a predictable manner to changes in food availability (e.g. Durant et al. 2003, Frederiksen et al. 2004). The form of the relationship between a measurable behavioral or demographic parameter and local food supply largely determines the sensitivity and utility of that parameter as an indicator of marine ecosystem change (Cairns 1987). For example, the breeding success of several species of seabirds has been shown to be a non-linear function of food density (Philips et al. 1996, Suddaby & Ratcliffe 1997, Piatt & Harding 2007), with productivity linearly correlated with food over a limited range of poor to moderate food abundance, but plateauing and independent over a range of higher abundance.

Similarly, there is a non-linear relationship between food density and the amount of time common murres Uria aalge spend at the colony during the chick-rearing period (Harding et al. 2007). Breeding common murres have a fairly flexible time budget, with the non-brooding parent able to increase foraging time in exchange for time spent at the colony when food is scarce (Burger & Piatt 1990, Uttley et al. 1994, Zador & Piatt 1999). Conversely, more time can be spent at the colony when food is abundant and foraging time is minimal. This flexibility results in a relationship where colony attendance increases rapidly as prey density increases over a range of low to moderate food densities until attendance levels off to become independent of prey over a range of moderate to higher densities (Harding et al. 2007). This plateau in attendance presumably reflects a trade-off between the costs (e.g. adult predation risk) and benefits (e.g. defending nest
sites) of time spent at the colony (Cairns 1987, Jones et al. 2002, Davoren & Montecucchi 2003).

Time and energy demands associated with reproduction are generally thought to be a maximum during the chick-rearing period for altricial species (Ricklefs 1983), and parents may adjust their foraging time and behavior to cope with these increased demands (e.g. Jansen et al. 2002, Shaffer et al. 2003). For example, studies on the behavior of breeding murres have shown an increase in foraging effort and foraging rates, a decrease in time spent at the colony, alteration in diving behavior (e.g. dive interval), and a switching of prey species during the chick-rearing period (Gaston 1985, Croll et al. 1991, Zador & Piatt 1999, Benvenuti et al. 2002, Jones et al. 2002). Given this increased demand for food, we assumed that time-activity budgets of chick-rearing parents should be more sensitive to prey availability than incubating birds. To our knowledge, however, this assumption had never been tested.

In the present study we used empirical data on the parental time budgets of common murres to examine how time allocation changes with breeding status. We predicted that chick-rearing birds would decrease colony attendance at a higher threshold of food density than incubating parents. We defined this behavioral threshold as the level of food density below which there is a positive correlation between attendance and food density, and above which there is no such relationship. In order to ensure a broad range of food densities required to assess functional relationships, we designed a 5 yr study around 3 colonies with contrasting oceanographic conditions and an order of magnitude range in local food density (Abookire & Piatt 2005, Speckman et al. 2005). We used 15 colony-years of data gathered in this study to characterize the functional relationship between time spent at the colony and food density and contrast the relationship between incubation and chick-rearing periods. We discuss the implications of these results for the use of seabirds as indicators of change in the marine environment and make specific recommendations for monitoring programs.

MATERIALS AND METHODS

Study sites and background. This study was conducted during 5 consecutive seasons (1995 to 1999) at 3 common murre Uria aalge colonies in lower Cook Inlet, Alaska (Speckman et al. 2005, Piatt & Harding 2007), providing us with 15 colony-years of data. The colonies are separated from each other by about 100 km, and are in oceanographically distinct habitats (Speckman 2004). Chisik Island is adjacent to stratified, relatively warm estuarine waters with low primary productivity; Gull Island is adjacent to relatively cool, stratified and highly productive waters that are fed by cold currents from the south; and the Barren Islands are surrounded by mixed, cold oceanic waters that result from upwelling of Gulf of Alaska water as it enters Cook Inlet (Speckman et al. 2005). Common murres breeding at these colonies have shown contrasting population trends over the last 25 yr (Piatt & Anderson 1996, Zador & Piatt 1999).

By studying 3 colonies with order-of-magnitude differences in food availability in the surrounding waters (Abookire & Piatt 2005, Speckman et al. 2005), our study constituted a natural experiment to resolve the relationship between seabirds and their food supply (see Harding et al. 2007 for more details).

Local prey density. We measured local fish densities around each of 3 seabird colonies by conducting hydroacoustic surveys on a grid of transects arranged within a 50 km radius of each site (details are found in Speckman 2004, Speckman et al. 2005, Harding et al. 2007). Distances surveyed among areas were similar, averaging about 1100 linear km of transect for all areas combined in each year except for 1995 (750 km surveyed; Speckman 2004, J. F. Piatt unpubl. data). Hydroacoustic surveys were conducted during a 3 wk period in each year (1995: 10 to 23 August; 1996: 14 to 31 July; 1997: 19 July to 8 August; 1998: 21 July to 12 August; 1999: 25 July to 16 August), usually encompassing periods of late incubation and early chick rearing for common murres (overall colony/year mean date of hatch was 10 August; J. F. Piatt & A. B. Kettle unpubl. data). We assumed therefore that hydroacoustic biomass estimates reflect food densities during both incubation and chick-rearing.

Hydroacoustic data were collected with a single beam 120 kHz BioSonics DT4000 system with a 6° beam angle. Before each cruise, the acoustic system was calibrated using a 33.2 mm tungsten carbide sphere with expected target strength of –40.6 dB. To identify acoustic signals and measure the size of individual fish, we conducted 163 mid-water trawls (see Abookire & Piatt 2005, Speckman et al. 2005). Acoustic data were analyzed using SonarData Echoview software (Ver. 2.10.48) and integrated with a minimum threshold of –70 dB to obtain relative measures of acoustic biomass (S_A). These were converted to absolute estimates of fish density (fish m⁻³) by dividing S_A by σ (backscattering cross-sectional area of single prey) for species with the following known target strengths (TS): pollock TS = 21.1Log(L) – 70.5, herring TS = 202.0Log(L) – 67.6, and capelin TS = 28.4Log(L) – 81.8 (all from Gauthier & Horne 2004), sandlance TS = 20.0Log(L) – 80 (Thomas et al. 2002), and cod TS = 20.0Log(L) – 65 (Rose & Leggett 1988), which accounted for 99.2% of all fish caught. The proportion of catch,
expressed as catch per unit effort, standardized to the number captured per km trawled, was used to convert acoustic backscatter to species-specific fish density (g m$^{-3}$) (Speckman 2004). Geometric mean acoustic densities were calculated from transformed data as mean (log $x + 1$) values, and then transformed back to original density units (Johannesson & Mitson 1983).

**Parental behavior.** We measured parental time spent at the colony during the chick-rearing period in each of the 15 colony-years and during incubation in 14 colony-years (data not collected at the Barren Islands in 1995). Data were collected by direct observations of murres on Chisik Island and indirectly with a time-lapse video camera on Gull Island (see Zador & Piatt 1999). Murres at the Barren Islands were observed directly in 1995 and by time-lapse video from 1996 to 1999. Video resolution (5 frames s$^{-1}$ at the Barrens, 6 frames s$^{-1}$ at Gull Island) was sufficient to record all arrivals and departures of birds at the colony.

Birds at each colony were observed on a plot containing 7 to 12 breeding pairs of murres from 07:00 to 20:00 Alaska Daylight Time on 2 to 3 observation days during both the incubation and chick-rearing phases. We observed the same nest sites within each summer, although failed nests were replaced in later watches. Observation days were generally scheduled to sample the early, middle, and late parts of both the incubation and chick-rearing periods.

We noted each parent’s arrival and departure time at the colony. Attendance was measured in bird-minutes per hour. For example, if 1 incubating or brooding parent attended its nest for a full hour, and the off-duty partner attended for half of that hour, we calculated 90 bird-minutes of attendance for that hour. Fewer than 60 bird-minutes of attendance would mean that the egg or chick was left unattended for some period of time. Nest site was a sample unit, with mean colony attendance per nest calculated separately for the incubation and chick-rearing periods.

**Statistical analysis.** Our prediction—that below a certain threshold food density is positively related to colony attendance, whereas above this threshold there is no such relationship—mathematically implies a non-linear model of the relation between these 2 variables. This model, heuristically depicted by Cairns (1987), can be more precisely described quantitatively as a piecewise or broken-stick model (Toms & Lesperance 2003) that represents the joining of 2 segments, the first of which is represented by a quadratic equation and the second of which is a flat asymptote or plateau of no slope. We used a quadratic model, rather than a linear one, for the first segment to allow for a smooth transition to the plateau. Two alternatives to this non-linear model can be contemplated. One is a null model of no relation, which is essentially the plateau segment of the non-linear model. The other is a linear model, which is analogous to just the first segment of the non-linear model and implies that the range of observed food densities affects time spent at the colony.

We compared the fit of these 3 models (Table 1) to colony mean values of incubation and chick-rearing attendance data using the Akaike information criterion, adjusted for finite sample size (AICc), and for which the model with the lowest AICc best represents the data (Burnham & Anderson 2002). Each model was statistically represented with a least-squares regression model where the error sums of squares, sample size, and number of estimated parameters all influenced the AICc calculation (Burnham & Anderson 2002). For each model we also present an AICc weight, which reflects the relative likelihood of that model being the best fitting model among those considered and where all AICc weights within an analysis sum to 1. These AICc weights allowed us to employ model-averaging procedures, which are useful when competing models fit the data similarly (Burnham & Anderson 2002).

### Table 1. *Uria aalge.* Comparison of the relationship between food density and time spent at the colony during the incubation and chick-rearing periods. Three predicted relationships were tested by comparing the fit of colony-mean annual values to the models illustrated using the Akaike information criterion (AIC). The best fitting model for each predicted relationship appears in **bold.**

<table>
<thead>
<tr>
<th>Relationships</th>
<th>Predicted models evaluated</th>
<th>Values from non-linear relationships</th>
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<tbody>
<tr>
<td>Food density x-axis</td>
<td>Non-linear</td>
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<tr>
<td>Colony attendance y-axis</td>
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<tr>
<td>Incubation</td>
<td>ΔAICc value</td>
<td>1.32</td>
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<td></td>
<td>AICc weight</td>
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<td>r²</td>
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<tr>
<td>Chick-rearing</td>
<td>ΔAICc value</td>
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<td></td>
<td>AICc weight</td>
<td>0.65</td>
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<tr>
<td></td>
<td>r²</td>
<td>0.71</td>
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</tbody>
</table>
RESULTS

Local food density

Mean prey density varied among the 15 colony-years (mean = 0.0353 g m$^{-3}$ ± 0.006 SE, CV = 0.69). Overall mean prey density (1995 to 1999) differed significantly among the 3 colonies (ANOVA: $F_{2,12} = 5.91, p = 0.016$), with food density at Gull Island usually higher than that at either Chisik Island or the Barren Islands (Tukey multiple comparison test: $p < 0.05$; Chisik mean = 0.0138 g m$^{-3}$ ± 0.002 SE; Barren mean = 0.0383 g m$^{-3}$ ± 0.008 SE; Gull mean = 0.0540 g m$^{-3}$ ± 0.012 SE).

Functional relationships

There was a weak relationship between time spent at the colony during incubation and food density, and, overall, the null model best fit the data. However, the model-averaged depiction of the relationship between food density and attendance has a semblance of non-linearity (Fig. 1). Birds actually maintained a fairly constant level of colony attendance over a broad range of food densities (null relationship) and reduced the time spent at the colony only when food reached the extreme lower range of densities measured in this study (Fig. 1). When examining parameter estimates from this poorer fitting non-linear model ($\Delta$AICc = 1.32), the threshold of 0.0334 g m$^{-3}$ food density is lower than the threshold observed during chick-rearing. Above this threshold, birds maintained attendance at a rate of 75.20 bird-minutes h$^{-1}$ over a broad range of higher densities. This equates to 4 h spent at the nest site by the non-incubating bird in a 16 h day.

In contrast, time spent at the colony during chick-rearing varied non-linearly with food availability (Table 1, Fig. 1). Overall, the non-linear model best fit the chick-rearing data ($\Delta$AICc > 1.0 for competing models). Time spent at the colony increased linearly with food over a poor to moderate range of prey densities, but was largely independent of food density above 0.058 g m$^{-3}$, the estimated threshold from this best-fitting model. This threshold corresponded to an asymptotic attendance rate of 72.13 bird-minutes h$^{-1}$ over a wide range of moderate to high food densities (in contrast to 75.20 bird-minutes h$^{-1}$ during incubation), suggesting that the non-brooding parent would have to spend 12 min h$^{-1}$ at the nest site, an equivalent of ca. 3 h of colony time in a 16 h day. The off-duty parent therefore spends ca. 1 h (in a 16 h day) less time at the colony over moderate to good feeding conditions than incubating parents.

DISCUSSION

The relationship between colony attendance of *Uria aalge* and local food density differed between the incubation and chick-rearing period in 3 important ways: (1) there was a strong non-linear relationship between food density and colony attendance during chick-rearing and a weaker relationship during incubation; (2) incubating birds were able to maintain relatively constant rates of attendance over a wider range of food densities than chick-rearing birds, and only reduced colony attendance under extremely poor feeding conditions, if at all; and (3) incubating birds spent more time attending nest sites at the colony than provisioning birds. The first 2 differences indicate that chick-rearing parents are more sensitive indicators of food abundance than incubating parents, and further suggest that measurement of time allocation during the incubation period will have limited value as an indicator of ecosystem change. We assume that incubating birds were able to balance social requirements of time spent at the colony with energy demands at a lower threshold of food density than parents provisioning chicks.
The decrease in time spent at the colony during chick-rearing most likely reflects an increase in time spent foraging. Provisioning parents must increase foraging effort in order to provide an average of 4 daily meals to their chick (Harris & Wanless 1988, Burger & Piatt 1990) and also to satisfy the resulting increase in their own energy requirements (Gaston 1985, Benvenuti et al. 2002). Alternatively, the lower colony attendance during chick-rearing could be explained by reduced benefits of time spent at the colony. This seems unlikely, however, because the number of immature and non-breeding murres at a colony increases during late chick-rearing (Gaston & Nettleship 1982, Harris et al. 1986), and the importance of nest-site defense is therefore presumably high.

Knowledge of the shape or form of functional relationships is essential for interpreting species-specific responses to a changing environment. Behavioral or demographic parameters can provide a useful indication of environmental change only if we can predict the range of food availability to which they respond. It is also important to determine the optimal time of the breeding season for monitoring indicator parameters. Functional relationships are usually non-linear (Holling 1959, Hassel & May 1974), and therefore most measures of foraging effort only reflect a change in food availability when densities are low and food is limiting. Chick-rearing birds have higher food requirements than incubating birds and therefore broaden the range over which food density is related to colony attendance. We suspect that other behavioral parameters that reflect food acquisition may also respond to a broader range of food densities during the chick-rearing period.

Direct measures of foraging effort using activity recorders or telemetry (e.g. Benvenuti et al. 2002, Falk et al. 2002) may provide a more accurate index of local food abundance than observations of colony attendance (Cairns 1987, Monaghan et al. 1994), but we observed a strong correlation between chick-rearing colony attendance and food density over a relatively wide range of low to moderate prey densities. Furthermore, methods for collecting data on time budgets are non-invasive, relatively inexpensive, and straightforward. This means they would be relatively easy to incorporate into long-term monitoring programs that use integrated approaches to detect change in the marine environment (e.g. Hare & Mantua 2000, Golet et al. 2004).

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LITERATURE CITED


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*Editorial responsibility: Howard Browman (Associate Editor-in-Chief), Storebø, Norway*
INTRODUCTION

Seabirds comprise one of the most numerous and highly visible components of coastal marine environments worldwide. Because of their ubiquity, range of life-history strategies, relative ease of access while at breeding locations, and collective breadth of diet, measures of seabird diet, growth, demography, abundance, and diversity have variously been proposed as indicators of environmental quality (Furness & Greenwood 1993, Furness & Camphuysen 1997). Ideally, comprehensive, long-term monitoring programs—both at-sea and on-colony—would return demographic and ecological indicators at time and space scales relevant to the birds as well as the underlying forcing factors inherent in any regional ecosystem. Practically, this is too expensive, with the result that worldwide only a handful of colony sites have long-term monitoring programs, and even fewer long-term at-sea programs exist.
One potential solution is to involve citizen volunteers in data collection. Beached bird surveys, because they can be built around standardized protocols and independently verifiable data (i.e. carcass identifications), offer such an opportunity. Worldwide, beached bird survey data have been used to provide data on oiling rates (Wiese & Robertson 2004), to detect changes in bycatch of fisheries (Forney et al. 2001), and to indicate mortality events associated with biotoxins (Scholin et al. 2000). When performed by trained volunteers, beached bird surveys can yield high quality data over a geographic scale not attainable in any other way.

Changes in the rate at which seabirds are beached, aside from human-caused events (e.g. oil spills), are a complex function of bio-physical coupling in the coastal marine environment. At regional scales, the seasonal pattern of upwelling influences the distribution, abundance, and quality of prey (Roemmich & McGowan 1995, Anderson & Piatt 1999), and thus of seabird predators both live (Veit et al. 1996) and dead (Granadeiro et al. 1997). Stressful situations, including episodic failures of upwelling (e.g. El Niño events) as well as chronic changes in upwelling strength (e.g. regime shifts), can affect both the relative presence of live birds as well as their mortality, and thus their beaching rates (Bayer et al. 1991, Wilson 1991). At local scales, storm events, particularly in winter, are known to cause mortality spikes in marine bird populations, commonly referred to as winterkill (Schreiber 2002, Newton 2006). A combination of wind, wave, and thermal stress associated with storm events causes birds to exert more energy to survive at the same time that local food sources may become more difficult to find (Finney et al. 1999). Finally, when marine birds die at sea, they become surface drifters, influenced by both surface currents and local winds (Granadeiro & Silva 1993, Flint & Fowler 1998, Wiese 2003).

Study system

The California Current System (CCS) is an eastern boundary current system that extends from Vancouver Island to Baja California and is home to millions of seabirds, including both resident breeders and winter migrants (Briggs et al. 1987). In most years, equatorward upwelling winds prevail in the spring and summer. When surface currents are directed offshore and upwelling is strong, colder, saltier, and nutrient-rich waters dominate the nearshore along the US West Coast (Huyer 1983), resulting in a highly productive coastal ecosystem (Roemmich & McGowan 1995). Downwelling prevails in fall and winter, with the most intense downwelling typically found in the northern half of the CCS. The wind-forced ‘spring transition’ from winter to summer conditions is frequently a sudden event (Strub et al. 1987), bringing distinct changes in coastal sea level, surface currents, nutrients, and nearshore sea surface temperatures along the entire west coast (Huyer 1983).

The 2005 anomaly

In 2005, there were widespread anomalies in the physical and biological properties of the CCS. Prominent characteristics included a mild winter and weak downwelling winds over the northern part of the CCS, but an anomalously stormy winter over the southern and central CCS (Gleason 2006). Spring brought winter-like conditions to the northern CCS, including a high frequency of downwelling wind periods that persisted until late May (Barth et al. 2007). In contrast, winds were favorable to upwelling, albeit weakly so, off the California coast from March to May (Schwing et al. 2006). At 45°N, the spring transition to upwelling winds and surface currents came on May 24, some 50 d later than the long-term average (Kosro et al. 2006). However, a ‘biological spring transition’ was delayed an additional 50 d off Newport, Oregon, until subsurface upwelled water first penetrated the strongly stratified surface layer on July 13 (Kosro et al. 2006). The biological responses to delayed upwelling included anomalously low primary production, low recruitment of intertidal invertebrates (Barth et al. 2007), an intrusion of southern copepod species into northern CCS pelagic communities (Mackas et al. 2006), shifts in pelagic fish communities (Brodeur et al. 2006), and a breeding failure of Cassin’s auklets Ptychorhamphus aleuticus in Central California (Sydeman et al. 2006).

The present paper explores seabird die-offs within the central and northern CCS in 2005, using beached bird data from 3 programs spanning from Monterey Bay, California, to Cape Flattery, Washington (Fig. 1). In particular, we establish the geographic and temporal scope of 2005 patterns relative to long-term averages, and examine the correlation between seasonal physical factors and species-specific elevations in beaching rate.

MATERIALS AND METHODS

Beached bird data. Beached bird data were collected from 3 regional programs: in Washington by the Coastal Observation and Seabird Survey Team (COASST) program; in Oregon by Robert Loeffel, a retired Oregon Department of Fish and Wildlife biologist, who maintains a long-term beached bird survey in Newport; and in Central California by the Coastal
Ocean Mammal and Bird Education and Research Surveys (BeachCOMBERS) program in Monterey Bay (Fig. 1). For all programs, trained individuals surveyed predefined lengths of beach from one to several times monthly in most to all months of the year. All carcasses found during a survey were identified to the lowest possible taxon using keys specific to beachcast birds (Ainley et al. 1993, Hass & Parrish 2002) and carcasses were marked or removed to avoid recounting.

In Washington, COASST volunteers conducted surveys monthly on dates of their choosing, such that between-survey intervals were roughly equivalent for each site. All carcasses were individually marked, photographed, and left on the beach. COASST sites were grouped into 2 regions: the south coast of Washington (Columbia River to Copalis River; 12 sites) and the north coast of Washington (Copalis River to Cape Flattery; 16 sites). Data span from November 2000 to December 2005.

In Oregon, surveys were largely performed by a single individual (Robert Loeffel), with assistance from a small group of trained assistants. From 1980 to 1983, surveys were performed at a jogging pace and flotsam piles were not searched, potentially leading to underrepresentation of carcasses in the data. After 1983, protocols were standardized to a walking pace. Exploration of the data revealed that carcass counts of study species were not significantly different across this protocol change, so all data were used. Two beach sites totaling 7.4 km (Henderson Creek to Thiel Creek and Thiel Creek to Beaver Creek) near Newport, Oregon, were surveyed most consistently and were used in this analysis. Only surveys within 3 d of each other were used. Total carcasses were summed within month and divided by number of surveys to calculate average carcasses encountered per month. Data span from January 1980 to December 2005.

In Central California, BeachCOMBERS conducted monthly surveys at 11 beach segments of 3.7 to 5.2 km in length within the Monterey Bay National Marine Sanctuary (total = 51.1 km). During the first week of each month, 2 trained surveyors working during an ebbing tide recorded all carcasses using a modified strip transect search pattern. Survey effort was centered on the wrack line of the previous high tide, and surveyors used binoculars to scan upper beach wrack for distant carcasses. Unidentified species were collected or photographed to verify identification. Data span from May 1997 to December 2005.

**Species of interest.** We chose to examine trends of 4 species (1) for which enough data were available to detect trends in depositional patterns (i.e. >10% of species composition across survey regions), (2) which maximized trophic diversity, and (3) which accounted for the majority of anomalous die-offs recorded in 2005. We excluded the highly migratory species, such
as shearwaters and fulmars, which may have been affected by extrinsic factors occurring outside the study area.

Cassin’s auklets *Ptychorhamphus aleuticus* are small-bodied divers that consume mainly zooplankton. An estimated 3.5 million Cassin’s auklets breed along the entire West Coast, with a population concentration in British Columbia (~75%; Manuwal & Thoresen 1993). Cassin’s auklets apparently migrate south in late fall to winter off California (Briggs et al. 1987), returning to colonies by March (Bertram et al. 2005).

Rhinoceros auklets *Cerorhinca monoceros* are actually puffins and feed on a mixture of fish and large zooplankton. As with Cassin’s auklets, this species breeds from southern California to Alaska, but the vast majority of the West Coast population, nearly 1 million birds, is found in Washington and further north (Gaston & Dechesne 1996). During winter, rhinoceros auklets migrate south, hundreds of thousands of them aggregating off California, north of Point Conception (Briggs et al. 1987). By April or May, these birds have returned to northern breeding sites.

Upwards of 4 million common murres *Uria aalge*, a deep-diving piscivore, are found along the West Coast. The population has a bimodal distribution, with breeding centers in northern California through northern Oregon (24%) and in Alaska (~70%; Ainley et al. 2002). The post-breeding distribution is poorly known, although a general movement to inshore waters within the CCS, including Monterey Bay and the Strait of Juan de Fuca, has been noted (Briggs et al. 1987).

Brandt’s cormorant *Phalacrocorax penicillatus* is the largest of the 4 focal species. A shallow-diving piscivore, Brandt’s cormorant is found throughout the CCS, with thousands breeding in Oregon and tens of thousands concentrated in Central and Southern California (Wallace & Wallace 1998). During the non-breeding season, Brandt’s cormorants extend their range north, where large numbers overwinter in Washington and British Columbia, migrating south in April through June.

**Analyses.** Data from all 3 programs were standardized by beach length, as carcasses km\(^{-1}\) mo\(^{-1}\), to create species-specific monthly encounter rates (a proxy for deposition), the basic unit of data for all analyses. Data are presented in 3 forms: (1) program means, mo\(^{-1}\), for each species and region, standardized to maximum monthly values (at 100%), (2) 2005 monthly anomalies, calculated as the monthly encounter rate minus the monthly program mean, and (3) cumulative seasonal values, yr\(^{-1}\).

Based on the background pattern of beaching and the timing of physical change in the CCS system, we divided the data into 3 seasonal groupings: winter (November to February), spring (March to June), and summer (July to October). During winter, the downwelling signal is strongest in the northern CCS, the upwelling signal is weakest in the central to southern CCS (Huyer 1983), and storm events are most likely to occur. During this time, all 4 bird species are found in high numbers in the southern CCS, particularly at wintering sites such as Monterey Bay. The transition from winter to spring is punctuated by the annual departure of the 2 species of auklets to breeding colonies in the northern CCS and beyond and a switch in ocean conditions from predominantly downwelling to predominantly upwelling (i.e. the spring transition). During spring, murres and cormorants return to breeding colonies within the CCS. Summer is post-breeding, when northern breeders (auklets) migrate into the southern CCS.

Long-term program means were contrasted to the 2005 data, using 1-sample, 2-sided t-tests. Correlation coefficients were used to explore concordance between select species × seasons and a range of physical and biological factors. These analyses were restricted to the Loeffel (26 yr) and BeachCOMBERS (8 yr) data sets, as the COASST data have only been gathered for 5 yr. Linear relationships are reported, unless exponential or power relationships explained an additional 10% or more of the variation.

**Physical data.** We used 3 indices of regional physical forcing: upwelling, vertical velocity, and zonal winds. Daily index values were summed over November to February and March to June. We chose from 1980 to 2005 to reflect the longest-running beached bird data set (Loeffel data from Newport, OR).

Upwelling indices along the US West Coast (www.pfeg.noaa.gov) are derived from sea level pressure (SLP) distributions and reflect the along-shore wind stress (Schwing et al. 1996). Cumulative seasonal values were used to characterize the mean forcing of cross-shore Ekman transports in the coastal zone, where positive values indicate upwelling and negative values indicate downwelling. We used the day of the year of spring transition as the onset of seasonal upwelling (Kosro et al. 2006).

We created a winter storminess index from the National Centers for Environmental Prediction (NCEP)—National Center for Atmospheric Research Reanalysis project (Kistler 2001; www.cdc.noaa.gov/cgi-bin/db_search/SearchMenus.pl). This data set was produced using a numerical weather prediction model assimilating surface, upper-air, and satellite-based observations for the period 1948 to the present. We used daily values of the pressure vertical velocity (σ) at 500 hPa for 6° latitude by 6° longitude boxes, centered 3 degrees offshore of Monterey and Newport, to characterize high-frequency storm activity (e.g. Norris 2000). Negative values indicate upward vertical velocities, hence more stormy conditions overall.
From the same source, and for the same spatio-temporal interval, mean zonal winds at the 300 hPa (jet-stream level) were also considered. These winds represent a measure of the regional atmospheric circulation. Seasonal mean anomalies in the zonal winds aloft correspond with their counterparts at the surface (r = 0.7 to 0.8). Westerly (easterly) wind anomalies aloft tend to be accompanied not only by downwelling (upwelling) anomalies at the coast (Barth et al. 2007), but also by equatorward (poleward) Ekman transports. The latter mechanism is potentially a significant influence on the latitude of the transition zone between sub-tropical and sub-arctic water masses and their attendant biological communities.

To explore a more local scale of physical forcing during the winter, we used hourly average surface wind speed and direction data obtained from the National Data Buoy Center website (http://ndbc.noaa.gov) for Station 46042 (27 nautical miles west of Monterey Bay, California) for 1997 to 2005 and Station NWPOB (Newport South Jetty, Newport, Oregon) for 1991 to 2005. Daily averages of the hourly wind speed squared (the pseudo-stress magnitude, in m² s⁻²) were computed from the hourly data using all available observations for each day at each station, respectively. Within the November through February period, for years in which data were constantly available, we chose all days in which mean pseudo-stress was 0.5 standard deviations or more above the long-term winter mean. We called these events storms; they lasted one to several days. We also examined more extreme storms, defined as those events exceeding a daily pseudo-stress of 10 m² s⁻². Finally, we tallied the number of days across the 4 mo winter season that winds were directed on-shore (180 to 270°). For each winter, we recorded the number of storms, the average duration (in days), the average daily intensity (m² s⁻²), the maximum event intensity (cumulative m² s⁻² over the storm), and the frequency of on-shore winds (days). The data set from Monterey was complete; however, the data from Newport had gaps such that the winters of 1997 and 1998 were excluded.

**Biological data.** We used biweekly, inner-shelf, copepod biomass (mg carbon m⁻³ of water sampled) data collected at a single station (NH-05, 5 nautical miles offshore) along the Newport Line (44.5°N), with a 0.20 mm vertical ring net towed from the bottom to the surface (Peterson & Keister 2003). Data were simplified to a single index—the x-axis ordination scores of a non-metric multidimensional scaling (NMDS), using Sorensen’s distance measure and incorporating log-transformed species abundance versus sample date (including 1969 to 1973, 1983, and 1996 to 2007). Rare species (occurring in <5 samples) were not included. In this measure, negative values correspond to cold water conditions and northern species (e.g. *Pseudocalanus minus*, *Acartia longiremis*, *Calanus marshallae*) and positive values represent warmer water southern species (e.g. *Paracalanus parvus*, *Ctenocalanus vanus*, *Mesocalanus tenuicornis*, *Clausocalanus spp.*). Monthly index values were summed over relevant months during the spring to summer period (March through June). Winter months contained too many years with 1 or more missing monthly sample to be useful.

**RESULTS**

**Regional patterns of beaching**

Along the US West Coast, baseline beaching rates for 3 of the 4 focal species were remarkably similar; the exception was Cassin’s auklet *Ptychorhamphus aleuticus* (Fig. 2B). Post-breeding mortality peaks (July to October) were evident for the rhinoceros auklet *Cerorhinca monocerata* and the common murre *Uria aalge* (Fig. 2A,C). For murres, a shift in the peak of mortality from south to north followed the shift in the timing of breeding for this species. The post-breeding signal was slightly modified in California by the summer gill net mortality that occurred in 1997 to 2000 (Forney et al. 2001). Rhinoceros auklet beaching peaked in the northern CCS during August to September, but was maximal in Monterey much earlier (April). This shift may represent earlier breeding in the south, or potentially mortality of northward migrating birds.

In northern Washington and Oregon, Brandt’s cormorant *Phalacrocorax peneillatus* mortality peaked during the post-breeding season (August to September); however, in southern Washington and California, the peak fell much earlier, in April to May (Fig. 2D). The California peak may be indicative of earlier breeding; however, the breeding range of this species is largely exclusive of the Washington coastline (Wallace & Wallace 1998), making the southern Washington early season peak more difficult to explain.

Clear baseline patterns were least apparent for Cassin’s auklets; however, the beaching rate was typically very low for this species (i.e. <0.05 birds km⁻²). Although a suggestion of CCS post-breeding peaks existed for the Washington and Oregon data, in California the peak fell much earlier, during April (Fig. 2A). This earlier peak coincided with the mortality peak in rhinoceros auklets in the same region, suggesting a location effect. Finally, all 4 locations showed winterkill.

**The 2005 die-off**

In 2005, anomalously high beaching rates for all 4 resident species were concentrated (1) in the winter
Fig. 2. (Above and facing page.) Encounter rates of (A) rhinoceros auklets, (B) Cassin’s auklets, (C) common murres, and (D) Brandt’s cormorants across the 4 sampling locations. Top row of panels: the average monthly encounter rate (a proxy for deposition) over the history of each program, standardized to maximum monthly value (at 100%) within each program. Northern Washington: white; southern Washington: light gray; Newport: dark gray; Monterey: black. Note that the 2 overlapping months (November, December) have the same mean values in the top panel graphs. Lower rows of panels: the encounter anomaly (month – mean), in birds km\(^{-1}\), for each of the 4 sampling locations (as listed) for November 2004 through December 2005. For positive anomalies, individual month between 120 and 300% of the mean value are shaded gray; anomalies >300% of the mean are in black. Background shading separates seasonal groupings used in the analysis: winter (November to February), spring to summer (March to June), and post-breeding (July to October).
and spring, (2) in the piscivorous species, and (3) especially in the southernmost location (California; Fig. 1). Rhinoceros auklets and Cassin’s auklets, the 2 zooplanktivorous species, beached primarily during the winter in California (Fig. 2A,B, Table 1). For Cassin’s auklets especially, anomalously high beaching resulted in an abundance of carcasses, as the underlying mean values during winter (particularly in January) were already high (Fig. 2B). In the northern CCS, these species either did not beach in appreciable numbers, or
Beginning of the post-breeding season in southern Washington and California (Fig. 2D, Table 1). Unseasonably high beaching continued through the post-breeding season in southern Washington, Oregon; Fig. 2D, top panel). Were expected (southern Washington, California) or not (northern Washington, Oregon; Fig. 2D, top panel). Normally, peak murre beaching rates occur during the post-breeding period (Fig. 2C, top panel). Thus, the 2005 murre mortality event occurred unseasonably early. Even in Oregon, where beaching rates were normal during spring, a large anomaly in July preceded the usual annual peak by a month (July 2005 = –8.466, p <0.0001; Fig. 2C). Beaching rates might be higher, as Ekman processes drove the sub-arctic–sub-tropical transition to the north. Food web structure and biomass would also be negatively affected by a late transition to upwelling and/or years in which spring upwelling was relatively weak. Because the cycle of strong upwelling along the West Coast occurs in spring, after the auklets have largely migrated north out of the system, we restricted this latter hypothesis to the predominantly local breeders, common murres and Brandt’s cormorants. Finally, physical forcing altered the rate at which carcasses were delivered to shore. These are not mutually exclusive; however, each leads to different hypotheses. If direct physical stress increased mortality, we predicted that in years with a higher frequency, duration, or intensity of storm events, and/or years with an elevated regional storminess index, beaching rates would be higher. If physical forcing acted through food web processes, we predicted that in years with negative zonal winds, beaching rates might be higher, as Ekman processes drove the sub-arctic–sub-tropical transition to the north. Food web structure and biomass would also be negatively affected by a late transition to upwelling and/or years in which spring upwelling was relatively weak. Because the cycle of strong upwelling along the West Coast occurs in spring, after the auklets have largely migrated north out of the system, we restricted this latter hypothesis to the predominantly local breeders, common murres and Brandt’s cormorants. Finally, if physical forcing changed the rate at which drifters (aka carcasses) were delivered to shore, we predicted that in years in which cumulative downwelling was stronger, beaching rates would be higher. Because downwelling occurs concurrently with storm events, it is not entirely possible to tease apart the direct and

<table>
<thead>
<tr>
<th>Location</th>
<th>COMU t-p</th>
<th>BRAC t-p</th>
<th>RHAU t-p</th>
<th>CAAU t-p</th>
</tr>
</thead>
<tbody>
<tr>
<td>North coast, WA (n = 5)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winter</td>
<td>1.852 n.s.</td>
<td>1.633 n.s.</td>
<td>-3.000 n.s.</td>
<td>-2.379 n.s.</td>
</tr>
<tr>
<td>Spring–Summer</td>
<td>-3.707 &lt;0.05</td>
<td>-3.920 &lt;0.05</td>
<td>1.471 n.s.</td>
<td>1.615 n.s.</td>
</tr>
<tr>
<td>Post-breeding</td>
<td>0.659 n.s.</td>
<td>1.235 n.s.</td>
<td>-0.751 n.s.</td>
<td>1.513 n.s.</td>
</tr>
<tr>
<td>South coast, WA (n = 5)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fall–Winter</td>
<td>1.283 n.s.</td>
<td>1.539 n.s.</td>
<td>-0.145 n.s.</td>
<td>0.509 n.s.</td>
</tr>
<tr>
<td>Spring–Summer</td>
<td>-3.600 &lt;0.05</td>
<td>-3.989 &lt;0.05</td>
<td>-1.355 n.s.</td>
<td>-3.823 &lt;0.05</td>
</tr>
<tr>
<td>Post-breeding</td>
<td>1.442 n.s.</td>
<td>-3.984 &lt;0.02</td>
<td>1.652 n.s.</td>
<td>0.585 n.s.</td>
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<tr>
<td>Newport, OR (n = 25, 26)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winter</td>
<td>2.895 &lt;0.01</td>
<td>2.328 &lt;0.05</td>
<td>0.448 n.s.</td>
<td>1.888 n.s.</td>
</tr>
<tr>
<td>Spring–Summer</td>
<td>2.049 n.s.</td>
<td>-19.641 &lt;0.0001</td>
<td>2.163 &lt;0.05</td>
<td>2.090 &lt;0.05</td>
</tr>
<tr>
<td>Post-breeding</td>
<td>-0.723 n.s.</td>
<td>1.999 n.s.</td>
<td>3.778 &lt;0.001</td>
<td>1.918 n.s.</td>
</tr>
<tr>
<td>Monterey, CA (n = 8)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winter</td>
<td>-5.088 &lt;0.002</td>
<td>-3.951 &lt;0.01</td>
<td>-6.838 &lt;0.001</td>
<td>-6.998 &lt;0.001</td>
</tr>
<tr>
<td>Spring–Summer</td>
<td>-3.306 &lt;0.01</td>
<td>-6.851 &lt;0.001</td>
<td>-0.142 n.s.</td>
<td>0.530 n.s.</td>
</tr>
<tr>
<td>Post-breeding</td>
<td>0.728 n.s.</td>
<td>-5.985 0.001</td>
<td>1.529 n.s.</td>
<td>0.001 n.s.</td>
</tr>
</tbody>
</table>

Exploring bio-physical linkages

Given the 2005 die-off events, 3 basic mechanisms might explain anomalously high deposition of birds on beaches in the CCS: (1) physical stress increased on-water mortality rates, (2) physical forcing acted through bottom-up food web processes, and (3) physical forcing altered the rate at which carcasses were delivered to shore. These are not mutually exclusive; however, each leads to different hypotheses. If direct physical stress increased mortality, we predicted that in years with a higher frequency, duration, or intensity of storm events, and/or years with an elevated regional storminess index, beaching rates would be higher. If physical forcing acted through food web processes, we predicted that in years with negative zonal winds, beaching rates might be higher, as Ekman processes drove the sub-arctic–sub-tropical transition to the north. Food web structure and biomass would also be negatively affected by a late transition to upwelling and/or years in which spring upwelling was relatively weak. Because the cycle of strong upwelling along the West Coast occurs in spring, after the auklets have largely migrated north out of the system, we restricted this latter hypothesis to the predominantly local breeders, common murres and Brandt’s cormorants. Finally, if physical forcing changed the rate at which drifters (aka carcasses) were delivered to shore, we predicted that in years in which cumulative downwelling was stronger, beaching rates would be higher. Because downwelling occurs concurrently with storm events, it is not entirely possible to tease apart the direct and
indirect effects of storms. To explore which, if any, of these mechanisms might have been operating, we hindcast, using the 2 data sets with a longer timeline, i.e. California and Oregon, and examined the correlations among physical proxies of winter storms and spring upwelling, and beaching rates of each species within the relevant season.

Winter

In general, the influence of winter conditions on beaching rates of our 4 focal species appeared to be weak (Table 2). In California, we deleted Cassin’s auklets from the analysis, as the majority of the years had beaching rates of zero. For the remaining 3 species, the strongest correlations were with zonal winds (Table 2), although no single physical variable was highly associated with beaching rates across all species. Cormorant, murre, and auklet beaching rates were higher when zonal winds were easterly (Table 2, Fig. 3A), possibly suggesting that northward Ekman transport may have disassociated the food web for these species. The 2005 data point was an outlier in all cases and drove the correlation in the case of auklets. Only murres had any association with the remaining regional-scale variables, vertical velocity (Fig. 3B) and upwelling index (not shown). In both cases, more murres beached in stormy (i.e. lower vertical velocity, stronger downwelling) years. Local storminess, at least as indicated by surface winds, had no influence on beaching rates, with the possible exception of frequency of onshore windy days and rhinoceros auklets (Table 2). However, this latter association was entirely driven by the 2005 point (large number of...
onshore windy days and high encounter rate); when this point is removed, the relationship weakens considerably. Lagging the data 1 mo, such that storminess in November through January influenced beaching rates in December through February did not improve the associations. Thresholding storms to only those events exceeding 10 m$^2$s$^{-2}$ also had no effect on strengthening the association between the number, duration, or intensity of storms and seabird beaching. In Oregon, associations between winter physical variables and seabird beaching rates were essentially nonexistent (Table 2); beaching rates were entirely unresponsive to regional- or local-scale variables.

### Spring to summer

In California, both the timing and cumulative intensity of upwelling appeared to influence beaching rates of both species (Table 3), especially for Brandt’s cormorants. Later transitions and weaker upwelling were associated with higher deposition (Fig. 4), as would be expected if birds were starving as a result of altered nearshore productivity. Correlation coefficients between beaching and cumulative upwelling were sub-

### Table 3. Correlation coefficients ($R^2$) between cumulative encounter rates (birds km$^{-1}$) during spring to summer (MA: Mar and Apr; MAM: Mar to May, MAMJ: Mar to Jun), and a range of proxies of nearshore productivity during spring. Relationships in a direction other than expected (see Table 2) are in italics. Power ($y = cx^d$) relationships are indicated by an asterisk; otherwise, all correlations are linear. Sample size (n), in yr, is listed following each location. See Table 1 for taxonomic names

<table>
<thead>
<tr>
<th>Spring transition (day of the year)</th>
<th>Upwelling index</th>
<th>Copepod index</th>
</tr>
</thead>
<tbody>
<tr>
<td>MA</td>
<td>MAM</td>
<td>MAMJ</td>
</tr>
<tr>
<td>Monterey, CA (n = 8)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Common murres</td>
<td>0.112</td>
<td>0.162*</td>
</tr>
<tr>
<td>Brandt’s cormorants</td>
<td>0.568</td>
<td>0.710*</td>
</tr>
<tr>
<td>Newport, OR (n = 26)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Common murres</td>
<td>0.002</td>
<td>0.078</td>
</tr>
<tr>
<td>Brandt’s cormorants</td>
<td>0.232</td>
<td>0.115</td>
</tr>
<tr>
<td>Newport, OR (n = 8; 9 for copepod index)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Common murres</td>
<td>0.002</td>
<td>0.036</td>
</tr>
<tr>
<td>Brandt’s cormorants</td>
<td>0.638</td>
<td>0.023</td>
</tr>
</tbody>
</table>

Fig. 4. Spring to summer (MAM: Mar to May, MAMJ: Mar to Jun) encounter rates of local breeders versus spring upwelling intensity (UW) and onset (ST). (A) Common murres in Monterey (birds = [4E + 15] × UW$^{-3.7964}$), (B) Brandt’s cormorants in Monterey (birds = [2E + 19] × UW$^{-4.8305}$), (C) Brandt’s cormorants in Newport (dashed line, 1998 to 2005: birds = 0.0063ST + 0.456), and (D) common murres in Newport (dashed line, 1998 to 2005: birds = –0.0001UW + 0.202). Open circles in Panels C and D are 1998 to 2005 data.
Parrish et al.: Beached birds in the CCS

stantially improved with a power model, suggesting that at the low end, only a slight additional weakening in upwelling was associated with a large biological response (Fig. 4A,B). In fact, the relationships appeared to be driven largely by these ‘bad’ bird years (2005, 1998). Removing these points from the data set destroyed the correlations. Finally, when cumulative upwelling was restricted to only early spring (March to April), correlations were lower for both species, perhaps indicating that early season physics did not necessarily set the stage for later beaching events, or that extended periods of weakened upwelling were necessary to provoke bottom-up indirect effects.

The strength of the association between spring to summer nearshore physics and seabird beaching rate was not, however, apparent in Oregon (Table 3, Fig. 4), with the possible exception of the timing of upwelling onset and Brandt’s cormorant. To infer whether the lack of association was a result of meso-scale geographic differences (central versus northern CCS) and/or the difference in temporal scope (8 versus 26 yr), we also reran the correlations restricted to the 1998 to 2005 window. Shortening the time series did improve correlations between Brandt’s cormorant beaching rates and both the intensity and, especially, onset timing of upwelling (Table 3). As with the California results, later transition dates and weaker upwelling were associated with higher beaching rates. Correlations between murre and cormorant beaching, and the Newport line index of copepod diversity were stronger, albeit still weak (Table 3). As predicted, in years with a higher incidence of cold-water (i.e. northern) species in the zooplankton community, beaching rates were lower (Fig. 5). A southern community composition resulted in higher beaching rates, although high beaching was not restricted to only southern community-dominated years (e.g. 1997 for murres). Finally, the strength of the association was strongest when May was included in the copepod index value (Table 3).

DISCUSSION

The patterns found across the 3 beached bird data sets in 2005 appear to echo patterns described by anomalous ocean and atmospheric conditions reported by others (Schwing et al. 2006, Barth et al. 2007). Pervasive die-offs of Brandt’s cormorant *Phalacrocorax penicillatus* and the common murre *Uria aalge* in the spring to summer reflected weak upwelling and the delay in both physical and biological spring transition (Kosro et al. 2006, Mackas et al. 2006). However, the elevated rate of auklet (*Ptychoramphus aleuticus, Cerorhinca monocerata*) beaching in the central CCS during the winter and the apparent absence of common murre mortality in Oregon did not follow from known physical conditions.

Do the responses of birds to changing ocean conditions in 2005 fit a more general model of physical forcing of beached bird patterns? In general, annual deposition of common seabird species within the CCS were only weakly related to physical forcing factors. Correlations in the central CCS site—Monterey—were uniformly higher than those at the northern CCS site—Newport (Tables 2 & 3). Associations were tighter between physical forcing and biological response in the spring relative to the winter (Tables 2 & 3). During the winter, only regional factors (i.e. zonal winds) appeared to influence all species, perhaps telesecking through the food web (e.g. Fig. 5). On the other hand, local winter forcing, typified by storm duration and intensity, did not appear to affect the timing or abundance of beaching (Table 2).

In exploring the potential linkages between physical forcing and beaching rates, we hypothesized 3 non-exclusive mechanisms: (1) increased mortality rates as a consequence of direct physical stress, (2) increased mortality rates as a consequence of bottom-up food web processes, and (3) increased delivery rate of carcasses to the beach. Our analyses suggest that direct
physical stress, specifically winter storms, was not a strong factor affecting annual beaching rate (Table 2). In fact, only common murres at the California site showed any association with our regional storminess index, vertical velocity (Table 2). Thus, while is it certainly true that seabird beaching is higher during the winter (Camphuysen et al. 1999), there were no simple relationships between measures of storminess and bird beaching.

Bottom-up food web processes appeared to be the strongest signal in our data. Delays in the onset of seasonal upwelling and upwelling intensity were both associated with beaching in those species largely resident in the system, especially Brandt’s cormorants (Table 3, Fig. 4). Changes in upwelling timing and intensity in eastern boundary current systems are well known forcing factors affecting system production, from primary productivity to upper trophic population dynamics (Barber & Chavez 1983, Duffy et al. 1988, Ainley et al. 1995), so the apparent relationship to beaching rates is not surprising.

What was non-intuitive is the weak (cormorants) to non-existent (murres) association between upwelling and beaching rates at our northern CCS site. Restricting the analysis to only the Monterey data set interval improved the correlations for cormorants (Table 3), suggesting that decadal-scale shifts (e.g. Pacific Decadal Oscillation) may play a role in beached bird abundance. However, determining the degree of this potential association would require a time series exceeding our Oregon (26 yr) data. At the very least, these data, together with the shorter term COASST data, appear to suggest that beached birds may reflect the apparent physical differences from north to south within the CCS (e.g. Mueter et al. 2002).

One potentially important difference between Monterey and Newport is that seabirds aggregate at the former as a foraging and resting hotspot (Briggs et al. 1987), but only breed (especially cormorants and murres) at the latter. Thus, what ends up on the beach in Monterey versus Newport in the winter may reflect more of the post-breeding distribution—and thus, choices—of the live birds, rather than the local-to-regional physics allowing carcasses to reach the beach. Thus, while extreme on-shore storms during the winter in Newport may create ready conditions for elevated carcass delivery, an observed increase in carcasses is only possible if there are birds in the area to suffer that mortality.

Food web processes were potentially invoked by the relationship between zonal winds and beaching rates, evident at the California, but not the Oregon, site. Here, the hypothesis is that easterly winds aloft may be associated with a northward shift in the extent of southern pelagic communities. Although our analysis suggested that birds washed ashore in years with a predicted northward shift (Monterey in winter; Table 2) and that southern copepods were more abundant and northern copepods were less abundant in years with higher bird beaching (Newport in spring; Table 3); this thread falls across 2 sites and 2 seasons, making direct conclusions suspect. Barth et al. (2007) have suggested that winds aloft can be related to changes in the strength and onset of coastal upwelling—particularly in 2005—thus, this mechanism may also explain elevated spring to summer beaching rates.

Finally, we found no direct evidence that physical processes resulted in a change in the rate of carcass delivery to the beach. With the possible exception of murres, increased winter downwelling did not result in higher carcass abundances (Table 2), and neither did years with more abundant on-shore wind days (Table 2). Wiese & Ryan (2003) did find a significant effect of weather index (first principal component of air temperature, wind direction, and wind velocity) on beaching rates of oiled carcasses in Newfoundland. During colder months, with stronger on-shore winds, more carcasses came ashore, indicating that at least in some areas local physical forcing assessed monthly may play a role in regulating carcass delivery. The dominant variability in wind forcing over the CCS occurs at time scales of several days (Hickey 1989). Event-scale reversals in wind direction on the order of 5 to 7 d (Hickey & Banas 2003) cause drifters (and thus potentially carcasses) to move towards (away from) the coastal zone (MacFadyen et al. 2005). Thus, it is possible that the temporal scale at which the beached bird data were collected (aggregated monthly) is not sufficient to distinguish the relationship between physical processes and carcass delivery rates.

Are beached birds good indicators of ocean conditions? The present paper has clearly demonstrated that, although the answer can be yes, it is not necessarily so. This indicates that the forces provoking movement in the live bird populations, as well as the physics of birds as drifters, must be understood at local-to-regional levels in order to comprehend the beached bird signal. Having said that, it is also clear that during 2005 anomalous conditions in the physical environment resulted in a dramatic and non-linear response across the seabird community, with the end result that an additional amount of tens of thousands of bird carcasses beached along the CCS during spring and early summer.

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INTRODUCTION

Warming of the climate system is unequivocal, as is now evident from observations of increases in global average air and ocean temperatures, widespread melting of snow and ice, and rising global average sea level....Anthropogenic warming and sea level rise would continue for centuries due to the timescales associated with climate processes and feedbacks, even if greenhouse gas concentrations were to be stabilized. (IPCC 2007)

Climate change in the past 3 decades in the North Pacific is thought to have had major effects on marine ecosystems, from physical oceanography to population dynamics of a variety of species (e.g., Ebbesmeyer et al. 1991, Francis & Hare 1994, Anderson & Platt 1999, Hare & Mantua 2000). The eastern Bering Sea in particular has undergone dramatic warming in this century, as predicted by global climate models, that has apparently had significant effects on pelagic and benthic community structure and biomass yield (Grebmeier et al. 2006, Coyle et al. 2008, IPCC 2007, Stabeno et al. 2007). Yet, despite intense interest, the mechanisms linking meteorological and oceanographic variability to marine biology and productivity are poorly known, owing largely to the high costs of extensive ship-based oceanographic studies designed specifically to document change and to discover its cause.

Insights into relationships among marine communities, food webs, and oceanographic features can often be found by examining characteristics of species at
higher trophic levels because they integrate processes at multiple lower trophic levels. Diet studies of predators can be especially informative because forage species and food webs are commonly affected by physical processes and variability. In the Bering Sea, least auklets *Aethia pusilla* have been shown to be especially useful in elucidating ecosystem properties that have much broader implications than simply for the birds and their prey (e.g. Springer & Roseneau 1985).

Least auklets are one of the most numerous and widely distributed species of seabirds in the Bering Sea—they number in the millions and nest at island colonies from the Aleutian Islands to Bering Strait (Jones 1993). They are planktivores that specialize on the large calanoid copepods *Neocalanus cristatus*, *N. plumchrus*, *N. flemingeri*, and *Calanus marshallae* in summer, and supplement them with other taxa of zooplankton, such as hyperiid amphipods, euphausiids, crab, shrimp, and fish larvae, and other miscellaneous organisms (Bedard 1969, Hunt et al. 1981, Bradstreet 1985, Springer & Roseneau 1985, Roby & Brink 1986, Hunt & Harrison 1990, Flint & Golovkin 2002). The composition of the copepod portion of their diets is determined by the relative abundances of the various species, which are in turn influenced by physical processes that structure the Bering Sea into hydrographic and biotic domains with distinct species assemblages (Iverson et al. 1979, Cooney 1981, Coachman 1986, Springer et al. 1996). Interannual variation in physical conditions and primary production can also affect copepod population abundances (Smith & Vidal 1984, 1986). Furthermore, in regions where all 4 species of copepods are available within the foraging range of least auklets, selectivity for one or another species appears to be determined not by differences in nutritional/energetic content, which are small, but by the ability of birds nesting in distinct colonies to find profitable solutions for dietary proclivities (Springer & Roseneau 1985, Flint & Golovkin 2002).

Oceanographic conditions in the southeastern Bering Sea in late July to August 2004, documented by traditional shipboard methodologies, sharply partitioned continental shelf and oceanic domains and created an abrupt and extremely narrow ecotone between them (Coyle et al. 2008). That is, waters of oceanic origin were confined to the very outer part of the continental shelf, with little or no excursion onto the shelf or mixing with waters of the middle shelf domain. Least auklet diets from the Pribilof Islands during summer 2004, which we present here, were indicative of this unusual hydrographic structure. Therefore, we examined our auklet diet data from the Pribilof Is. for 1996 to 2006, and reviewed data from earlier years (St. George I.—1977, 1984, 1985; St. Paul I.—1976, 1977, 1984, 1992), to see if there was evidence that such conditions had occurred at other times in the past 3 decades. This is among the few data sets that can be used to document the temporal and spatial scale of conditions important to the structure of the pelagic community of continental shelf waters, to the food web supporting least auklets and other planktivorous species at the Pribilof Is., and thus to our view of how climate change may alter characteristics of the marine ecosystem of the Bering Sea. The Pribilof Is. are well situated for such studies: central-place foragers like least auklets on St. George I. are closer to deep basin waters and the associated oceanic plankton community than auklets on St. Paul I., which is somewhat higher on the continental shelf, and thus, birds from the 2 islands sample the region differently and provide contrasting and complementary views of the larger ecosystem.

**MATERIALS AND METHODS**

Samples for estimating least auklet diets were obtained during the nesting season (June through early August) from 1996 to 2006, from adults trapped at colonies on St. George I. and St. Paul I. (Fig. 1, Table 1), largely as part of a long-term seabird monitoring program conducted by the Alaska Maritime National Wildlife Refuge (e.g. Dragoo et al. 2006). Contents of sublingual pouches, consisting of fresh zooplankton destined for chicks, were collected when the birds regurgitated upon being trapped. In 2003 and 2004 on St. Paul I., adipose tissue samples for fatty acid signature analysis were also taken by live biopsy from the

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**Fig. 1.** Pribilof Islands and other locations discussed in the text.
synsacral region of the birds (Iverson et al. 2007, this volume). All birds were released after sampling. Regurgitation samples were preserved in 70% ethanol in the field and enumerated at the University of Alaska Fairbanks using methods described by Springer & Roseneau (1985). Prey species were identified to the lowest taxonomic level practical, which precluded separating the closely related copepod species *Neocalanus plumchrus* and *N. flemingeri*. Adipose tissues were placed in chloroform buffered with BHT (an antioxidant) and frozen until analyzed using methods described by Iverson et al. (2007).

### RESULTS

#### Diets at St. George I.—adult regurgitations of chick meals

Diets of least auklets during our study at St. George I. were in most respects typical of those reported in earlier years—that is, large calanoid copepods dominated diets in nearly all intervals in all years, with other taxa present in varying, lesser proportions (Fig. 2a, Table 2). Among the copepods, *Neocalanus cristatus* and *N. plumchrus/flemingeri* were generally, but not

<table>
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Fig. 2. *Aethia pusilla*. Least auklet diets at the Pribilof Islands—(a) St. George I. and (b) St. Paul I., from 1996 to 2006
<table>
<thead>
<tr>
<th>Year Interval</th>
<th>Neocalanus cristatus Mean</th>
<th>N. plumchrus/ flemingeri Mean</th>
<th>Calanus marshallae Mean</th>
<th>Hyperid amphipods Mean</th>
<th>Euphausiids Mean</th>
<th>Juvenile crusts Mean</th>
<th>Other invertebrates Mean</th>
<th>Larval fish Mean</th>
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<tr>
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<td></td>
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<td>0.15</td>
<td>15.49</td>
<td>0.66</td>
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always, more important than Calanus marshallae. Only in late July 2003 did copepods contribute relatively little to auklet diets.

**Diets at St. Paul I. — adult regurgitations of chick meals**

In contrast to St. George I., copepods were frequently (7 of 9 intervals) rare or absent from auklet diets at St. Paul I. from 2002 to 2005 (Fig. 2b, Table 2). This was remarkably dissimilar to diets there from 1996 to 2001 and to those previously reported from the Pribilof Is. or elsewhere. Copepods were hardly encountered in any of the 3 intervals sampled in 2003, and in 2004 and 2005 they were plentiful in early July, but declined abruptly and precipitously later in those summers. Furthermore, copepods were not abundant in late July 2002, the only interval sampled that summer. By 2006, copepods were again abundant in mid-July, a time by which, in the previous 2 yr at least, they had already essentially disappeared. At times when copepods were not plentiful, least auklets ate primarily hyperiid amphipods, euphausiids, and juvenile crabs (Table 2).

Calanus marshallae was absent in diets, or nearly so, in all intervals we sampled from 2002 to 2004, and in mid-July 2006, when Neocalanus spp. were present (Table 2). C. marshallae was plentiful in early July 2005, when Neocalanus were absent, but disappeared from diets by the middle of the month.

**Diets at St. Paul I. — adult fatty acids**

Calanoid copepod fatty acids are distinguished from fatty acids of all other marine species by the extremely large proportions of long-chain monounsaturated fatty acids and fatty alcohols (especially the isomers 20:1n-11, 20:1n-9, 22:1n-11, and 22:1n-9) arising from de novo biosynthesis (reviewed in Dalsgaard et al. 2003); this is consistent with our own data on the fatty acid composition of both Neocalanus spp. and Calanus marshallae (S. J. Iverson unpubl. data). These fatty acid biomarkers of copepods in least auklet adipose tissue were found at very high levels on St. Paul I. in early June in both 2003 and 2004 (Fig. 3), indicating that copepods had been available to them approximately 2 to 4 wk (the approximate integration period of dietary fatty acids) before the first chick meals were collected in early July. By July 2004, these fatty acid isomers had declined, but not to as low levels as by July 2003, which is consistent with the later decline of copepods in 2004 that was evident from chick meals.

**Fig. 3. Aethia pusilla. Characteristic copepod fatty acid biomarkers (mean ± SE) measured in adipose tissue biopsies obtained from adult least auklets in June (early) and July (late) of 2003 and 2004 on St. Paul I.**

**DISCUSSION**

**Interannual and inter-island variability**

The diets of least auklets Aethia pusilla at St. George I. that we observed from 1996 to 2006 were similar to those reported for the chick periods in 1977, 1984, and 1985 (Hunt et al. 1978, Bradstreet 1985, Roby & Brink 1986). Copepods predominated in all sampling periods except late July 2003. Among all copepods, Neocalanus spp. predominated in all but 1 collection, when they were replaced by Calanus marshallae. St. George I. lies near the oceanic domain, the habitat of Neocalanus spp., which are endemic to oceanic waters of the North Pacific and Bering Sea and are supplied to the outer continental shelf by advection. Calanus marshallae replaces Neocalanus on the shelf, where it is the only large calanoid species (Cooney 1981). Neocalanus are larger than C. marshallae and might have been selected preferentially over C. marshallae by auklets if both were equally available (i.e., Neocalanus might be more profitable in an energetic sense). Lack of C. marshallae in diets, therefore, would not necessarily indicate a lack of C. marshallae in the environment. Thus, Neocalanus spp. were apparently much less abundant/profitable than C. marshallae within the foraging range of auklets at St. Paul I. at times in 1997, 2000, 2001 and 2005. In the same vein, the switch from N. plumchrus/flemingeri in early July to N. cristatus in late July 2004 at St. George I.
likely reflected a change in the profitability of these species: all samples were collected from the Ulakaia Hill colony, minimizing the possibility that dietary specialization by birds at individual colonies might have accounted for the difference (Springer & Roseneau 1985, Flint & Golovkin 2002).

A much different picture emerged at St. Paul I., where copepods predominated in diets from 1996 to 2001, but thereafter occurred only during early summer. They were nearly gone, at the latest, by early August 2002, by early July 2003, and by mid-July 2004 and 2005. In 2006, Neocalanus and Calanus marshallae were again abundant in diets in mid-July, a time by which they had essentially disappeared in the previous 2 yr. Diets from 2002 to 2005 contrasted not only with those from 1996 to 2001 and 2006, but also with those in 1976, 1977, 1984, and 1992, when copepods dominated throughout the chick period (Hunt et al. 1978, Bradstreet 1983, Flint & Golovkin 2002).

As noted earlier, St. Paul I. lies higher on the continental shelf than St. George I. and is therefore not as near to the deep basin, and the source of Neocalanus spp. Moreover, the location of St. Paul I. places it somewhat more within the realm of Calanus marshallae, a shelf species, than St. George I. Although auklets at St. Paul I. commonly have access to copepods in summer, obviously there can be situations when foraging areas influenced by oceanic waters, i.e. where Neocalanus would be expected, are apparently beyond the profitability range of these small seabirds. St. Paul I. lies just 75 km north of St. George I., and although the foraging range of least auklets can be as great as 80 to 100 km, depending on prey distributions (Obst et al. 1995, Flint & Golovkin 2002), from 2002 to 2005 Neocalanus were out of range of birds from St. Paul I. much of the time. And, not only were Neocalanus commonly unavailable to auklets at St. Paul I. from 2002 to 2005, there were few C. marshallae either.

Causes of copepod anomalies

The unusual paucity of Calanus marshallae in continental shelf waters and the sharp demarcation between shelf and oceanic zooplankton communities from 2002 to 2005 were documented by traditional sampling with plankton nets in a single cruise in late July through September 2004 (Coyle et al. 2008). Depleted Neocalanus abundances around St. Paul I. at that time were apparently caused by a very sharp boundary between oceanic and shelf water masses (the Middle Front) that restricted the oceanic zooplankton community to the deeper offshore region beyond the reach of foraging least auklets from St. Paul I. The presence of Neocalanus spp. in diets at St. George I. clearly demonstrated that the problem was one of copepod distribution rather than copepod production. In contrast, the lack of C. marshallae reflected chronic failures of spring cohorts to persist through summer across a broad region of the shelf in recent years (Coyle et al. 2008).

Transport of shelf water into the vicinity of the Pribilof Is. in summer freshens the upper 50 m of the water column and enhances the strength of the Middle Front (Stabeno et al. 2008) that lies in the vicinity of the 100 m isobath and runs just south of the Pribilof Is. (Coachman & Charnell 1979). Stabeno et al. (2008) proposed one scenario for July to August 2004, in which middle shelf waters expanded southward and westward, dominating the region around the Pribilofs. This kept oceanic water and its zooplankton community away from the Pribilofs (Coyle et al. 2008), sufficiently far that Neocalanus spp. were beyond the foraging range of least auklets from St. Paul I. Auklet diets revealed that such a condition apparently occurred many times in the 2000s, and in 2003 it was so strong that auklets at St. George I. also had limited access to oceanic copepods by late July.

Unusually high atmospheric temperatures over the Bering Sea in the 2000s have had a dramatic effect on warming of the upper layer of the water column over the middle shelf (Stabeno et al. 2007), which has apparently had major consequences to the structure of the zooplankton community there. In 2004, a warm year in a series of warm years, the shelf community was dominated by smaller species of copepods and other taxa of zooplankton compared to 1999, a cooler year in a series of cool years (Coyle et al. 2008). Coyle et al. (2008) have proposed that the hot and deep upper layer effectively capped the water column, and in the absence of extreme storms that might have broken down the strong stratification, essential post-bloom primary production was so depressed that spring cohorts of Calanus marshallae starved later in summer. Post-bloom new (nitrate) primary production over the middle shelf during summer can augment total annual production by as much as 10 to 50%, depending on the frequency and intensity of storms that break down stratification and mix nutrient-laden water sequestered beneath the pycnocline into the euphotic zone (Sambrotto et al. 1986). But, in 2004 for example, the stratification coefficient had a mean value of 90 J m⁻³, or 2 to 3 times greater than that believed to be optimal for summer primary productivity, and thus, zooplankton productivity (Coyle et al. 2008). As a consequence, a floral community of phytoflagellates and other small taxa likely developed and persisted in 2004 and in other recent years with similar conditions, which fostered the shift from larger species of zooplankton to smaller ones.
There is a notable relationship between one index of environmental conditions in the southeastern Bering Sea, May sea surface temperature (SST), and the presence of copepods in auklet diets at St. Paul I. (Fig. 4). In 8 yr of average or cool May SST, Neocalanus spp. and/or Calanus marshallae were available to auklets at St. Paul I. However, warm years for which we have diet data were divided into 2 groups: those prior to 2000 (1977 and 1996), when copepods were available despite positive SST anomalies in May, and those after 2000 (2002 to 2005), when copepods were variably scarce. The difference was not simply a consequence of sampling dates—that is, in 1977 and 1996, copepods were available at times in summer when they were scarce in the 2000s. The difference appears to involve the degree of warming that occurred after May in these 2 eras. For example, in 1996, despite early warming of the surface layer, the temperature of the upper layer above the thermocline did not rise to the levels seen from 2002 to 2005, and the total integrated heat content of the water column was correspondingly lower (Stabeno et al. 2008). Similar data from 1979 to 1981 (Sambrotto et al. 1986) suggest that this situation likely prevailed in 1977 as well. These relationships identify a process-oriented conceptual model that could be used to generate hypotheses for future research.

**Consequences of copepod anomalies**

For least auklets, the low abundance of their principal copepod prey also had adverse physiological effects, as revealed by elevated levels of corticosterone, an adrenal hormone indicative of nutritional stress (Benowitz-Fredericks et al. 2008). Corticosterone levels of auklets at St. Paul I. were high in June and July 2003, corresponding to the early decline in copepods that year. In 2004, levels were comparatively low in June and early July, but rose rapidly by late July after copepod abundance collapsed. Field data on aspects of least auklet nesting success or the fitness of chicks at St. Paul I. are not available to evaluate the direct effects of shifts in diets. However, at St. Matthew I. in the central Bering Sea, least auklet chicks grew significantly faster when copepods (Calanus marshallae) were abundant in meals brought by adults (Springer et al. 1986); there are strong relationships between least auklet demographic parameters and the amount of copepods in chick diets in the Aleutian Islands (Jones & Williams 2007); and at St. Lawrence I. in the northern Bering Sea, the daily survival rate of least auklet chicks was proportional to the amount of copepods in their diets (Gall et al. 2006). Work on other species of seabirds has found strong negative correlations between stress and various demographic parameters (Kitaysky et al. 2007). Thus, it is reasonable to suspect that the feeding environment for least auklets at St. Paul I. from 2002 to 2005 was detrimental to the health of the population.

In an important respect, the very low abundance of Calanus marshallae around the Pribilof Is. in recent years has been just one symptom of the much larger, expansive change in the structure of the pelagic community of the continental shelf of the eastern Bering Sea. Coyle et al. (2008) reported a shift in the size spectrum of zooplankton over the shelf from larger (e.g. C. marshallae) to smaller taxa, and suggested that if the condition persisted it would be expected to have numerous repercussions in the pelagic food web for various consumer species of commercial, aesthetic, and ecological importance. Effects of such a shift would be exacerbated around the Pribilof Is., and elsewhere along the outer shelf, by the early expansion of middle shelf waters seaward in summer and the associated offshore displacement of the community of larger oceanic plankton, including notably Neocalanus spp.

**CONCLUSIONS**

Least auklets at St. Paul I., and probably other planktivores in the region of the Pribilof Is., were subjected to prey (copepod) shortage from 2002 to 2005, apparently brought on by unusually high water temperatures over the continental shelf. A single oceanographic research cruise in summer 2004 documented characteristics of the physical environment and plankton communities that were anomalous compared to previous observations in cooler years. By studying diets of least auklets at the Pribilofs, we extended the temporal and spatial scales of our knowledge of these conditions, and this gave us a much improved under-
Understanding of responses of the ocean ecosystem to climate warming. There is no evidence that such conditions occurred between the mid-1970s and 2002.

Least auklets sample their environment very efficiently and effectively—despite a limitation on the depth to which they can dive (about 15 m), they are able to forage over considerable distances (up to at least 80 km from their colonies)—and they provide a valuable index of abundance of ecologically important species of zooplankton. The information contained in their diets is large and the cost of acquiring it is small. They should therefore be included and emphasized in any plan to monitor environmental variability in the Bering Sea.

The stories that scientists have to tell about expectations for future impacts of global warming on ecosystems are enriched with integrated observations that link changes in oceanographic conditions with predator and prey data. Collections and analyses of diet data from least auklets in the Bering Sea provide a wealth of information from which we can better understand the ecosystem-scale consequences of climate change. This story tells us that if warming trends continue (e.g. Overland & Wang 2007), there may be serious repercussions to auklets and other planktivorous species in the eastern Bering Sea. Communities and ecosystems are not static, but change over time, yet changes such as those reported here and by others, apparently in response to unusual warming of the Bering Sea in this century, appear to be altering in fundamental ways the structural and functional elements of the ecosystem. We do not know how or if these changes might alter food webs crucial to this highly productive sea over the long term, but they should be a cause for concern to people who depend upon its vast resources and to those charged with their management.

Acknowledgements. We thank numerous field assistants of the US Fish and Wildlife Service and University of Alaska Fairbanks for collecting auklet diet samples, K. Turco for enumerating prey in the samples, and G. Van Vliet and 3 anonymous reviewers for helpful comments. Funding for this study was provided by the US Fish and Wildlife Service Report AMNWR 04/15, Homer, AK.

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Aquatic bird disease and mortality as an indicator of changing ecosystem health

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ABSTRACT: We analyzed data from pathologic investigations in the United States, collected by the USGS National Wildlife Health Center between 1971 and 2005, into aquatic bird mortality events. A total of 3619 mortality events was documented for aquatic birds, involving at least 633,708 dead birds from 158 species belonging to 23 families. Environmental causes accounted for the largest proportion of mortality events (1737 or 48%) and dead birds (437,258 or 69%); these numbers increased between 1971 and 2000, with biotoxin mortalities due to botulinum intoxication (Types C and E) being the leading cause of death. Infectious diseases were the second leading cause of mortality events (20%) and dead birds (20%), with both viral diseases, including duck plague (Herpes virus), paramyxovirus of cormorants (Paramyxovirus PMV1) and West Nile virus (Flavivirus), and bacterial diseases, including avian cholera (Pasteurella multocida), chlamydiosis (Chlamydia psittici), and salmonellosis (Salmonella sp.), contributing. Pelagic, coastal marine birds and species that use marine and freshwater habitats were impacted most frequently by environmental causes of death, with biotoxin exposure, primarily botulinum toxin, resulting in mortalities of both coastal and freshwater species. Pelagic birds were impacted most severely by emaciation and starvation, which may reflect increased anthropogenic pressure on the marine habitat from over-fishing, pollution, and other factors. Our study provides important information on broad trends in aquatic bird mortality and highlights how long-term wildlife disease studies can be used to identify anthropogenic threats to wildlife conservation and ecosystem health. In particular, mortality data for the past 30 yr suggest that biotoxins, viral, and bacterial diseases could have impacted >5 million aquatic birds.

KEY WORDS: Emerging infectious diseases · Aquatic birds · Seabirds · Ecosystem · Health · Bird mortality · Sentinel species · Conservation medicine · Botulism · Viral disease · Bacterial disease

INTRODUCTION

Increasingly, wildlife biologists, veterinarians, and ecologists are reporting significant wildlife mortality events (Dobson & Foufopoulos 2001, Friend et al. 2001); many of these are later determined to be caused by infectious diseases or acute or chronic pollution. In some cases, diseases have caused population declines and have threatened species diversity (Warner 1968, Lyles & Dobson 1993, Berger et al. 1998, Daszak & Cunningham 1999). Diseases that have recently increased in incidence or impact, or have recently moved into a new host population or geographic region are termed ‘emerging diseases’, following the terminology adopted widely for a number of human diseases (Lederberg et al. 1992, Smolinski et al. 2003). Like emerging diseases of humans, emerging diseases of wildlife are often directly linked to anthropogenic environmental changes.

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that provide the driving force behind their recent change in incidence, impact, geography, or host (Schrag & Wiener 1995, Daszak et al. 2001).

Despite the recognition of emerging diseases as a potentially key threat to wildlife populations, research on the links among anthropogenic activities, on changes in ecological health, and on disease emergence has largely concentrated on terrestrial ecosystems, with a few notable exceptions. Marine diseases serve as indicators of global climate change (Harvell et al. 2002), and marine species of high conservation concern are affected by increasingly well-studied emerging diseases (Harvell et al. 1999), such as morbilliviruses in dolphins (Domingo et al. 1990), canine distemper viruses in seals (Stone 2000), and fibropapillomas in sea turtles (Williams et al. 1994). For aquatic birds, there has been a great deal of interest in the effects of acute and chronic pollution (petroleum, pesticides, heavy metals, or other industrial by-products), collisions with man-made structures (buildings, power lines, or wind turbines), refuse ingestion, fishing line or net entanglement, and changes in food availability and climate on their populations (Sydeman et al. 1994, Camphuysen & Heubeck 2001, Carter 2003, Newman et al. 2003, 2006, Burger & Gochfeld 2004). However, there have been few large-scale studies of trends in infectious and non-infectious diseases in this fauna (Friend et al. 2001, Muzzafar & Jones 2004).

In order to better understand the disease, environmental, and anthropogenic threats that pose the greatest dangers to aquatic bird populations, we have analyzed 30 yr of diagnostic evaluations from dead aquatic birds (seabirds, shorebirds, waders, and sea ducks) recovered in the US or US territories and diagnosed by wildlife pathologists from the US Geological Service, National Wildlife Health Center (NWHC). Our analyses provide a review of the magnitude as well as the temporal and spatial patterns of diseases and suggest several anthropogenic drivers of these diseases in aquatic birds.

MATERIALS AND METHODS

We selected aquatic bird (seabirds, shorebirds, waders, and sea ducks) mortality data in the US and US territories from 2 databases (‘Diagnostic Database’ and ‘Epizoo’) maintained by the NWHC since 1971. The Diagnostic Database contains information from necropsies on individual birds conducted at the NWHC when no mass mortality was reported. The Epizoo database contains information about mortality events observed in the field and reported by biologists, researchers, diagnostic laboratories, or the general public. In most cases, carcasses were sent to the NWHC for necropsy. Field necropsy data and diagnoses are entered into this database when biologists or field veterinarians have followed the appropriate necropsy and sample collection guidelines and diagnostic results from the appropriate diagnostic laboratories have been provided. For all mass mortality events, information provided to the NWHC included: (1) a gross necropsy report, (2) a complete set of formalin-fixed tissues for histology, and (3) additional refrigerated and frozen tissues for toxicology and infectious disease testing.

For all cases used in the present study, a final diagnosis was determined by a NWHC pathologist.

Each event in the Diagnostic Database or Epizoo used in the present study was described by the following information: record identification number, date of collection, date on which the event started and ended (if applicable), eco-region, flyway, county and state of collection, name of refuge or park (if applicable), contact persons, species name, common name, recent or anticipated population changes, number of sick individuals by species, clinical signs, number of dead individuals by species, estimated number of dead individuals, estimated population, environmental conditions, habitat changes, recent weather changes, history of disease events at this site, and final diagnosis. The general cause of mortality for individuals or in events was further refined into the categories noted in Table 1.

Note that we considered botulism an environmental cause of death rather than a lethal infectious disease because the majority of avian mortality due to this disease is actually caused by ingestion of the toxin, rather than primary infection of the gastrointestinal tract by Clostridium botulinum bacteria (Rocke & Friend 1999). We have discussed the implications of this categorization in the discussion. A diagnosis of ‘pathology’ was used if there was evidence of histological changes observed by microscopy that was suggestive of insult such as a disease or toxin exposure. However, because no toxin or disease could be identified as having contributed to the observed histological lesion, these birds were grouped independently from other causes of mortality. A diagnosis of ‘emaciation/starvation’ was made if birds were physically emaciated, no gross or microscopic lesions or injuries were identified during necropsy, and no other causes of mortality could be determined (diseases, toxins, biotoxins, etc.). An ‘undetermined’ diagnosis was given to any case in which no cause of mortality could be determined.

For the purposes of the present study, we included only species that inhabit oceans for >8 mo of the year and did not include freshwater-inhabiting ‘waterfowl’ species. Based on their habitat use and natural history, species were divided into groups for additional analyses: (1) pelagic/offshore species that use primarily
pelagic habitats, (2) near-shore/coastal species that spend most of their time within several km of the coastline, and (3) freshwater species that use both marine and freshwater habitats. We cross-referenced each individual from the Diagnostic Database to rule out dual reporting in the Epizoo database. We used MATLAB (MathWorks) to perform descriptive statistics and to create charts and graphs. Analyses were also performed to examine basic geographic patterns of seabird mortality by mapping mortality incident locations in ESRIArcMap9.0 Geographic Information System (ESRI). Because there are different numbers of inland and shoreline states, we examined the percentage of each general category that contributed to the mortality events in inland and shoreline states.

RESULTS

Causes of mortality

Between 1971 and 2005, 3619 mortality events were reported in aquatic birds, for which 1 or more birds were examined by wildlife pathologists to diagnose the cause of mortality. Of the mortality events (involving multiple birds at a single location; Fig. 1a) or individual bird deaths (Fig. 1b), California reported the largest number of mortality events, while California and Nevada reported the largest number of dead aquatic birds. The 3619 mortality events involved 633,708 dead birds from 158 species belonging to 23 families: Alcidae, Anhingidae, Anatidae, Ardeidae, Charadriidae, Ciconiidae, Cinclidae, Diomedeidae, Fregatidae, Gaviidae, Haematopodidae, Hydrobatidae, Laridae, Pelecanidae, Phaethontidae, Phalacrocoracidae, Phoenicopteridae, Procellariidae, Recurvirostridae, Scolopacidae, Stercorariidae, Sulidae, and Threskiornithidae (Supplementary Material available at www.int-res.com/articles/suppl/m352p299_app.xls, Table 1). The frequency and causes of mortality events by family are reported here in Table 1. The causes of mortality events and the total number of dead birds based on habitat are reported in Table 2. The largest number of mortality events was observed in Laridae, Scolopacidae, and Ardeidae, and was found in the nearshore/coastal habitat use category.

<table>
<thead>
<tr>
<th>Family</th>
<th>Anthropogenic (n) (%)</th>
<th>Environmental (n) (%)</th>
<th>Infectious (n) (%)</th>
<th>Pathology with no etiology (n) (%)</th>
<th>Toxicosis (n) (%)</th>
<th>Undetermined (n) (%)</th>
<th>Total numbers (n)</th>
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<td>Anatidae</td>
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<td>62 (26)</td>
<td>26 (10)</td>
<td>45 (19)</td>
<td>6 (2)</td>
<td>25 (11)</td>
<td>11 (9)</td>
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<td>34 (25)</td>
<td>22 (16)</td>
<td>16 (12)</td>
<td>23 (16)</td>
<td>22 (16)</td>
<td>15 (11)</td>
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<td>1 (5)</td>
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<td>15 (45)</td>
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<td>10 (26)</td>
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<td>88 (35)</td>
<td>30 (12)</td>
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<td>3 (70)</td>
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<td>228 (45)</td>
<td>45 (9)</td>
<td>8 (1)</td>
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<td>83 (43)</td>
<td>27 (14)</td>
<td>51 (26)</td>
<td>6 (3)</td>
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<td>0 (0)</td>
<td>0 (0)</td>
<td>1 (100)</td>
</tr>
<tr>
<td>Recurvirostridae</td>
<td>2 (2)</td>
<td>80 (75)</td>
<td>15 (14)</td>
<td>3 (3)</td>
<td>1 (1)</td>
<td>5 (5)</td>
<td>106 (106)</td>
</tr>
<tr>
<td>Scolopacidae</td>
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<td>435 (80)</td>
<td>38 (7)</td>
<td>15 (3)</td>
<td>23 (4)</td>
<td>31 (6)</td>
<td>547 (547)</td>
</tr>
<tr>
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<td>450 (45)</td>
<td>233 (23)</td>
<td>83 (8)</td>
<td>86 (9)</td>
<td>114 (11)</td>
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<tr>
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<td>1 (33)</td>
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<td>0 (0)</td>
<td>1 (33)</td>
<td>1 (33)</td>
<td>3 (70)</td>
</tr>
<tr>
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<td>26 (45)</td>
<td>3 (5)</td>
<td>8 (14)</td>
<td>9 (16)</td>
<td>10 (17)</td>
<td>58 (58)</td>
</tr>
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<td>Cincidae</td>
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<td>1 (100)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>1 (100)</td>
</tr>
<tr>
<td>Total</td>
<td>3619</td>
<td></td>
<td></td>
<td></td>
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</table>
Environmental causes were the most important class of mortality events, accounting for 1737 or 48% of those in the database. Environmental causes were also responsible for the largest proportion of dead birds (437 258 or 69%) in this database (Fig. 2a,b). Over three-quarters of the environmental causes of mortality were due to biotoxin poisoning, representing 78% of the aquatic bird deaths in this category (Fig. 2c). Of all 344 045 deaths due to biotoxins, only 12 were not caused by botulism (Clostridium botulinum) toxin. This supports our categorization of botulism as a non-infectious disease for the purposes of this study, because the majority of individual bird deaths due to C. botulinum are actually due to birds ingesting up the environmentally present toxin, rather than due to primary bacterial infection.
Infectious causes (Fig. 2b) resulted in the second largest category: 1 of 5 of aquatic bird mortalities (125,471 or 20%). The most commonly diagnosed infectious diseases were viral, representing 54% of all deaths due to infectious disease (Fig. 2d) and 10.5% of all aquatic bird deaths. The most commonly diagnosed viral diseases were (duck plague Herpes virus, paramyxovirus of cormorants Paramyxovirus PMV1, and West Nile virus Flavivirus). The most commonly diagnosed bacterial diseases were (avian cholera Pasteurella multocida, chlamydiosis Chlamydia psittaci, and salmonellosis Salmonella sp.), representing almost all deaths due to infectious diseases. Fungal and parasitic diseases were found to be relatively minor causes of mortality events (7 and 1%, respectively) in the context of both infectious and non-infectious causes of death (Fig. 2d). The most common organisms included: fungal (aspergillosis

![Image of pie chart](image_url)

**Fig. 2.** Specific and general causes of aquatic bird deaths from 1971 to 2005. (a) Cause of death per mortality event shown in percent of 3619 aquatic bird mortality events. (b) Cause of death per bird of 633,708 aquatic birds. (c) Specific cause of death per bird of 441,045 aquatic bird mortalities due to environmental causes. (d) Specific cause of death per bird of 125,471 aquatic bird mortalities due to infectious diseases.

Aquatic bird mortality attributable to anthropogenic interactions accounted for 5% (180) of the mortality events or 1% (558) of the dead birds; toxicosis accounted for 7% (258) of the mortality events or 3% (17 704) of the dead birds; pathology with no known etiology accounted for 11% (384) of the mortality events or 4% (22 544) of the mortality events or 3% (21 064) of the dead birds (Fig. 2a,b).

Mortality events of pelagic/offshore species were most frequently linked to environmental events (74; 34%) or undiagnosed pathology (58; 26%). Pelagic seabird deaths (104 855) were most commonly associated with environmental causes (79 177), and, of these, 99% was due to emaciation/starvation. Toxicosis accounted for 11 623 deaths, of which 99% was due to petroleum exposure, and undetermined causes represented 11 136 individual pelagic bird deaths (Table 2, Fig. 3).

Nearshore/coastal species mortality events were most frequently caused by biotoxin exposure (1377; 41%) and bacterial diseases (418; 12%), while the largest numbers of bird deaths were attributable to biotoxin exposure (139 823; 33%), emaciation/starvation (85 195; 20%), and viral diseases (66 432; 16%) (Fig. 3b,c,e,f).

Mortality events associated with species that use both marine and freshwater habitats were most frequently caused by biotoxin exposure (1468; 44%) and bacterial diseases (419; 13%), while the largest numbers of bird deaths were attributable to biotoxin exposure (341 376; 65%), viral diseases (66 434; 13%), and bacterial diseases (43 123; 8%). Other causes of death included pathology of undiagnosed origin (22 032 birds; 4%), emaciation/starvation 2% (9909), weather events 2% (9220), and fungal disease 2% (8689). Oil exposure was a relatively minor problem 3% (1571). The most frequently reported diseases for both nearshore/coastal species and those using both marine and freshwater habitats include avian cholera, paramyxovirus, West Nile virus, and salmonellosis.

Temporal and geospatial trends in mortality

Between 1971 and 1995, the number of mortality events per 5 yr interval increased from <50 events to >700 events. Environmental, infectious and toxicosis categories were the causes of mortality that increased...
most prominently among these years (Table 3). From 1995 to 2000, the overall number of mortality events decreased slightly, while the number of events associated with botulism continued to increase and the number of infectious diseases reached a plateau.

Numbers of aquatic birds that died from environmental etiologies increased in magnitude and peaked in 2000 (49,444). Infectious disease-related bird deaths peaked in 2005 (11,595), after a decline between 1995 and 2000. By 2005, fewer numbers of events were reported to the NWHC overall and the numbers of dead birds from all causes decreased to slightly <100,000 from the peak numbers of mortalities (257,707) reported in 2000 (Table 3).

Finally, we compared the frequency of each category of mortality events occurring in inland versus shoreline states (Table 4) because a high incidence of mortality events was observed in inland states (Fig. 1a). The numbers of mortality events and total dead birds are higher for inland states than for shoreline states. The numbers of biotoxin-associated events and total mortalities for inland states are greater than twice those for shoreline states. There were more than twice as many incidences of mortality events and total dead birds due to bacterial infections and from unknown causes in shore states, while emaciation/starvation was more than 4 times more frequent in shore states compared to inland states and was the cause of almost one-third of aquatic bird deaths.

### DISCUSSION

#### Causes of mortality

Our analysis of 30 yr of necropsy data for aquatic birds in the US indicates that environmental factors are the major cause of mortality events and of individual bird deaths. This broad category includes ‘emaciation/starvation’, which was the leading cause of environmentally related mortalities among pelagic/offshore species. The frequency of mortalities from emaciation/starvation has risen since 1971, demonstrating that it is an important pelagic bird issue from a temporal perspective as well. Other research has suggested that declines in marine fish and marine resources have affected upper level marine predators such as seabirds and killer whales (Piatt & Anderson 1996, Estes et al. 1998) and that this is correlated with declines in fish catches over the last 3 decades (Piatt et al. 2002). Some authors have linked large-scale seabird wrecks, failed breeding efforts, or a lack of nest initiation among seabirds in North America (from central California, the Pacific Northwest, British Columbia, Alaska, Newfoundland) and Europe (North Sea, Irish Sea, Shetland Islands) over the past 5 to 10 yr to changes in distribution and abundance of prey (Bourne 1976, Sydeman et al. 1994, Piatt & Anderson 1996, Piatt & Van Pelt 1997) or anomalous oceanographic conditions (Ainley & Boekelheide 1990, Bodkin & Jameson 1991, Daoust et

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Table 3. Number, mean, and SE of aquatic bird mortality events and aquatic bird deaths for 5 yr intervals from 1971 to 2005. Data for years preceding 1971 are sparse, so no means and SE were calculated—only the total is given. Of the total numbers 532 mortality events (including 27,047 dead birds) had no reporting year, so these are not included in these tables.

<table>
<thead>
<tr>
<th>5 yr period ending in:</th>
<th>Anthropogenic</th>
<th>Environmental</th>
<th>Infectious</th>
<th>Pathology with no etiology</th>
<th>Toxicosis</th>
<th>Undetermined</th>
<th>Total number</th>
</tr>
</thead>
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<td>11</td>
<td>0</td>
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<td>11</td>
<td>45</td>
</tr>
<tr>
<td>1975</td>
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<td>1.8 ± 0.8</td>
<td>3.8 ± 2.5</td>
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<td>1.8 ± 1.0</td>
<td>0.2 ± 0.2</td>
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<tr>
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<td>17.2 ± 9.4</td>
<td>6.6 ± 3.1</td>
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<td>1.6 ± 1.0</td>
<td>2.4 ± 0.9</td>
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<tr>
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<td>36.6 ± 8.5</td>
<td>11.2 ± 1.7</td>
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<td>7.2 ± 2.1</td>
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<td>2005</td>
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<td>51.4 ± 15.6</td>
<td>29.6 ± 8.1</td>
<td>2.2 ± 0.9</td>
<td>4.8 ± 0.6</td>
<td>11.6 ± 4.6</td>
<td>508</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3087</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>5 yr period ending in:</th>
<th>Number of dead birds</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pre-1971</strong></td>
<td>4</td>
</tr>
<tr>
<td>1975</td>
<td>0*</td>
</tr>
<tr>
<td>1980</td>
<td>0</td>
</tr>
<tr>
<td>1985</td>
<td>1 ± 1</td>
</tr>
<tr>
<td>1990</td>
<td>360 ± 213</td>
</tr>
<tr>
<td>1995</td>
<td>406 ± 228</td>
</tr>
<tr>
<td>2000</td>
<td>190 ± 190</td>
</tr>
<tr>
<td>2005</td>
<td>57 ± 38</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
</tr>
</tbody>
</table>

*No dead birds reported despite a mortality event being reported
Table 4. Comparison of specific causes of aquatic bird mortality events and aquatic bird deaths between inland and shoreline states

<table>
<thead>
<tr>
<th>Causes of mortality</th>
<th>Percent of specific causes of:</th>
<th>Mortality events</th>
<th>Dead birds</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Inland Shore</td>
<td>Inland Shore</td>
</tr>
<tr>
<td>Bacterial</td>
<td>5.6</td>
<td>14.9</td>
<td>4.4 11.0</td>
</tr>
<tr>
<td>Bacterial or viral</td>
<td>0.2</td>
<td>0.2</td>
<td>0.0 0.1</td>
</tr>
<tr>
<td>Biotoxin</td>
<td>66.7</td>
<td>28.9</td>
<td>81.3 24.9</td>
</tr>
<tr>
<td>Fungal</td>
<td>0.4</td>
<td>3.5</td>
<td>1.6 1.3</td>
</tr>
<tr>
<td>Gunshot</td>
<td>0.9</td>
<td>0.7</td>
<td>0.0 0.7</td>
</tr>
<tr>
<td>Heavy metal</td>
<td>0.4</td>
<td>1.0</td>
<td>0.0 0.0</td>
</tr>
<tr>
<td>Natural biology</td>
<td>0.1</td>
<td>0.6</td>
<td>0.0 0.3</td>
</tr>
<tr>
<td>Net entrapment</td>
<td>0.0</td>
<td>0.6</td>
<td>0.0 0.5</td>
</tr>
<tr>
<td>Nutritional</td>
<td>0.5</td>
<td>0.3</td>
<td>0.0 0.0</td>
</tr>
<tr>
<td>Oil</td>
<td>0.2</td>
<td>2.8</td>
<td>0.0 4.3</td>
</tr>
<tr>
<td>Open</td>
<td>5.3</td>
<td>11.4</td>
<td>0.4 6.5</td>
</tr>
<tr>
<td>Parasites</td>
<td>1.5</td>
<td>2.2</td>
<td>0.2 0.3</td>
</tr>
<tr>
<td>Pathology</td>
<td>6.2</td>
<td>12.6</td>
<td>5.1 1.9</td>
</tr>
<tr>
<td>Pesticide</td>
<td>0.4</td>
<td>2.3</td>
<td>0.0 0.6</td>
</tr>
<tr>
<td>Poison</td>
<td>0.6</td>
<td>0.8</td>
<td>0.0 0.2</td>
</tr>
<tr>
<td>Powerline collision</td>
<td>0.5</td>
<td>0.6</td>
<td>0.0 0.1</td>
</tr>
<tr>
<td>Emaciation/Starvation</td>
<td>1.6</td>
<td>7.2</td>
<td>0.6 28.3</td>
</tr>
<tr>
<td>Trauma</td>
<td>1.7</td>
<td>3.9</td>
<td>0.1 0.6</td>
</tr>
<tr>
<td>Undetermined</td>
<td>0.4</td>
<td>2.1</td>
<td>0.3 0.3</td>
</tr>
<tr>
<td>Viral</td>
<td>5.3</td>
<td>2.2</td>
<td>5.0 16.3</td>
</tr>
<tr>
<td>Weather</td>
<td>1.8</td>
<td>1.3</td>
<td>1.1 1.9</td>
</tr>
</tbody>
</table>

al. 1998). Our data suggest that this cause of death has increased in importance, although it is not possible to confirm whether the starvation was primarily due to a lack of prey related to overfishing or climate issues, or another cause that was not evident upon necropsy.

The leading cause of environmentally related mortalities and events among nearshore/coastal and freshwater bird species was biotoxin exposure and, specifically, botulinum intoxication (Types C and E) or an untyped botulism (most likely Type C or E). However, it is important to note that our inclusion of botulism as an environmental, rather than infectious, cause of death is critical to distinguishing which general cause of death is the most important (if botulism is considered infectious, the dominant cause of overall mortality in our database would be infectious diseases). While it is true that infection with Clostridium botulinum is an infectious disease, this is rarely the cause of death in wild waterbirds; rather, the ingestion of environmental botulinum toxin (produced either directly in the gastrointestinal tract of infected birds, or from environmental multiplication of C. botulinum) is the most common cause of death. Importantly, the environmental causes of death most commonly reported in scientific publications and non-scientific media (chemical pollution) are less significant in our database than either botulinum intoxication or infectious diseases.

Our analysis confirms that infectious diseases are an important cause of mortality events and individual bird deaths (in the 1000s per annum) in the US alone, especially among nearshore/coastal and freshwater aquatic birds. Mass mortality events were caused more often by bacterial events than by viral events; however, the number of dead aquatic birds is greater due to viral etiologies. Previous authors have suggested that bacterial diseases are a significant burden on aquatic bird populations (Reece 1989); however, our data do not demonstrate this. Population-scale effects of microbial and parasitic infections in aquatic birds are poorly understood (Reece 1989, Muzzafar & Jones 2004), and, although bacterial pathogens are often documented in aquatic birds, it is often unclear whether they have played a role in mortality events or in beach-cast birds. The recognition of the West Nile virus as a cause of death in aquatic birds is interesting. This introduced pathogen is responsible for high mortality rates in a number of terrestrial species, and its impact on aquatic birds adds another dimension to the toll of introduced pathogens on North American ecosystems.

A suite of other anthropogenic environmental factors have caused aquatic bird mortality, including marine pollution in the form of oil spills, pesticides, heavy metals, trauma, gunshot, collisions with power lines, and fishing net or fishing line entanglement. Although 1000s of pelagic birds have been impacted by net entrapment over the past 30 yr, these mortalities were not part of this database and should be considered as an additional significant impact to aquatic birds, although not represented here. A more complete assessment of pelagic bird mortalities would include this data as well. Finally, we did not find algal blooms to be a frequent cause of mortality in the current database, but recent advances in diagnostic techniques that detect the presence of algal toxins may explain why others have more recently reported aquatic bird mortality due to algal blooms (Williams et al. 1992, Sherman 2001, Sherman & Epstein 2001).

Temporal trends in mortality

A number of temporal trends can be gleaned from our datasets. First, there was a striking increase in the number of birds submitted for diagnostic evaluation from 1971 through 2000, followed by a decrease during the last 5 yr of the study. The rise in reports likely reflects increases in (1) interest in aquatic bird conservation, (2) human inhabitants and human visitation to coastal locations, (3) funding for monitoring and studies of this type from federal, state, and private sources, (4) interest in the impact of oil pollution on aquatic birds, as well as (5) the expansion of diagnostic facilities such as the NWHC. It is unclear why the number of reports declined from 2000 to 2005, but changing
weather patterns resulting in drought, changes in population numbers, or changes in the use of traditional wintering and stop-over areas could have resulted in a change in the disease outbreak patterns observed.

While the overall temporal trend in number of birds submitted for diagnostic evaluation may be biased by changes in sampling effort and funding, comparison of temporal trends among causes of death are less biased due to the standardized necropsy and diagnostic methods used throughout the duration of this study. Thus, the increasing importance of infectious diseases and environmental causes of mortality events and bird deaths from 1971 to 2000 is likely a real trend, reflecting some underlying, but unknown, cause. Viral disease events were relatively unimportant until the mid-1990s, when West Nile virus emerged in the US. The only aquatic species reported to have West Nile virus as a major cause of mortality is the American white pelican Pelecanus erythrorhynchos. Individual mortalities were reported in many aquatic bird species, including double-crested cormorant Phalacrocorax auritus, great egret Ardea alba, great blue heron A. herodias, black-crowned night heron Nycticorax nycticorax, ring-billed gull Larus delawarensis, California gull L. californicus, Franklin’s gull L. pipixcan, and American avocet Recurvirostra americana. Viral diseases also play an increasingly important role in the health of aquatic birds, as has been suggested in other studies (Daoust et al. 1998, Sherman 2001, Sherman & Epstein 2001, Harvell et al. 1999, Converse & Kidd 2001, Friend et al. 2001).

**Limitations to the database**

While we can establish some very important trends from this database on aquatic bird mortalities, it is important to recognize certain limitations as well. The counts of dead birds that comprise the aquatic bird database may be inherently biased because only dead birds encountered by humans in the environment, and subsequently submitted for diagnosis, became data points. Therefore, a counting bias exists towards birds submitted for analysis from geographic locations where (1) public access exists; (2) human population densities are large enough to provide some level of ‘indirect’ surveillance for dead birds; (3) birds are large enough to be seen by people passing by; (4) locations are monitored regularly by natural resource agency personnel as in the case of Wildlife Refuges and National Parks; (5) predators (wild or domestic animals) do not remove all carcasses before they are recovered; (6) formalized beached-bird surveys are conducted on a regular basis; and (7) ecological conditions warrant increased surveillance (beach closures, algal blooms, oil spill events). We observed a discrepancy in the number of birds represented in the database based on preferred ecological habitats. Numbers of birds in the database that use both marine and freshwater habitats (521 670) and coastal marine habitats (419 881) outnumbered birds from pelagic marine habitats (104 855), demonstrating that some bias exists based on natural history. Finally, there were considerable changes in sampling effort over the period of the present study, which likely affect the rigor of analyses of temporal trends in overall mortality.

These biases suggest that the number of mortality events and especially the number of individual birds found dead greatly under-represent the true magnitude of aquatic bird mortality in the US. It has been demonstrated for common murres Uria aalge collected during oil spills and from carcass-persistence studies that only a small proportion (<10 to 15%) of birds that are oiled or are part of ‘carcass drift studies’ wash ashore (Ford et al. 1987, Piatt & Ford 1996, Ford et al. 2004). Consequently, fewer birds are actually recovered by personnel monitoring beaches. Most dead birds either sink at sea or, once deposited on the beach, are scavenged by wildlife or domestic animals, washed back out to sea and missed by observers monitoring the coastline, or washed ashore on coastlines that are inaccessible or not monitored by people (Piatt & Van Pelt 1997, Carter 2003, Hampton & Zafonte 2007).

**CONCLUSIONS**

Our analysis provides an important first attempt to use data from diagnostic evaluations and necropsies to understand broad trends in aquatic mortality in the US. The results suggest that environmental causes (including the biotoxin produced by Clostridium botulinum) are the most important cause of death and that infectious diseases are also significant in overall mortality. By applying a conservative correction for the under-reporting bias (only 10 to 15% of aquatic birds that die are recovered, based on carcass-recovery studies), we believe that the final numbers of birds impacted by botulinum toxin and infectious diseases may have been at least 4 million over the study period and that aquatic bird mortality from all sources may have been >6 million birds. Considering the possibility that recovery rates for carcasses are closer to 5% than the assumed 10 to 15% and that large numbers of aquatic birds aggregate in certain coastal ecosystems at certain times of year, these numbers could be an order of magnitude higher. Other authors have suggested that infectious diseases are responsible for significant effects on marine bird populations (Friend et al. 2001);
our database does not permit statistical testing of this hypothesis but demonstrates that very large amount of aquatic bird mortalities are attributable to infectious diseases. Most importantly, our analyses highlight the value of long-term collection of mortality data, even where biases exist, in order to better understand the threats to aquatic birds, wildlife conservation, and ecosystem health. To increase knowledge of population level impacts of diseases in our changing marine ecosystem, wildlife disease surveillance efforts from multiple sources will need to be combined and analyzed. For example, national wildlife disease surveillance programs, beached-bird monitoring programs, rehabilitation center data, and aquatic bird monitoring programs all provide information about morbidity and mortality, breeding effort, breeding success, and changes in population sizes. Combining these data will allow a more thorough evaluation of impacts to aquatic bird species and provide a potentially robust early warning system for larger scale marine perturbations. This has serious implications for aquatic bird health, but also for human health, as we use aquatic birds as sentinels for contamination of the marine ecosystems that people depend on for food, recreation, and their well-being.

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