THEME SECTION

Seabirds as indicators of marine ecosystems

Idea: **John F. Piatt, William J. Sydeman**
Coordination: **William J. Sydeman, John F. Piatt, Howard I. Browman**

CONTENTS

Introduction: a modern role for seabirds as indicators

John F. Piatt[1,*], William J. Sydeman[2], Francis Wiese[3]

[1]US Geological Survey, Alaska Science Center, 1011 East Tudor Road, Anchorage, Alaska 99503, USA
[2]Farallon Institute for Advanced Ecosystem Research, PO Box 750756, Petaluma, California 94975, USA
[3]North Pacific Research Board, 1007 West Third Avenue, Suite 100, Anchorage, Alaska 99501, USA

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

*Email: john_piatt@usgs.gov

often confusing over the short term compared to bio-
logical 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 vari-
ability. 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 vari-
ety 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 con-
tribute to this approach, offering unique insights into
ecosystem status and change. In terms of marine spe-
cies, 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 measure-
ments 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, Fur-
ness & 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 vil-*

losus 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 demo-
graphic, 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 acquisi-
tion 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 environ-
ments.

The importance of scale became increasingly obvi-
ous while looking for spatial patterns in pelagic distri-
bution 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 cli-
mate 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, phyto-
plankton, 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 sea-
birds or their biological attributes (in this case breed-
ing 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 Montevecchi 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.

LITERATURE CITED

Aebischer NJ, Coulson JC, Colebrook JM (1990) Parallel long-term trends across four marine trophic levels and weather. Nature 347:753−755

Anderson PJ, Piatt JF (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar Ecol Prog Ser 189:117−123

Bertram DF, Mackas DL, Mckinnell SM (2001) The seasonal cycle revisited: interannual variation and ecosystem consequences. Prog Oceanogr 49:283−307

Botsford LW, Castilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. Science 277:509−515

Cairns DK (1987) Seabirds as indicators of marine food supplies. Biol Oceanogr 5:261−271

Carpenter SR, Folke C (2006) Ecology for transformation. Trends Ecol Evol 21:309−315

Chavez FP, Ryan J, Lluch-Cota SE, Ñiquen MC (2003) From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science 299:217−221

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

management. Ecol Appl 6:665–691

Croxall JP, Reid K, Prince PA (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. Mar Ecol Prog Ser 177: 115–131

Francis RC, Hare SR, Hollowed AB, Wooster WS (1998) Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fish Oceanogr 7:1–21

Furness RW, Camphuysen CJ (1997) Seabirds as monitors of the marine environment. ICES J Mar Sci 54:726–737

Hare ST, Mantua N J (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog Oceanogr 47:103–145

Hatch SA, Sanger GA (1992) Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. Mar Ecol Prog Ser 80:1–14

Kitaysky AS, Wingfield JC, Piatt JF (1999) Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. Funct Ecol 13:577–584

Kruse GH, Livingston P, Overland JE, Jamieson GS, McKinnell S, Perry RI (eds) (2006) Report of the PICES/NPRB workshop on integration of ecological indicators of the North Pacific with emphasis on the Bering Sea. North Pacific Marine Science Organization (PICES), Sidney, BC, PICES Scientific Report 33

Lee DE, Nur N, Sydeman WJ (2007) Climate and demography of the planktivorous Cassin's auklet off northern California: implications for population change. J Anim Ecol 76: 337–347

Mangel M, Talbot LM, Meffe GK, Agardy MT, Alverson DL (1996) Principles for the conservation of wild living resources. Ecol Appl 6:338–362

Montevecchi WA (1993) Birds as indicators of change in marine prey stocks. In: Furness RW, Greenwood DJ (eds) Birds as monitors of environmental change. Chapman & Hall, London, p 217–266

Montevecchi WA, Myers RA (1997) Centurial and decadal oceanographic influences on changes in northern gannet populations and diets in the north-west Atlantic: implications for climate change. ICES J Mar Sci 54:608–614

Piatt JF, Anderson P (1996) Response of common murres to the 'Exxon Valdez' oil spill and long-term changes in the Gulf of Alaska marine ecosystem. In: Rice SD, Spies RB, Wolfe DA, Wright BA (eds) Symposium 18: Proc 'Exxon Valdez' Oil Spill Symposium, Anchorage, AK, February 2–5, 1993. American Fisheries Society, Bethesda, MD, p 720–737

Roth JE, Mills KL, Sydeman WJ (2007) Chinook salmon—seabird co-variation off central California: possible forecasting applications. Can J Fish Aquat Sci 64:1080–1090

Sydeman WJ, Hester MM, Thayer JA, Gress F, Martin P, Buffa J (2001) Climate change, reproductive performance and diet composition of marine birds in the southern California Current System, 1969–1997. Prog Oceanogr 49: 309–329

Sydeman WJ, Brodeur RD, Bychkov A, Grimes C, McKinnell S (2006) Marine habitat 'hotspots' and their use by migratory species and top predators in the North Pacific Ocean: introduction. Deep Sea Res II 53:247–249

Seabirds as environmental indicators: the advantages of combining data sets

Morten Frederiksen[1,3,*], Roderick A. Mavor[2], Sarah Wanless[1]

[1]Centre for Ecology and Hydrology, Hill of Brathens, Banchory AB31 4BW, UK
[2]Joint Nature Conservation Committee, Dunnet House, 7 Thistle Place, Aberdeen AB10 1UZ, UK

[3]*Present address:* National Environmental Research Institute, Dept. of Arctic Environment, University of Aarhus,
Frederiksborgvej 399, 4000 Roskilde, Denmark

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.

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

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 variation in food supply, relatively easy to study and have a high public profile (e.g. Bost & le Maho 1993, Montevecchi 1993). However, selecting appropriate indicator variables is not straightforward, since ideally they should fulfil several potentially conflicting criteria, such as (1) be easily measured, (2) be sensitive to stresses on the system and respond in a predictable manner, (3) be

integrative, and (4) have low variability in response (Dale & Beyeler 2001). In addition, indicators should be reasonably easy for decision makers and the general public to interpret, and preferably relevant for resource management policy. The relative weighting of these criteria will depend on whether it is primarily aimed at indicating the general health of an aspect of the environment, or tailored to reflect a specific aspect or the response to a specific stressor.

Suggested or implemented seabird-based indicators usually include single variables measured at one site or summed over a defined area. For example, the proportion of oiled birds among common guillemots *Uria aalge* found dead on North Sea beaches has been adopted as an 'Ecological Quality Objective' by the OSPAR Commission for the Protection of the Marine Environment of the North-East Atlantic (Rogers & Greenaway 2005). Such univariate indicators are often easy to measure and interpret, thus fulfilling some of

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 to extract a common signal, 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).
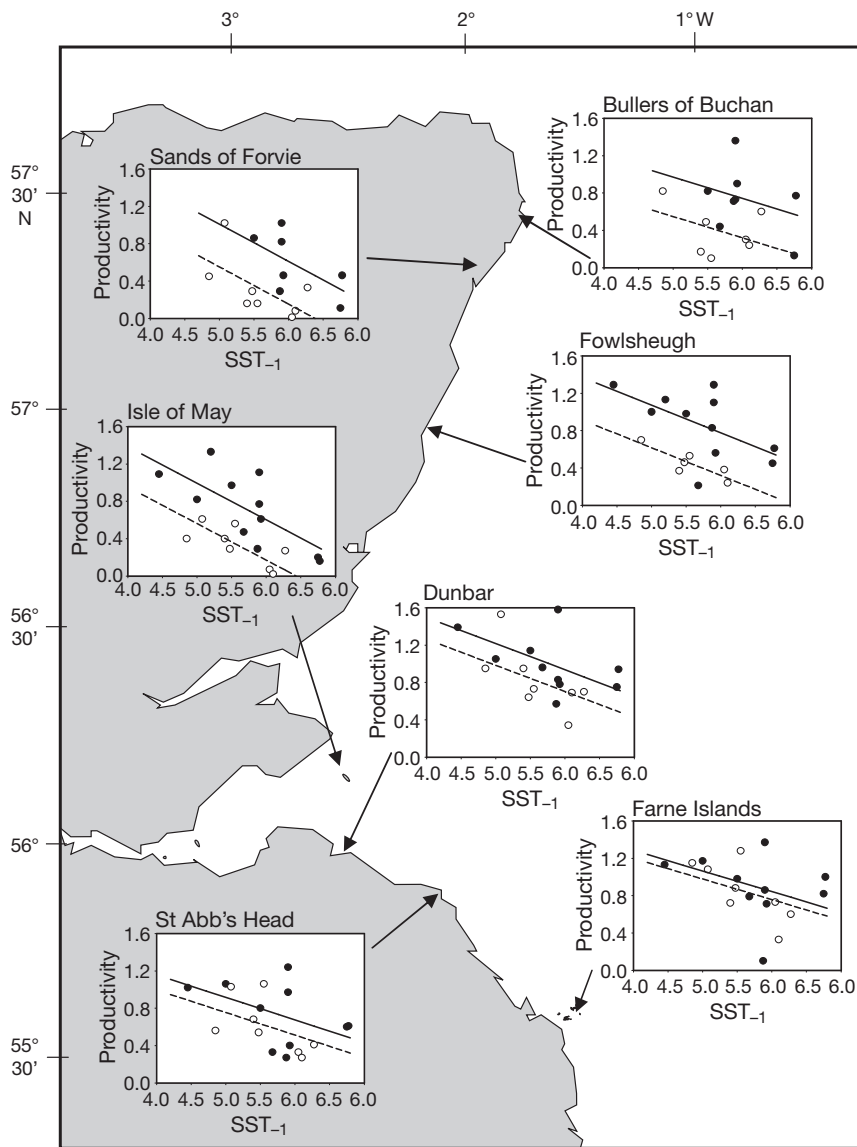
Fig. 1. *Rissa tridactyla*. Breeding productivity (number of fledged chicks per nest) of black-legged kittiwakes at 7 colonies in the NW North Sea, as related to local late winter sea surface temperature (SST) in the previous year in °C (SST$_{-1}$) and the presence of a sandeel fishery, 1986 to 2004. Regression lines from a model with no interaction between fishery and SST$_{-1}$. Solid lines and ●: non-fishery years; dashed lines and ○: fishery years. Details of the regressions in Table 1

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).

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

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 ≤ 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

Table 2. Linear regressions of breeding productivity of 4 seabirds on Isle of May, and of their first principal component (PC1), against an index of larval sandeel *Ammodytes marinus* abundance in the previous spring, 1986 to 2003. Loadings of the 4 original time series on the PC1 are also given. Note that coefficients are not directly comparable

Species	Coefficient	p	R^2	Loading
European shag	0.1383	0.015	32%	0.50
Black-legged kittiwake	0.1152	0.017	31%	0.86
Razorbill	0.0076	0.49	3%	0.51
Atlantic puffin	0.0162	0.26	8%	0.89
PC1	0.4119	0.022	29%	–

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).

Table 1. *Rissa tridactyla*. Results from general linear models relating black-legged kittiwake breeding productivity to the presence of a sandeel *Ammodytes marinus* fishery and local late winter SST in the previous year (SST_{-1}), for 7 colonies in the NW North Sea and the regional mean, 1986 to 2004. Locations of colonies are shown in Fig. 1

Colony	n	Fishery Coefficient	p	SST_{-1} Coefficient	p	R^2
Bullers of Buchan	15	–0.4274	0.028	–0.2279	0.22	35%
Sands of Forvie	15	–0.4584	0.013	–0.3993	0.020	47%
Fowlsheugh	17	–0.4575	0.003	–0.2970	0.013	57%
Isle of May	19	–0.4327	0.001	–0.3919	0.0006	66%
Dunbar	18	–0.2325	0.11	–0.2795	0.025	35%
St Abb's Head	18	–0.1629	0.26	–0.2411	0.057	25%
Farne Islands	18	–0.0862	0.57	–0.2213	0.095	18%
Regional mean	19	–0.3222	0.0035	–0.3155	0.001	61%

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)
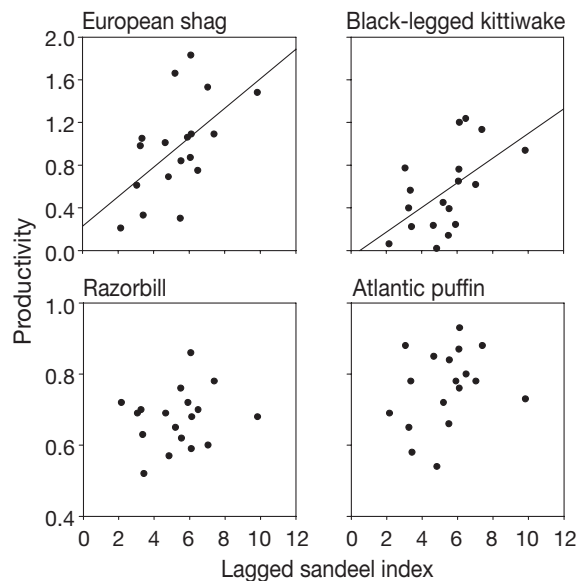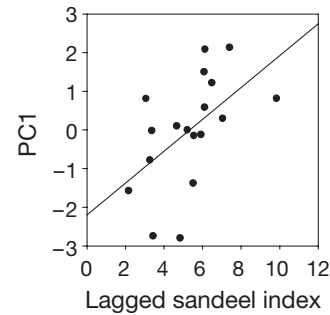

Fig. 3. Breeding productivity (number of fledged chicks per nest) of 4 seabird species at the Isle of May as related to an index of larval sandeel abundance in the previous spring, 1986 to 2003. Regression line indicates a significant relationship (see Table 2 for details). PC1: first principal component

There were also substantial gains in terms of generality. 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

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

Variable	Principal components	
	PC1	PC2
Proportion explained	57%	19%
Breeding productivity		
European shag	0.40	0.69
Black-legged kittiwake	0.53	0.63
Common guillemot	0.84	−0.42
Razorbill	0.75	−0.41
Atlantic puffin	0.85	0.24
Fledging mass		
Common guillemot	0.92	−0.13
Atlantic puffin	0.84	−0.04

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).

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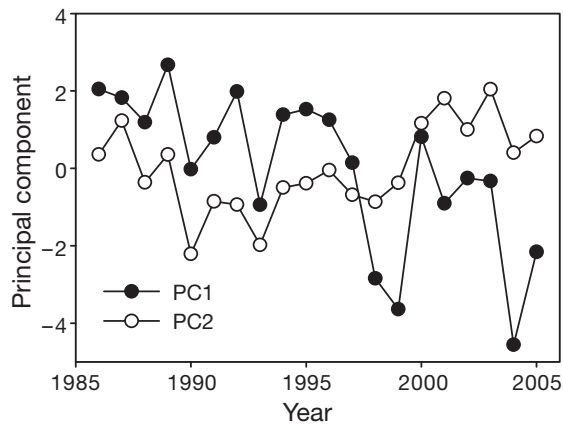
Fig. 4. The first 2 principal components (PC1 and PC2) of 7 seabird breeding performance variables at the Isle of May, 1986 to 2005. Variables included are breeding productivity of 5 species and mean fledging mass of 2 species (see Table 3)

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 (Browman & 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.

LITERATURE CITED

Bost CA, le Maho Y (1993) Seabirds as bio-indicators of changing marine ecosystems: new perspectives. Acta Oecol 14:463–470

Boyd IL, Murray AWA (2001) Monitoring a marine ecosystem using responses of upper trophic level predators. J Anim Ecol 70:747–760

Browman HI, Stergiou KI (eds) (2004) Theme section: perspectives on ecosystem-based approaches to the management of marine resources. Mar Ecol Prog Ser 274:269–303

Dale VH, Beyeler SC (2001) Challenges in the development and use of ecological indicators. Ecol Indic 1:3–10

Frederiksen M, Wanless S, Harris MP, Rothery P, Wilson LJ (2004) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. J Appl Ecol 41:1129–1139

Frederiksen M, Wright PJ, Harris MP, Mavor RA, Heubeck M, Wanless S (2005) Regional patterns of kittiwake *Rissa tridactyla* breeding success are related to variability in sandeel recruitment. Mar Ecol Prog Ser 300:201–211

Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S (2006) From plankton to top predators: bottom-up control of a marine food web across four trophic levels. J Anim Ecol 75:1259–1268

Greenstreet SPR, Armstrong E, Mosegaard H, Jensen H and others (2006) Variation in the abundance of sandeels *Ammodytes marinus* off southeast Scotland: an evaluation of area-closure fisheries management and stock abundance assessment methods. ICES J Mar Sci 63:1530–1550

Harris MP, Wanless S, Murray S, Mackley E (2005) Isle of May seabird studies in 2004. JNCC Report No. 375, JNCC/CEH, Peterborough/Banchory

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

Lepš J, Šmilauer P (2003) Multivariate analysis of ecological data using CANOCO. Cambridge University Press

Mavor RA, Parsons M, Heubeck M, Schmitt S (2005) Seabird numbers and breeding success in Britain and Ireland, 2004. UK Nature Conservation Report No. 29, Joint Nature Conservation Committee, Peterborough

McGarigal K, Cushman S, Stafford S (2000) Multivariate statistics for wildlife and ecology research. Springer, New York

Montevecchi WA (1993) Birds as indicators of change in marine prey stocks. In: Furness RW, Greenwood JJD (eds) Birds as monitors of environmental change. Chapman & Hall, London, p 217–266

Niemi GJ, McDonald ME (2004) Application of ecological indicators. Annu Rev Ecol Evol Syst 35:89–111

Niemi G, Wardrop D, Brooks R, Anderson S and others (2004) Rationale for a new generation of indicators for coastal waters. Environ Health Perspect 112:979–986

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

Reid K, Croxall JP, Briggs DR, Murphy EJ (2005) Antarctic ecosystem monitoring: quantifying the response of ecosystem indicators to variability in Antarctic krill. ICES J Mar Sci 62:366–373

Rice JC, Rochet MJ (2005) A framework for selecting a suite of indicators for fisheries management. ICES J Mar Sci 62:516–527

Rogers SI, Greenaway B (2005) A UK perspective on the development of marine ecosystem indicators. Mar Pollut Bull 50:9–19

Wanless S, Wright PJ, Harris MP, Elston DA (2004) Evidence for decrease in size of lesser sandeels *Ammodytes marinus* in a North Sea aggregation over a 30-yr period. Mar Ecol Prog Ser 279:237–246

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

W. A. Montevecchi*

Cognitive and Behavioural Ecology Program, Memorial University, St. John's, Newfoundland A1B 3X9, Canada

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 nonlinearly 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]t 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 cumu-lated 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
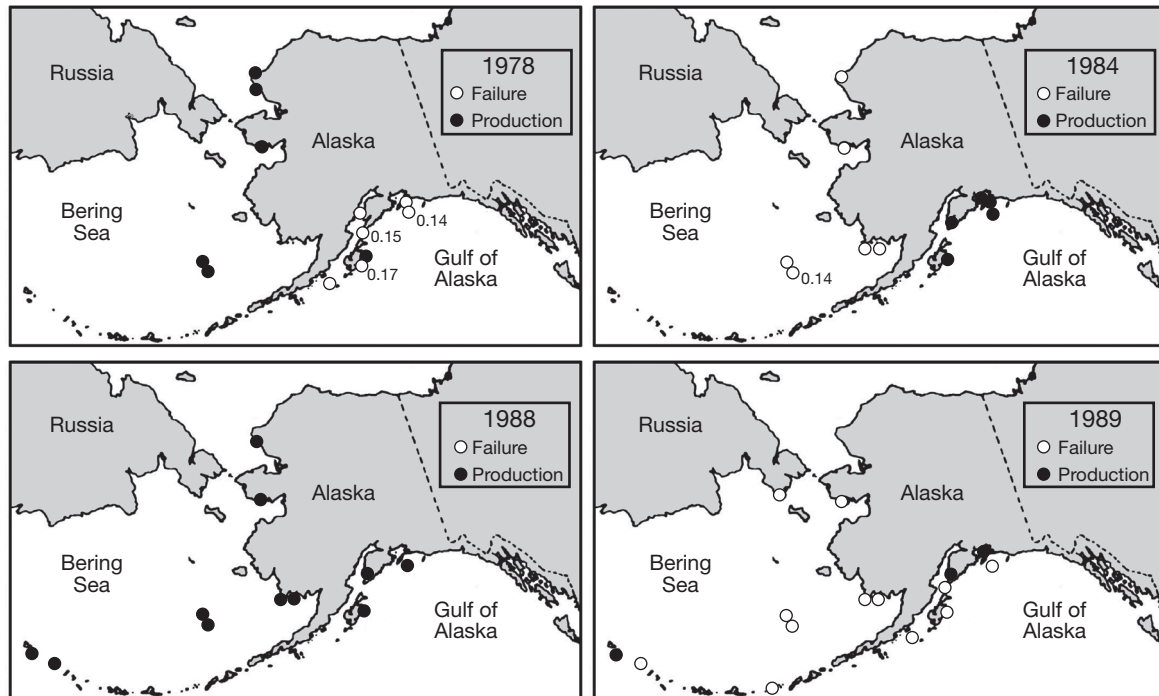

Fig. 1. *Rissa tridactyla.* Inter-annual ocean-basin patterns of breeding success (●) and failure (○) of black-legged kittiwakes at colonies in the North Pacific (after Hatch et al. 1993)

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.

Fig. 2. Funk Island, off the NE coast of Newfoundland, Canada, is the site of the most oceanic and third largest of the 6 colonies of gannets in North America. Hydrographic Stn 27 is 20 km E of St. John's, Newfoundland, in the Avalon Channel of the Labrador Current

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

Year	Date	With 1 species	With >1 species	Total
1977	12 Jul	105	0	105
1978	11–20 Aug	496	12	508
1979	31 Jul–6 Aug	162	4	166
1980	1–9 Aug	217	7	224
1982	9–13 Aug	191	25	216
1983	5–13 Aug	488	2	490
1984	9–19 Aug	225	8	233
1985	4–10 Sep	184	16	200
1986	7–15 Aug	493	22	515
1987	22–26 Aug	144	8	152
1988	12–20 Aug	525	36	561
1989	21–26 Aug	380	27	407
1990	18 Jul–11 Aug	340	38	378
1991	13 Jul–16 Aug	411	21	432
1992	5–10 Aug	293	8	301
1993	5–12 Aug	258	18	276
1994	11–14 Aug	50	3	53
1995	4–11 Aug	279	2	281
1996	5–8 Aug	348	3	351
1997	1–8 Aug	244	2	246
1998	3–17 Aug	446	14	460
1999	26 Jul–6 Aug	98	1	99
2000	6–12 Aug	183	0	183
2001	31 Jul–6 Aug	202	12	214
2002	8–12 Aug	275	8	283
2003	26 Jul–6 Aug	391	2	393
2004	Jul 26-Aug 1	88	1	89
2005	3–11 Aug	200	0	200
2006	6–14 Aug	216	7	223
Totals 1977–2006		7932	307	8239
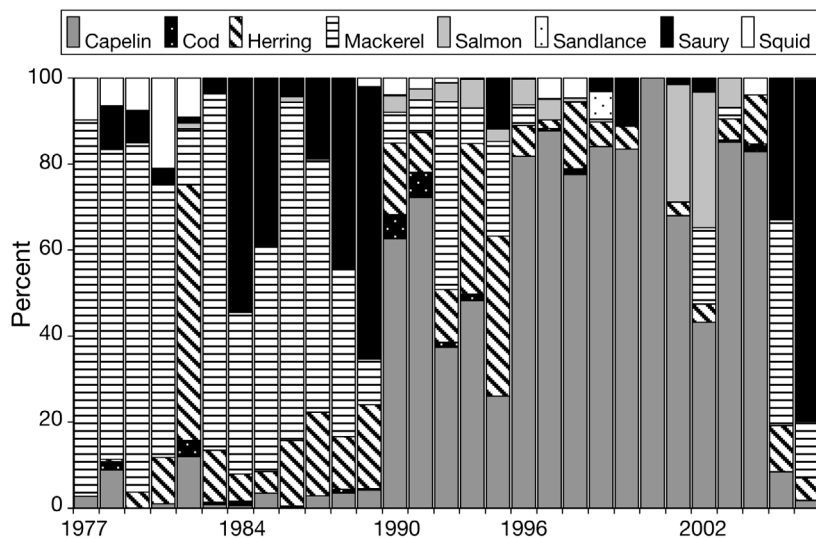
Fig. 3. *Sula bassana*. Estimated percentages of total mass of prey landed by northern gannets at the colony on Funk Island, 1977 to 2006

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 83 % 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
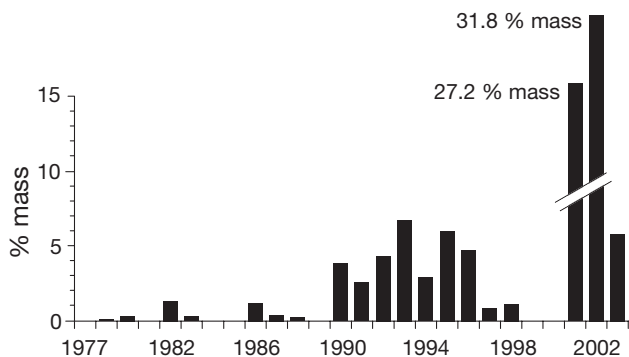
Fig. 4. *Salmo salar*. Estimated percentages of total mass of Atlantic salmon landed in the northern gannet colony on Funk Island from 1977 to 2006
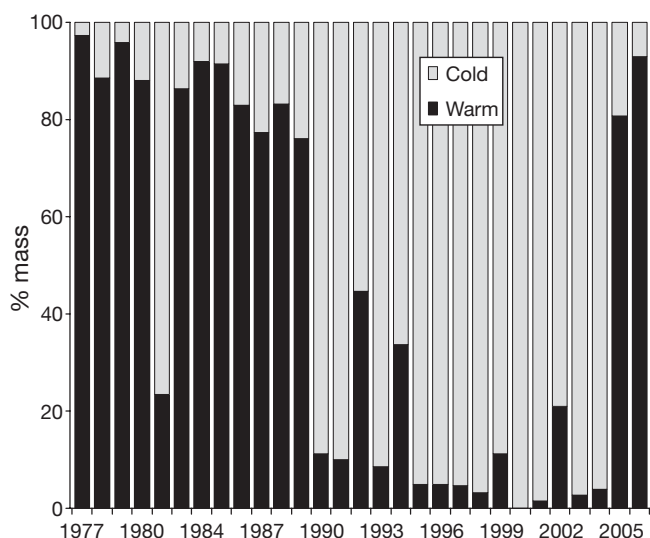

Fig. 5. *Sula bassana*. Warm-water prey (mackerel, squid, saury) from boreal and subtropical ocean regions and low arctic cold-water prey (herring, capelin, salmon, sandlance, cod), as percentages of total mass of prey landed by northern gannets in the colony on Funk Island, 1977 to 2006
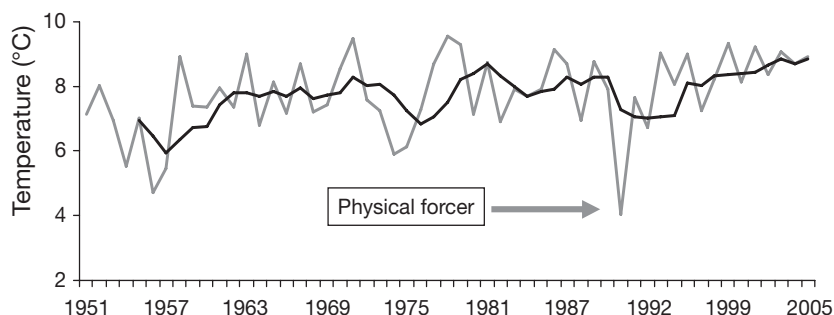
Fig. 6. June to July annual (gray) and 5 yr running average (black) of sea surface temperature anomalies obtained from Hydrographic Stn 27. Arrow indicates the most extreme negative anomaly on record that acted as a physical forcer in 1991 to induce a shift in the pelagic food web (DFO 2005)

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 morhoa* (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 novaeanglia* 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

Barrett RT, Røv N, Loen J, Montevecchi WA (1990) Diets of shags *Phalacrocorax aristotelis* and cormorants *P. carbo* in Norway and implications for gadoid stock recruitment. Mar Ecol Prog Ser 66:205–218

Boyd IL, Wanless S, Camphuysen CJ (eds) (2006) Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press, Cambridge

Burger AE, Piatt JF (1990) Flexible time budgets in breeding common murres: buffers against variable prey abundance. Stud Avian Biol 14:71–83

Cairns DK (1987) Seabirds as indicators of marine food supplies. Biol Oceanogr 5:261–271

Chardine JW (2000) Census of northern gannet colonies in the Atlantic Region in 1999. Can Wildl Serv Tech Rep Ser 361:1–16

Chavez FP, Ryan J, LLuch-Cota SE, Ñiquen CM (2003) From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science 299:217–221

Daunt F, Peters G, Scott B, Grémillet D, Wanless S (2003) Rapid-response recorders reveal interplay between marine physics and seabird behaviour. Mar Ecol Prog Ser 255:283–288

Daunt F, Wanless S, Peters G, Benvenuti S, Sharples J, Grémillet D, Scott B (2006) Impacts of oceanography on the foraging dynamics of seabirds in the North Sea. In: Boyd IL, Wanless S, Camphuysen CJ (eds) Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press, Cambridge, p 177–190

Davoren GK, Montevecchi WA (2003) Signals from seabirds indicate changing fish stocks. Mar Ecol Prog Ser 258:253–261

DFO (Department of Fisheries and Oceans Canada) (2005) 2004 state of the ocean: physical oceanographic conditions in the Newfoundland and Labrador Region. DFO Can Sci Advis Sec Sci Advis Rep 2005/018, available at: www.dfo-mpo.gc.ca/csas/Csas/status/2005/SAR-AS2005_018_E.pdf

Drinkwater KF (1996) Atmospheric and oceanographic variability in the northwest Atlantic during the 1980s and early 1990s. J Northw Atl Fish Sci 18:77–97

Garthe S, Benvenuti S, Montevecchi WA (2000) Pursuit-plunging by gannets (*Morus bassana*) feeding on capelin (*Mallotus villosus*). Proc R Soc Lond B 267:1717–1722

Garthe S, Montevecchi WA, Chapdelaine G, Rail JF, Hedd A (2007) Contrasting foraging tactics of seabirds breeding in different oceanographic domains. Mar Biol 151:687–694

Hare S, Mantua N (2000) Empirical evidence of North Pacific regime shifts in 1977 and 1989. Prog Oceanogr 47:103–145

Hatch SA (1996) Concordance of seabird population parameters: analytical methods and interpretation. In: Montevecchi WA (ed) Studies of high-latitude seabirds. 4. Trophic relationships and energetics of endotherms in cold water. Can Wildl Serv Occas Pap 21, p 37–48

Hatch SA, Byrd GV, Irons DB, Hunt GL Jr (1993) Status and ecology of kittiwakes (*Rissa tridactyla* and *R. brevirostris*) in the North Pacific. In: Vermeer K, Briggs KT, Morgan KH, Siegel-Causey D (eds) The status, ecology, and conservation of marine birds in the North Pacific. Can Wildl Serv Spec Publ, Ottawa, p 140–153

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

Miller AK, Sydeman WJ (2004) Rockfish response to low-frequency ocean climate change as revealed by the diet of a marine bird over multiple time scales. Mar Ecol Prog Ser 281:207–216

Montevecchi WA (1993) Birds as indicators of change in marine prey stocks. In: Furness RW, Greenwood JJD (eds) Birds as monitors of environmental change. Chapman & Hall, London, p 217–266

Montevecchi WA (2006) Simple is useful: binary responses of seabirds to changing prey and oceanographic conditions. Proc Pacific Seabird Group 33rd Annual Meeting, Girdwood, Alaska, Abstract available at: www.pacificseabirdgroup.org/downloads/Girdwood.pdf

Montevecchi WA, Berruti A (1991) Avian indication of pelagic fisheries and trophic changes in the southeast and northwest Atlantic. Acta 20th Congr Int Ornithol 4:2246–2256

Montevecchi WA, Myers RA (1995) Prey harvests of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales. Mar Ecol Prog Ser 117:1–9

Montevecchi WA, Myers RA (1996) Dietary changes of seabirds reflect shifts in pelagic food webs. Sarsia 80:313–322

Montevecchi WA, Tuck LM (1987) Newfoundland birds: exploitation, study, conservation. Nuttall Ornithological Club, Cambridge, MA

Montevecchi WA, Ricklefs RE, Kirkham IR, Gabaldon D (1984) Growth energetics of nestling northern gannets, *Sula bassana.* Auk 101:334–341

Myers RA, Akenhead SA, Drinkwater K (1990) The influence of the Hudson Bay runoff and ice melt on the salinity of the inner Newfoundland Shelf. Atmospere–Ocean 28:241–256

Ollason JG, Yearsley JM, Liu K, Ren R (2006) Modelling the behaviour of individuals and groups of animals foraging in heterogeneous environments. In: Boyd IL, Wanless S, Camphuysen CJ (eds) Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press, Cambridge, p 294–309

Österblom H, Bignert A, Fransson T, Olsson O (2001) A decrease in fledging body mass in common guillemot *Uria aalge* chicks in the Baltic Sea. Mar Ecol Prog Ser 224:305–309

Petrie B, Akenhead SA, Lazier S, Loder J (1988) The cold intermediate layer on the Labrador and Northeast Newfoundland Shelves, 1978–86. North Atlantic Fish Org Sci Council Stud 12:57–69

Piatt JF, Sydemann WJ, Wiese F (2007a) Introduction: a modern role for seabirds as indicators. Mar Ecol Prog Ser 352:199–204

Piatt JF, Harding AMA, Shultz M, Speckmann SG, Van Pelt TI, Drew GS, Kettle AB (2007b) Seabirds as indicators of marine food supplies: Cairns revisited. Mar Ecol Prog Ser 352:221–234

Schreiber RW, Schreiber EA (1984) Central Pacific seabirds and the El Niño southern oscillation: 1982 to 1983 retrospectives. Science 225:713–716

Scott BE, Sharples J, Wanless S, Ross ON, Frederiksen M, Daunt F (2006) The use of biologically meaningful climate and fisheries on seabird breeding success. In: Boyd IL, Wanless S, Camphuysen CJ (eds) Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press, Cambridge, p 46–62

Siegel S (1957) Nonparametric statistics. McGraw-Hill, New York

Staniland IJ, Trathan P, Martin AR (2006) Consequences of prey distributions for the foraging behaviour of top predators. In: Boyd IL, Wanless S, Camphuysen CJ (eds) Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press, Cambridge, p 131–142

Wanless S, Wright PJ, Harris MP, Elston DA (2004) Evidence for a decrease in size of lesser sandeels *Ammodytes marinus* in a North Sea aggregation over a 30-yr period. Mar Ecol Prog Ser 279:237–246

Wanless S, Harris MP, Redman P, Speakman JR (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. Mar Ecol Prog Ser 294:1–8

Wilson RP, Grémillet D, Syder J, Kierspel MAM and 7 others (2002) Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. Mar Ecol Prog Ser 228: 241–261

Seabirds as indicators of marine food supplies: Cairns revisited

John F. Piatt[1,*], Ann M. A. Harding[1,2], Michael Shultz[1], Suzann G. Speckman[3], Thomas I. van Pelt[1], Gary S. Drew[1], Arthur B. Kettle[4]

[1]US Geological Service Alaska Science Center, 1011 E. Tudor Rd., Anchorage, Alaska 99503, USA
[2]Alaska Pacific University, Environmental Science Department, 4101 University Dr., Anchorage, Alaska 99508, USA
[3]School of Aquatic and Fishery Sciences, University of Washington, 1122 NE Boat St., Seattle, Washington 98105, USA
[4]Alaska Maritime National Wildlife Refuge, US Fish and Wildlife Service, 2355 Kachemak Bay Dr., Homer, Alaska 99603, USA

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%, $r^2 = 0.89$) reflected prey variability, murre breeding success did not (CV = 29%, $r^2 < 0.00$). It appears that murres were able to buffer breeding success by reallocating discretionary 'loafing' time to foraging effort in response ($r^2 = 0.64$) 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

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
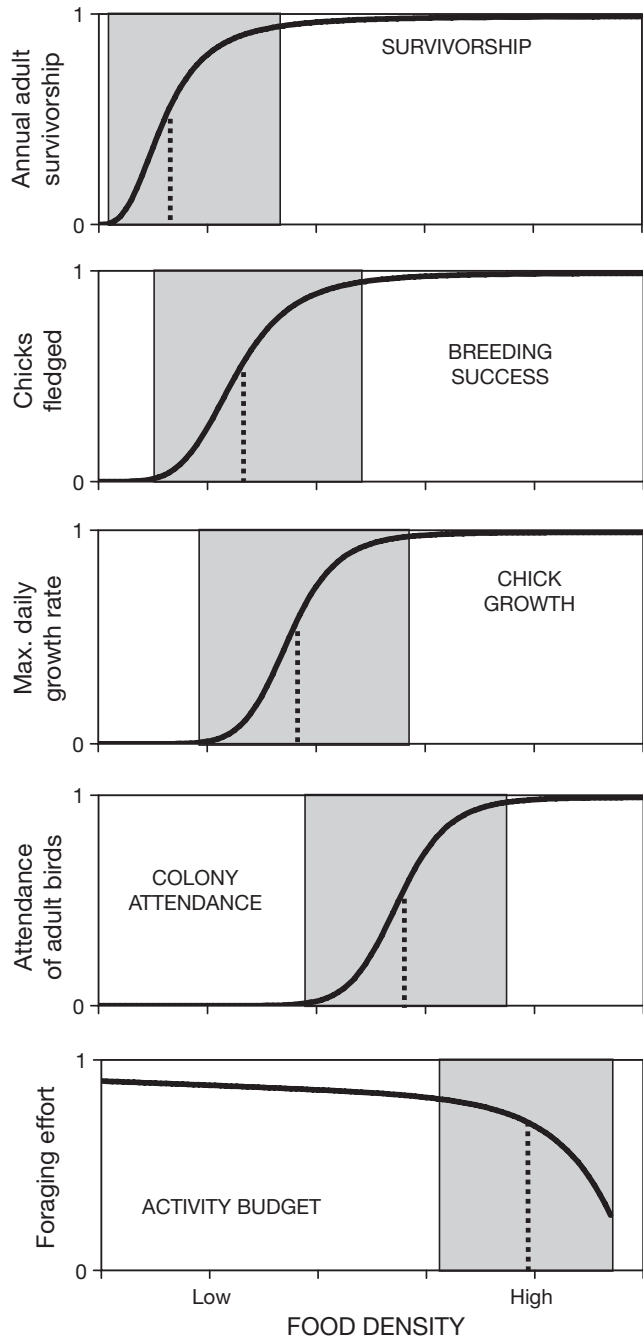
Fig. 1. Cairns' predicted relationships between population and behavioral parameters of seabirds and their food supply. Dashed vertical lines indicate approximate threshold or halfway point in parameter response to change in prey density. Modified from Cairns (1987)

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 hydro-acoustic 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

Fig. 2. Study areas in lower Cook Inlet, Alaska. Illustrated are tracks of hydro-acoustic and bird surveys conducted within about a 50 km radius (circles) of each colony

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 σ (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 (log$x$ + 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).
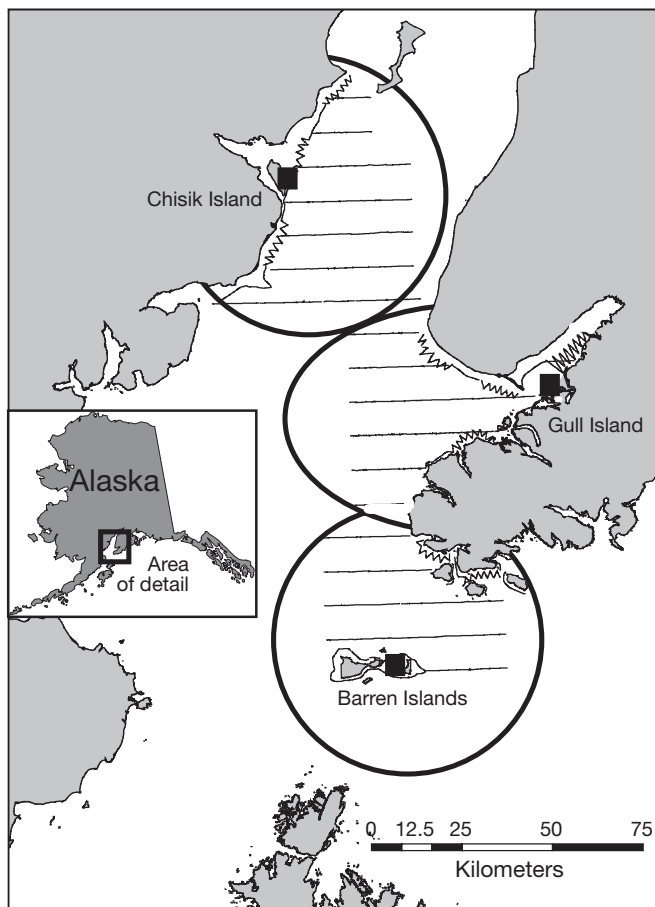
Behavioral activity budgets were determined from all-day observations of 8 to 12 nest-sites of adult murres and kittiwakes at each colony during the incubation and chick-rearing period in each of the 15 colony-years (see Harding et al. 2007 for more details). During observations, the time was recorded 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. Uttley 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 fledgling 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:

$$f = (a \times x)/(b + x)$$

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:

$$f = (a - d)/[1 + (x/c)^b] + d$$

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:

$$f = k_1 D \text{ if } D > D_T$$
$$f = k_2 D \text{ if } D < D_T$$

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 inflection point (Piatt 1990).

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

$$f = a \times \exp(-b \times x)$$

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 (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 AIC$_c$ calculation (Burnham & Anderson 2002). The model with the lowest AIC$_c$ was assumed to best represent the data. Models in which the difference in AIC$_c$ from the minimum value (ΔAIC$_c$) is <2 are considered plausible alternative models. For each model, we also calculated an AIC$_c$ weight (w) that reflects the relative likelihood of that model being the best-fitting model among those considered, and in which all 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. 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. AIC$_c$ analysis penalizes models with more equation parameters and small sample sizes, and so ΔAIC$_c$ 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. 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.
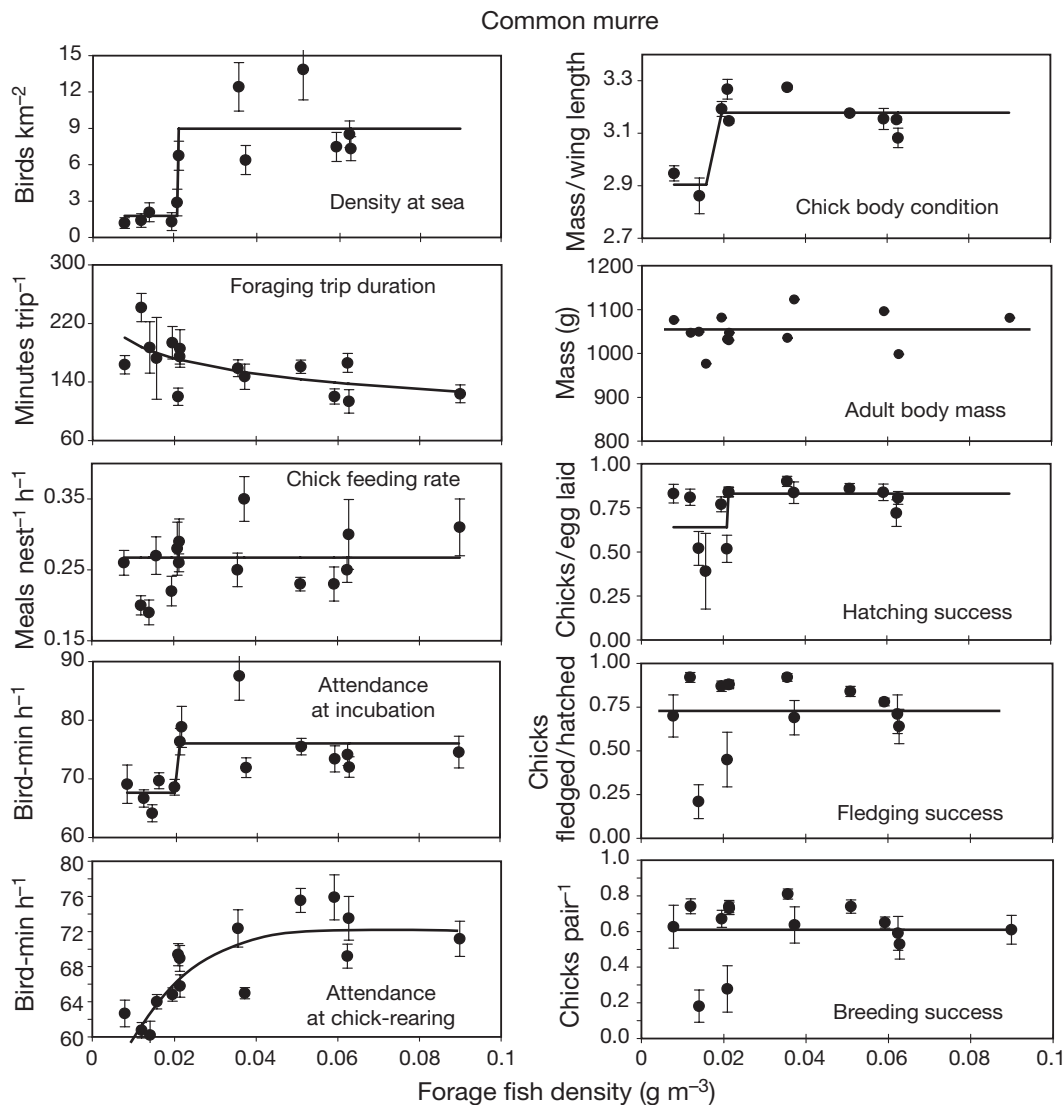
Fig. 3. *Uria aalge.* Response of different parameters of murre biology or behavior to variation in prey density. Graphs include predicted form (solid line) of relationship from the best-fitting model function (null, linear, hyperbolic, sigmoidal, step, or exponential decay) as determined by using Akaike's information criterion adjusted for sample size (AIC$_c$) analysis

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 chickrearing 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 ± 0.00033 g m^{-3} and in kittiwakes (n = 8) was 0.021 ± 0.00028 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).

Table 1. *Rissa tridactyla*, *Uria aalge.* Functional relationships between different measures of seabird biology or behavior and prey density, and variability in those measures among colony-years. n = number of colony-years of data. Types of parameters: Att = colony attendance; Gro = body condition or growth; Br = breeding success; Act = activity budget; For = foraging behavior. Relationships were modeled as null, linear, hyperbolic (hyper), sigmoidal (sigm), step, or exponential (exp) functions. *w*: Akaike weight; ns: not significant. Variability ranked as low (CV < 20%), medium (20% < CV < 40%), and high (CV > 40%), where CV is the coefficient of variation

Parameter	n	Type	Relationship with fish density							Variability	
			Model with highest explained variance				AIC_c best-fit model			CV	Rank
			Form	R^2	p	Threshold	Form	r^2	*w*		
Black-legged kittiwake *R. tridactyla*											
Attendance at chick-rearing	11	Att	–	0.03	ns	–	Null	0.00	0.77	7.1	Low
Adult body condition	15	Gro	–	0.00	ns	–	Null	0.00	0.65	7.5	Low
Clutch size	15	Br	–	0.07	ns	–	Null	0.00	0.59	12.3	Low
Chick growth rate (alpha/single)	12	Gro	sigm	0.73	0.012	0.018	Step	0.62	0.57	12.6	Low
Brood size at fledging	11	Br	step	0.59	0.005	0.020	Step	0.59	0.35	13.5	Low
Foraging trip duration	11	Act	exp	0.36	0.048	0.028	Exp	0.36	0.37	22.8	Medium
Laying success	15	Br	–	0.16	ns	–	Null	0.00	0.53	28.7	Medium
Hatching success	14	Br	step	0.30	0.043	0.018	Null	0.00	0.52	37.2	Medium
Chick feeding rate	10	For	step	0.31	0.075	–	Null	0.00	0.65	42.0	High
Forage fish biomass	15	–	–	–	–	–	–	–	–	68.7	High
Density at sea	12	For	sigm	0.86	<0.001	0.021	Hyper	0.68	0.36	72.3	High
Fledging success	13	Br	sigm	0.89	<0.001	0.020	Step	0.89	0.94	81.2	High
Breeding success	15	Br	step	0.63	<0.001	0.020	Step	0.63	0.88	87.0	High
Common murre *U. aalge*											
Adult body condition	13	Gro	–	0.04	ns	–	Null	0.00	0.72	3.8	Low
Fledgling body condition	10	Gro	step	0.79	0.006	0.018	Step	0.79	0.85	4.2	Low
Chick feeding rate	15	For	step	0.29	0.040	0.020	Null	0.00	0.38	15.5	Low
Hatching success	14	Br	step	0.39	0.016	0.021	Step	0.39	0.36	20.9	Medium
Foraging trip duration	15	Act	exp	0.41	<0.001	–	Exp	0.41	0.51	21.1	Medium
Fledging success	13	Br	–	0.07	ns	–	Null	0.00	0.71	28.3	Medium
Breeding success	14	Br	step	0.23	0.004	0.021	Null	0.00	0.63	29.2	Medium
Attendance at incubation	14	Att	step	0.53	0.003	0.021	Step	0.53	0.59	44.3	High
Attendance at chick-rearing	15	Att	sigm	0.71	0.003	0.020	Hyper	0.64	0.70	65.8	High
Forage fish biomass	15	–	–	–	–	–	–	–	–	68.7	High
Density at sea	12	For	sigm	0.77	0.006	0.021	Step	0.74	0.52	72.4	High

Difference in responses among species

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%), kitti-wakes 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 $\Delta AIC_c = 0$, but all models with $\Delta AIC_c < 2$ (in bold) and high AIC_c weights relative to other models have substantial support and offer plausible alternative models of functional relationships

| Measurement | n | AIC_c weights (w) | | | | | | $\Delta AICc$ | | | | | |
		Null	Linear	Hyper	Sigm	Step	Exp	Null	Linear	Hyper	Sigm	Step	Exp
Black-legged kittiwake *R. tridactyla*													
Attendance at chick-rearing	11	0.77	0.11	0.11	0.00	0.01	–	**0.00**	3.86	3.87	16.03	8.71	–
Adult body condition	15	0.65	0.18	0.14	0.00	0.02	–	**0.00**	2.57	3.06	11.67	6.88	–
Clutch size	15	0.59	0.21	0.14	0.01	0.06	–	**0.00**	2.05	2.92	9.13	4.65	–
Chick growth rate (alpha/single)	12	0.12	0.02	0.09	0.20	0.57	–	3.05	6.44	3.69	2.11	**0.00**	–
Brood size at fledging	11	0.24	0.16	0.24	0.01	0.35	–	**0.72**	**1.51**	**0.75**	7.33	**0.00**	–
Foraging trip duration	11	0.27	0.36	–	–	–	0.37	**0.66**	**0.07**	–	–	–	**0.00**
Laying success	15	0.53	0.26	0.14	0.01	0.07	–	**0.00**	**1.46**	2.71	8.93	4.09	–
Hatching success	14	0.52	0.10	0.20	0.01	0.16	–	**0.00**	3.26	**1.87**	7.28	2.40	–
Chick feeding rate	10	0.46	0.23	0.26	0.00	0.05	–	**0.00**	**1.40**	**1.16**	13.31	4.61	–
Density at sea	12	0.00	0.25	0.36	0.10	0.28	–	11.72	**0.72**	**0.00**	2.49	**0.50**	–
Fledging success	13	0.00	0.00	0.00	0.06	0.94	–	13.63	15.52	14.55	5.57	**0.00**	–
Breeding success	15	0.02	0.01	0.01	0.09	0.88	–	7.72	10.04	8.48	4.67	**0.00**	–
Common murre *U. aalge*													
Adult body condition	13	0.72	0.13	0.13	0.00	0.02	–	**0.00**	3.38	3.39	12.95	7.32	–
Fledgling body condition	10	0.06	0.01	0.07	0.01	0.85	–	5.31	8.50	5.09	9.03	**0.00**	–
Chick feeding rate	15	0.38	0.22	0.23	0.02	0.15	–	**0.00**	**1.07**	**1.00**	6.46	**1.79**	–
Hatching success	14	0.30	0.19	0.13	0.03	0.36	–	**0.36**	**1.29**	2.06	5.27	**0.00**	–
Foraging trip duration	15	0.05	0.45	–	–	–	0.51	4.82	**0.25**	–	–	–	**0.00**
Fledging success	13	0.71	0.13	0.13	0.00	0.03	–	**0.00**	3.34	3.47	11.95	6.32	–
Breeding success	14	0.63	0.13	0.14	0.00	0.10	–	**0.00**	3.14	3.00	12.07	3.74	–
Attendance at incubation	14	0.13	0.05	0.18	0.05	0.59	–	3.01	4.86	2.36	4.99	**0.00**	–
Attendance at chick-rearing	15	0.00	0.14	0.70	0.08	0.08	–	11.48	3.24	**0.00**	4.35	4.25	–
Density at sea	12	0.01	0.14	0.27	0.06	0.52	–	7.41	2.70	**1.33**	4.40	**0.00**	–

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 nonlinear 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).

Black-legged kittiwake
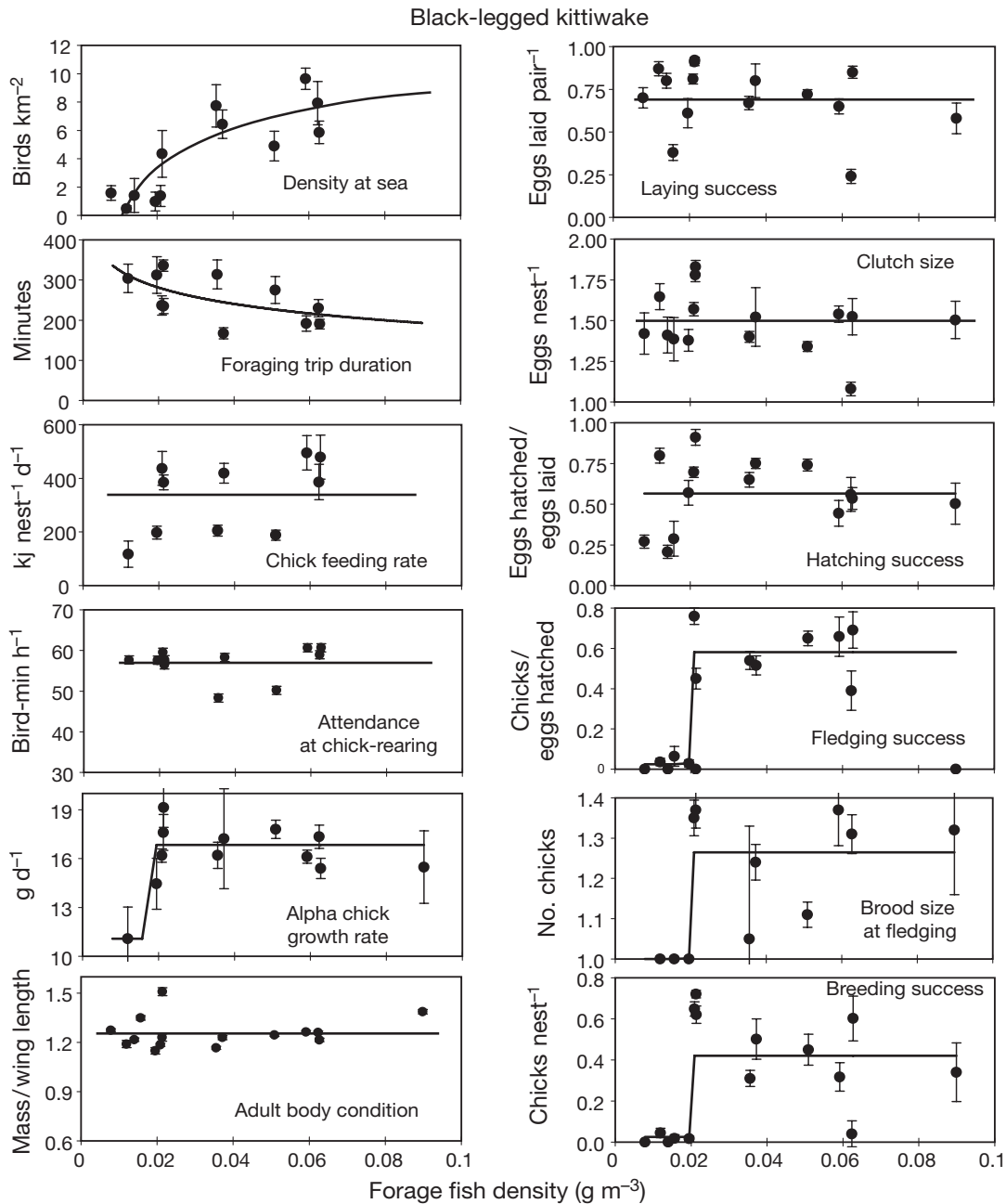
Fig. 4. *Rissa tridactyla.* Response of different parameters of kittiwake biology or behavior to variation in prey density. Graphs include predicted form (solid line) of relationship from the best-fitting model function (null, linear, hyperbolic, sigmoidal, step, or exponential decay) as determined by using Akaike's information criterion adjusted for sample size (AIC_c) analysis

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

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)
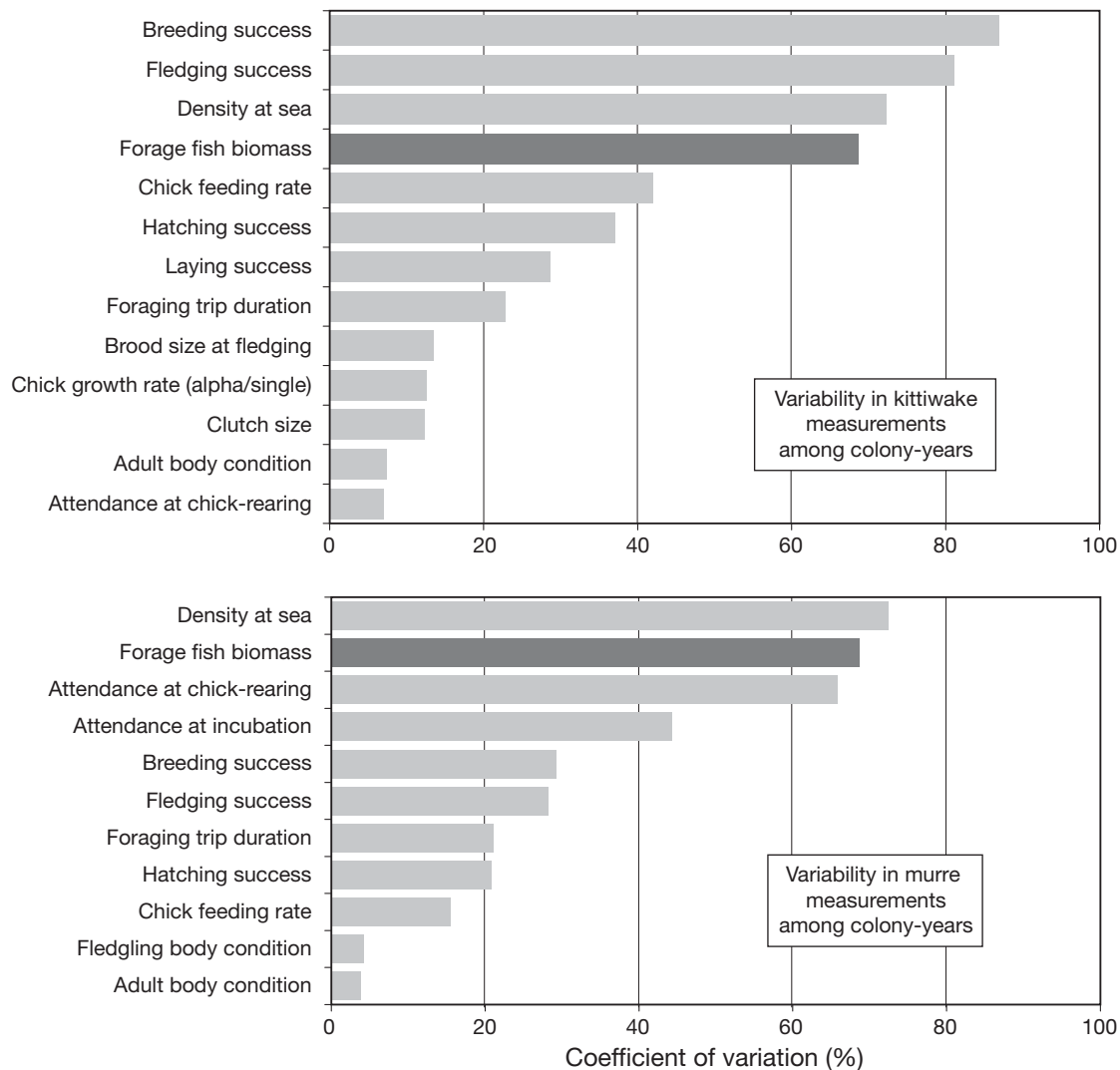
same? Perhaps because there is only one true physical threshold, and that is the fish school density above which seabirds can successfully acquire food energy at a rate that is sufficient to support daily metabolic demands (Piatt 1990). Tracking of prey at sea (aggregative response) *sets the baseline 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).

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). 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. Monaghan 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, Montevecchi 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 (Montevecchi 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 (Fredericksen 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 (Fredericksen 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. 2005, Fredericksen et al. 2006), which further suggests that seabirds are likely to track spatial and temporal variation in prey abundance.

LITERATURE CITED

Abookire AA, Piatt JF (2005) Oceanographic conditions structure forage fishes into lipid-rich and lipid-poor communities in lower Cook Inlet, Alaska, USA. Mar Ecol Prog Ser 287:229–240

Aebischer NJ, Coulson JC, Colebrook JM (1990) Parallel long-term trends across four marine trophic levels and weather. Nature 347:753–755

Anderson PJ, Piatt JF (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar Ecol Prog Ser 189:117–123

Benson J, Suryan RM, Piatt JF (2003) Assessing chick growth from a single visit to a seabird colony. Mar Ornithol 31: 181–184

Brooke ML (2004) The food consumption of the world's seabirds. Proc R Soc Lond (Suppl)271:246–248

Burger AE, Piatt JF (1990) Flexible time budgets in breeding common murres: buffers against variable prey availability. Stud Avian Biol 14:71–83

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York

Cairns DK (1987) Seabirds as indicators of marine food supplies. Biol Oceanogr 5:261–271

Dale VH, Beyeler SC (2001) Challenges in the development and use of ecological indicators. Ecol Indic 1:3–10

Eri013kstad KE, Fauchald P, Tveraa T, Steen H (1998) On the cost

of reproduction in long-lived birds; the influence of environmental variability. Ecology 79:1781–1788

Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S (2006) From plankton to top predators: bottom-up control of a marine food web across four trophic levels. J Anim Ecol 75:1259–1268

Furness RW, Camphuysen CJ (1997) Seabirds as monitors of the marine environment. ICES J Mar Sci 54:726–737

Gabrielsen GW (1994) Energy expenditure in Arctic seabirds. PhD thesis, University of Tromso

Gaston AJ, Jones IL (1998) The auks. Oxford University Press, Oxford

Golet GH, Irons DB (1999) Raising young reduces body condition and fat stores in black-legged kittiwakes. Oecologia 120:530–538

Golet GH, Irons DB, Estes JA (1998) Survival costs of chick rearing in black-legged kittiwakes. J Anim Ecol 67: 827–841

Gould PJ, Forsell DJ (1989) Techniques for shipboard surveys of marine birds. Fish and Wildlife technical report 25, US Dept. of Interior, Fish and Wildlife Service, Washington, DC

Hamer KC, Furness RW, Caldow RWG (1991) The effects of changes in food availability on the breeding ecology of great skuas *Catharacta skua* in Shetland. J Zool Lond 223: 175–188

Hamer KC, Monaghan P, Uttley JD, Walton P, Burns MD (1993) The influence of food supply on the breeding ecology of kittiwakes *Rissa tridactyla* in Shetland. Ibis 135: 255–263

Harding AMA, van Pelt TI, Piatt JF, Kitaysky AS (2002) Reduction of provisioning effort in response to experimental manipulation of chick nutritional status in the horned puffin *Fratercula corniculata*. Condor 104:842–847

Harding AMA, Piatt JF, Schmutz JA, Shultz MT, van Pelt TI, Kettle AB, Speckman SG (2007) Prey density and the behavioral flexibility of a marine predator: the common murre (*Uria aalge*). Ecology 88:2024–2033

Harris MP, Wanless S (1988) The breeding biology of guillemots *Uria aalge* on the Isle of May over a six year period. Ibis 130:172–192

Hatch SA, Byrd GV, Irons DB, Hunt GL (1993) Status and ecology of kittiwakes (*Rissa tridactyla* and *R. brevirostris*) in the North Pacific. In: Vermeer K, Briggs KT, Morgan KH, Siegel-Causey D (eds) The status, ecology, and conservation of marine birds of the North Pacific. Special Publication, Canadian Wildlife Service, Ottawa, p 140–153

Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can Entomol 91:293–320

Jodice PGR, Roby DD, Turco KR, Suryan RM and others (2006) Assessing the nutritional stress hypothesis: relative influence of diet quantity and quality on seabird productivity. Mar Ecol Prog Ser 325:267–279

Kitaysky AS, Wingfield JC, Piatt JF (1999) Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. Funct Ecol 13:577–584

Monaghan P, Uttley JD, Burns M, Thane C, Blackwood J (1989) The relationship between food supply, reproductive effort, and breeding success in Arctic terns *Sterna paradisea*. J Anim Ecol 58:261–274

Monaghan P, Walton P, Wanless S, Uttley JD, Burns MD (1994) Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding guillemots *Uria aalge*. Ibis 136:214–222

Montevecchi WA (1993) Birds as indicators of change in marine prey stocks. In: Furness RW, Greenwood DJ (eds)

Birds as monitors of environmental change. Chapman & Hall, London, p 217–266

Montevecchi WA (2007) Binary dietary responses of northern gannets *Sula bassana* indicate changing food web and oceanographic conditions. Mar Ecol Prog Ser 352:213–220

Murdoch WW, Oaten A (1975) Predation and population stability. Adv Ecol Res 9:1–131

Piatt JF (1990) Aggregative response of common murres and Atlantic puffins to their prey. Stud Avian Biol 14:36–51

Piatt JF, Harding AMA (2007) Population ecology of seabirds in Cook Inlet. In: Spies R (ed) Long-term ecological change in the northern Gulf of Alaska. Elsevier, Amsterdam, p 335–352

Piatt JF, Methven DA (1992) Threshold foraging behavior of baleen whales. Mar Ecol Prog Ser 84:205–210

Reid K, Croxall JP, Briggs DR, Murphy EJ (2005) Antarctic ecosystem monitoring: quantifying the response of ecosystem indicators to variability in Antarctic krill. ICES J Mar Sci 62:366–373

Robards MD, Piatt JF, Kettle AB, Abookire AA (1999) Temporal and geographic variation in fish communities of lower Cook Inlet, Alaska. Fish Bull 97:962–977

Romano MD, Piatt JF, Roby DD (2006) Testing the junk-food hypothesis on marine birds: effects of prey type on growth and development. Waterbirds 29:407–516

Sagar P, Horning DS (1998) Mass related survival of fledging sooty shearwaters *Puffinus griseus* at the Snares, New Zealand. Ibis 140:329–339

Speckman SG (2004) Characterizing fish schools in relation to the marine environment and their use by seabirds in lower Cook Inlet, Alaska. PhD thesis, University of Washington, Seattle, WA

Speckman S, Piatt JF, Minte-Vera C, Parrish J (2005) Parallel structure among environmental gradients and three trophic levels in a subarctic estuary. Prog Oceanogr 66:25–65

Stearns SS (1992) The evolution of life histories. Oxford University Press, New York

Suddaby D, Ratcliffe D (1997) The effects of fluctuating food availability on breeding Arctic terns (*Sterna paradisaea*). Auk 114:524–530

Suryan RM, Irons DB (2001) Colony and population dynamics of black-legged kittiwakes in a heterogeneous environment. Auk 118:636–649

Sydeman WJ, Hester MM, Thayer JA, Gress F, Martin P, Buffa J (2001) Climate change, reproductive performance and diet composition of marine birds in the southern California Current System, 1969–1997. Prog Oceanogr 49:309–329

Uttley JD, Walton P, Monaghan P, Austin G (1994) The effects of food abundance on breeding performance and adult time budgets of guillemots *Uria aalge*. Ibis 136:205–213

Van Pelt TI, Piatt JF, Lance BK, Roby DD (1997) Proximate composition and energy density of some North Pacific forage fishes. Comp Biochem Physiol A 118A:1393–1398

Wanless S, Harris MP, Redman P, Speakman JR (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. Mar Ecol Prog Ser 294:1–8

Weimerskirch H, Prince PA, Zimmermann L (2000) Chick provisioning by the yellow-nosed albatross: response of foraging effort to experimentally increased costs and demands. Ibis 142:103–110

Weimerskirch H, Zimmermann L, Prince PA (2001) Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross. Behav Ecol 12:22–30

Zador S, Piatt JF (1999) Time-budgets of common murres at a declining and increasing colony in Alaska. Condor 101:149–152

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

Sara J. Iverson[1],*, **Alan M. Springer[2], Alexander S. Kitaysky[3]**

[1]**Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada**
[2]**Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska 99775-7220, USA**
[3]**Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska 99775-7000, USA**

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, Montevecchi 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 on only 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 over-represented, 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 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 42, 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*), euphasiids *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 esti-

mated 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)
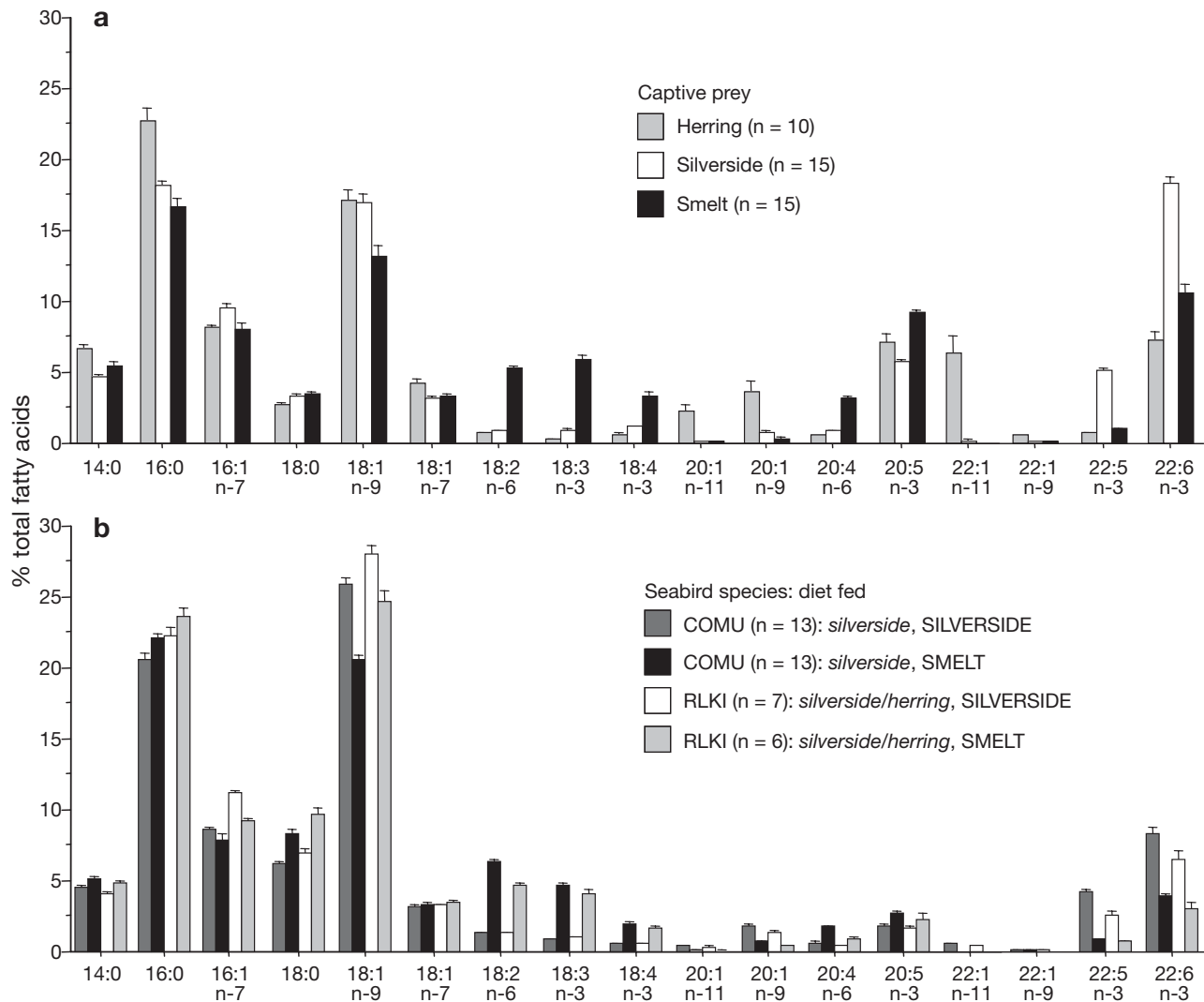
Fig. 1. Selected fatty acids (FAs; 17 of 67 identified) with the largest overall variance and an overall mean of ≥0.4 % of total FAs and that illustrate characteristic differences in patterns: (a) among the 3 prey items fed to captive seabird chicks and (b) in the adipose tissue of common murres *Uria aalge* (COMU) and red-legged kittiwakes *Rissa brevirostris* (RLKI) chicks fed different diets (prey in italics fed from 0 to 10 or 15 d post-hatching, prey in capitals fed for the main period, from Day 10 or 15 until Day 42 or 45). Bars are means and vertical lines are 1 SE

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
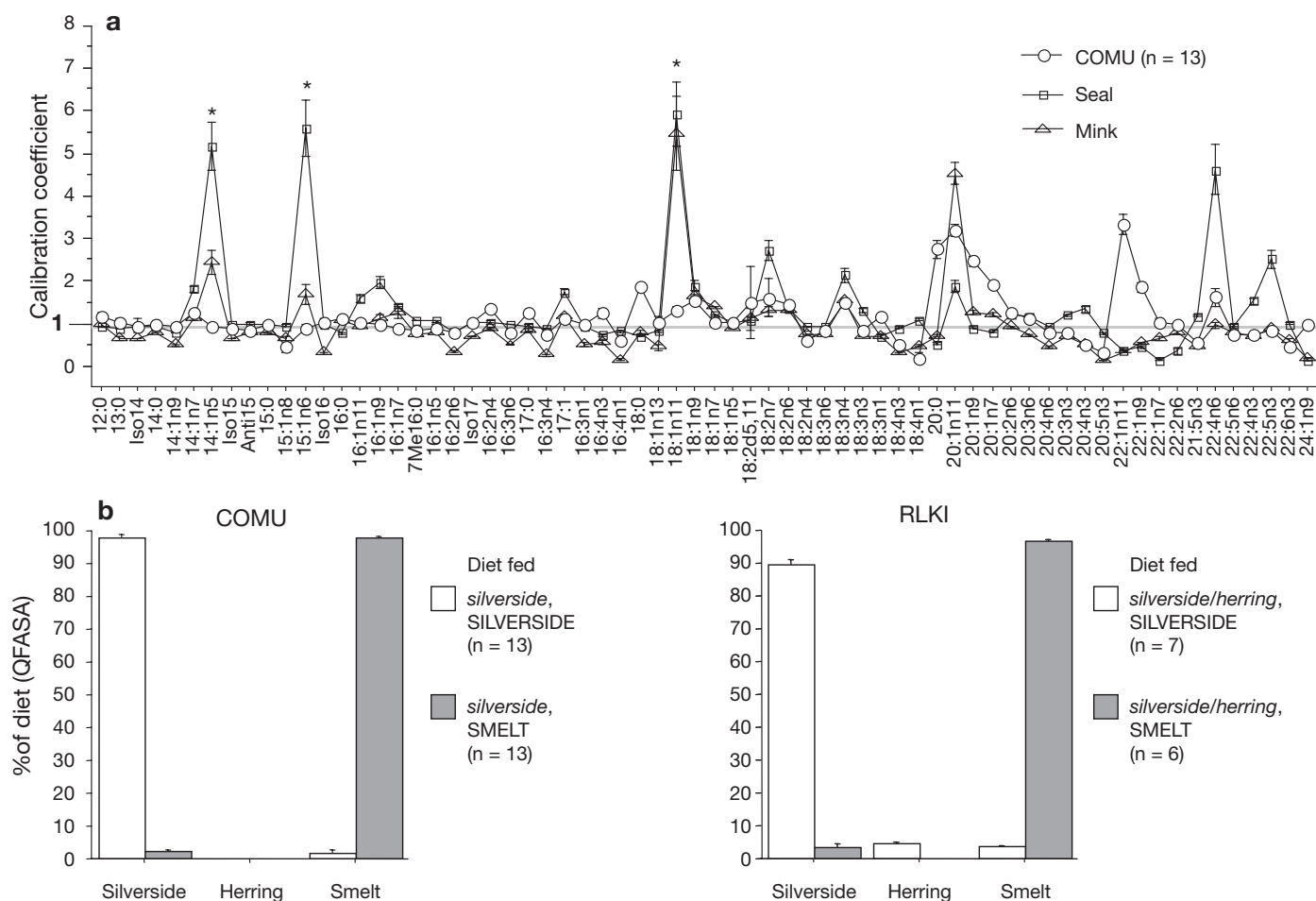
Fig. 2. (a) Seabird calibration coefficients (CCs) calculated from captive common murres (COMUs) fed a constant diet of silverside since hatching (means ± 1 SE). CCs calculated according to Iverson et al. (2004) as: % of each FA in each bird/average % of FAs in diet), but without trimmed means, as we did not use these in modeling diets of birds. Average CCs determined from previous studies of seals and mink (from Iverson et al. 2004) presented for comparison. The 1:1 line denotes deviation of a given FA in the predator from that consumed in diet. * = examples of FAs with large deviations from 1:1, but which occur at minor or trace amounts in marine lipids, with contributions from biosynthesis, and not used in quantitative fatty acid signature analysis (QFASA) modeling. (b) Estimated cumulative diets of captive COMU (at 45 d) and red-legged kittiwakes (RLKI; at 42 d) using the QFASA model and the COMU CCs from Panel a. Prey listed in italics were fed from 0 to 10 or 15 d post-hatching, and prey in capitals were fed for the main period, from Day 10 or 15 until Day 42 or 45. Bars are means of each species estimated in diets, and vertical lines are 1 SE

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 iden-

tified 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
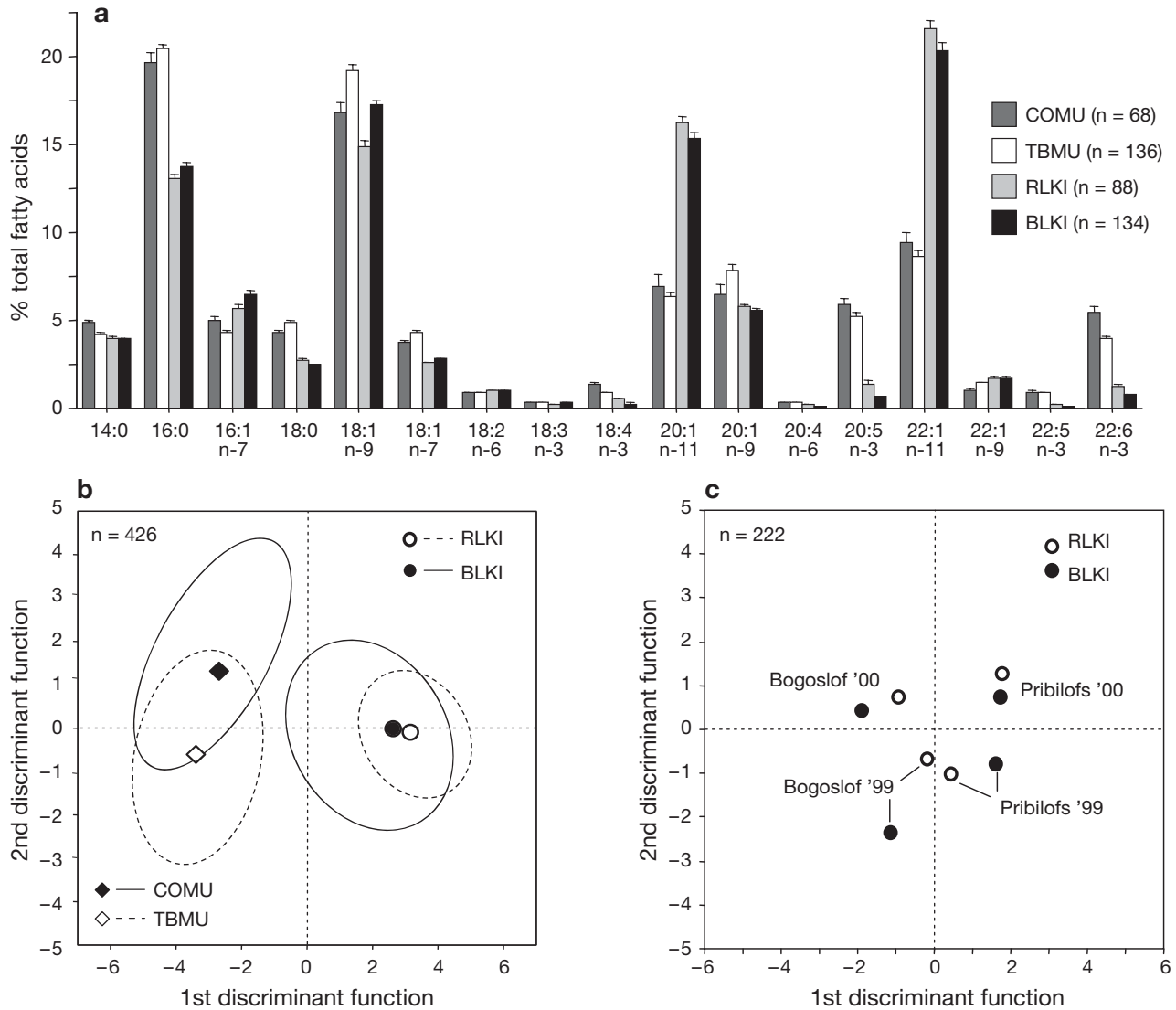
Fig. 3. (a) Selected FAs (17 of 67 identified) with the largest overall variance and an overall mean of ≥0.4% of total FAs that illustrate characteristic differences in patterns among free-ranging common and thick-billed murres (COMU and TBMU, respectively) and red-legged and black-legged kittiwakes (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 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.

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 stom-

achs. 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, sandlance, and northern smooth-tongue, and euphausiids. Squids, which were estimated to be of some importance to TBMU based on stomach contents
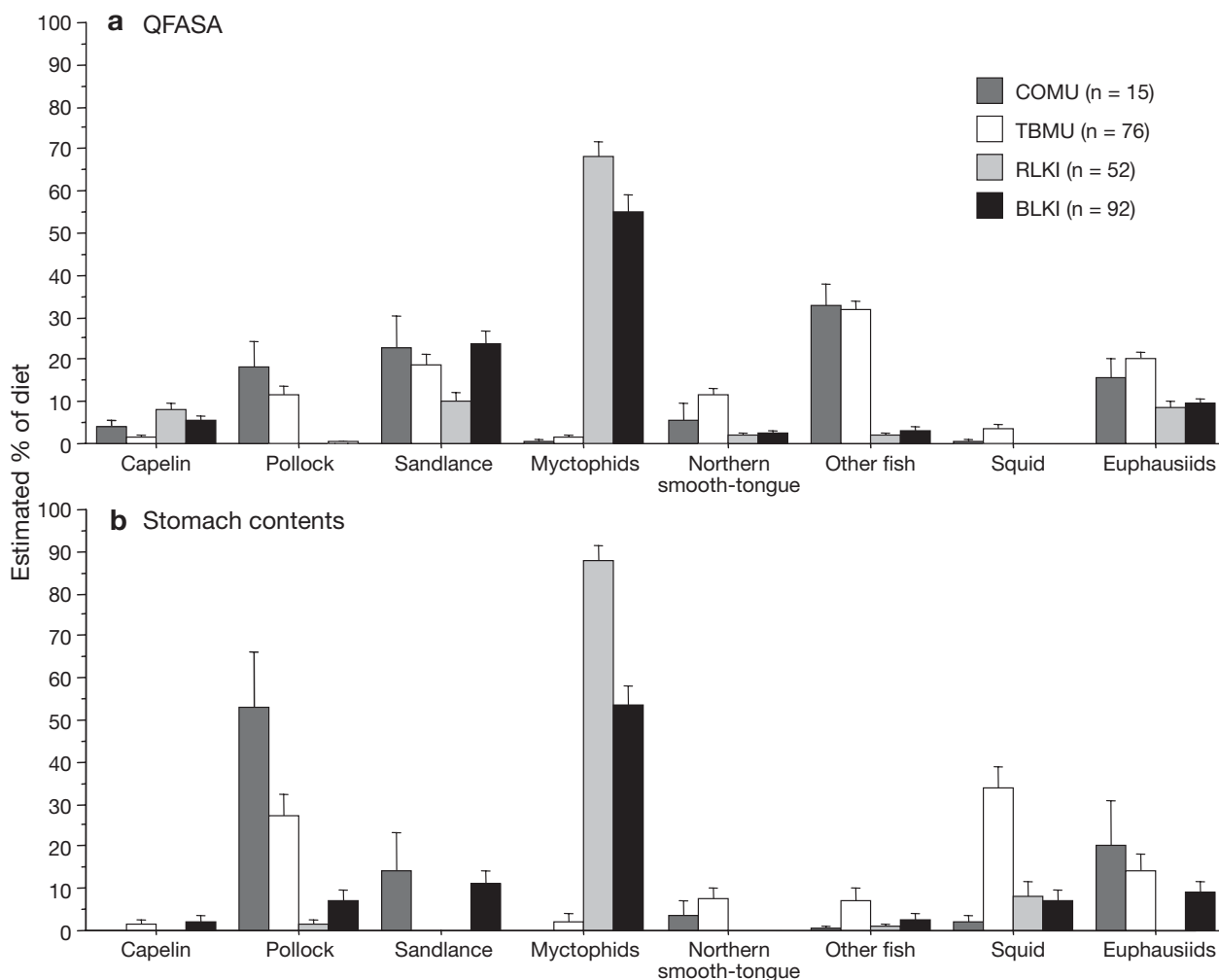
Fig. 4. (a) QFASA estimates of diets of free-ranging murres and kittiwakes (n = 235) in comparison to (b) diet estimates from stomach contents analysis in the same individuals. Prey species present in the database, but not detected in diets by either method are not illustrated. 'Other fish' were identified 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

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.

LITERATURE CITED

Bedard J (1969) Feeding of the least, crested and parakeet auklets on St. Lawrence Island, Alaska. Can J Zool 47:1025–1050

Benowitz-Fredericks ZM, Kitaysky AS (2005) Benefits and costs of rapid growth in common murre (*Uria aalge*) chicks. J Avian Biol 36:287–294

Boyd IL, Murray AWA (2001) Monitoring a marine ecosystem using responses of upper trophic level predators. J Anim Ecol 70:747–760

Budge SM, Iverson SJ, Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. Mar Mamm Sci 22:759–801

Cooper MH, Iverson SJ, Heras H (2005) Dynamics of blood chylomicron fatty acids in a marine carnivore: implications for lipid metabolism and quantitative estimation of predator diets. J Comp Physiol B 175:133–145

Croxall JP (2006) Monitoring preditor–prey interactions using multiple predator species: the South Georgia experience. In: Boyd IL, Wanless, S, Camphuysen CJ (eds) Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press, Cambridge, p 157–176

Enderson JH, Berger DD (1968) Chlorinated hydrocarbon residues in peregrines and their prey species from northern Canada. Condor 70:149–153

Furness BL, Laugksch RC, Duffy DC (1984) Cephalopod beaks and studies of seabird diets. Auk 101:619–620

Harvey JT, Loughlin TR, Perez MA, Oxman DS (2000) Relationship between fish size and otolith length for 63 species of fishes from the eastern North Pacific Ocean. NOAA Tech Rep 150

Hatch SA, Sanger GA (1992) Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. Mar Ecol Prog Ser 80:1–14

Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. J Anim Ecol 63:786–798

Hunt GL Jr, Burgesson B, Sanger GA (1981) Feeding ecology of seabirds of the eastern Bering Sea. In: Hood DW, Calder JA (eds) The eastern Bering Sea shelf: oceanography and resources, Vol. 2. NOAA, Juneau, AK, p 629–648

Iverson SJ (1993) Milk secretion in marine mammals in relation to foraging: Can milk fatty acids predict diet? Symp Zool Soc Lond 66:263–291

Iverson SJ, Springer AM (2002) Estimating seabird diets using fatty acids: protocol development and testing of ReFER hypotheses. Report to the National Pacific Marine Research Program, University of Alaska, Fairbanks, AK

Iverson SJ, Frost KJ, Lowry LL (1997) Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. Mar Ecol Prog Ser 151:255–271

Iverson SJ, Lang SLC, Cooper MH (2001) Comparison of the

Bligh and Dyer and Folch methods for total lipid determination in a broad range of marine tissue. Lipids 36: 1283–1287

Iverson SJ, Frost KJ, Lang SLC (2002) Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska: factors contributing to among and within species variability. Mar Ecol Prog Ser 241:161–181

Iverson SJ, Field C, Bowen WD, Blanchard W (2004) Quantitative fatty acid signature analysis: a new method of estimating predator diets. Ecol Monogr 74:211–235

Iverson SJ, Stirling I, Lang SLC (2006) Spatial and temporal variation in the diets of polar bears across the Canadian arctic: indicators of changes in prey populations and environment. In: Boyd IL, Wanless S, Camphuysen CJ (eds) Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press, Cambridge, p 98–117

Käkelä R, Käkelä A, Kahle S, Becker PH, Kelly A, Furness RW (2005) Fatty acid signatures in plasma of captive herring gulls as indicators of demersal or pelagic fish diet. Mar Ecol Prog Ser 293:191–200

Kitaysky AS, Kitaiskaia EV, Wingfield JC, Piatt JF (2001) Dietary restriction causes chronic elevation of corticosterone and enhances stress response in red-legged kittiwake chicks. J Comp Physiol B 171:701–709

McCafferty DJ, Boyd IL, Walker TR, Taylor RI (1999) Can marine mammals be used to monitor oceanographic conditions? Mar Biol 134:387–395

Mecklenburg CW, Mecklenburg TA, Thorsteinson LK (2002) Fishes of Alaska. American Fisheries Society, Bethesda, MD

Montevecchi WA (1993) Birds as indicators of change in prey stocks. In: Furness RW, Greenwood JJD (eds) Birds as monitors of environmental change. Chapman & Hall, London, p 217–266

Raclot T, Groscolas R, Cherel Y (1998) Fatty acid evidence for the importance of myctophid fishes in the diet of king penguins, *Aptenodytes patagonicus*. Mar Biol 132: 523–533

Roseneau DG, Byrd GV (1997) Using Pacific halibut to sample the availability of forage fishes to seabirds. In: Forage fishes in marine ecosystems. Proceedings of the international symposium on the role of forage fishes in marine ecosystems. University of Alaska, Fairbanks, AK, p 231–241

Sinclair E, Loughlin T, Pearcy W (1994) Prey selection by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea. Fish Bull (Wash DC) 92:144–156

Springer AM, Roseneau DG, Murphy EC, Springer MI (1984) Environmental controls of marine food webs: food habits of seabirds in the eastern Chukchi Sea. Can J Fish Aquat Sci 41:1202–1215

Springer AM, Roseneau DG, Lloyd DS, McRoy CP, Murphy EC (1986) Seabird responses to fluctuating prey abundance in the eastern Bering Sea. Mar Ecol Prog Ser 32: 1–12

Springer AM, Piatt JF, van Vliet G (1996) Sea birds as proxies of marine habitats and food webs in the western Aleutian Arc. Fish Oceanogr 5: 45–55

Steele JH (1974) The structure of marine ecosystems. Harvard University Press, Cambridge, MA

Votier SC, Bearhop S, MacCormick A, Ratcliffe N, Furness RW (2003) Assessing the diet of great skuas, *Catharacta skua*, using five different techniques. Polar Biol 26:20–26

Stress hormones link food availability and population processes in seabirds

A. S. Kitaysky[1],*, J. F. Piatt[2], J. C. Wingfield[3]

[1]Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA
[2]USGS Alaska Science Center, 1011 East Tudor Road, Anchorage, Alaska 99503, USA
[3]Department of Biology, University of Washington, Seattle, Washington 98195, USA

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-

*Email: ffask@uaf.edu

tive failure (Kitaysky et al. 2006) and/or affect their recruitment to breeding populations (Thompson & Ollason 2001). More importantly, breeding during sub-optimal 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 & Montevecchi 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 supplementations also reduced CORT secretion (Lanctot 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. Lanctot 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. Kitayski, 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 3 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 PBSG-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 pallasi*, 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 (Lebreton 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 sub-

sequent 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 Bonferonni 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, σ^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 AIC_c values, which is recommended when sample sizes are small relative to the number of parameters being estimated ($N/K \leq 40$; Burnham & Anderson 1998). The model with the lowest AIC_c was considered the best. Then we calculated the Akaike weights (W_i) for each model using the formula: $W_i = [\exp(-0.5 \times \Delta_i)]/\Sigma_{r=1}^{R}[\exp(-0.5 \times \Delta_r)]$. 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).
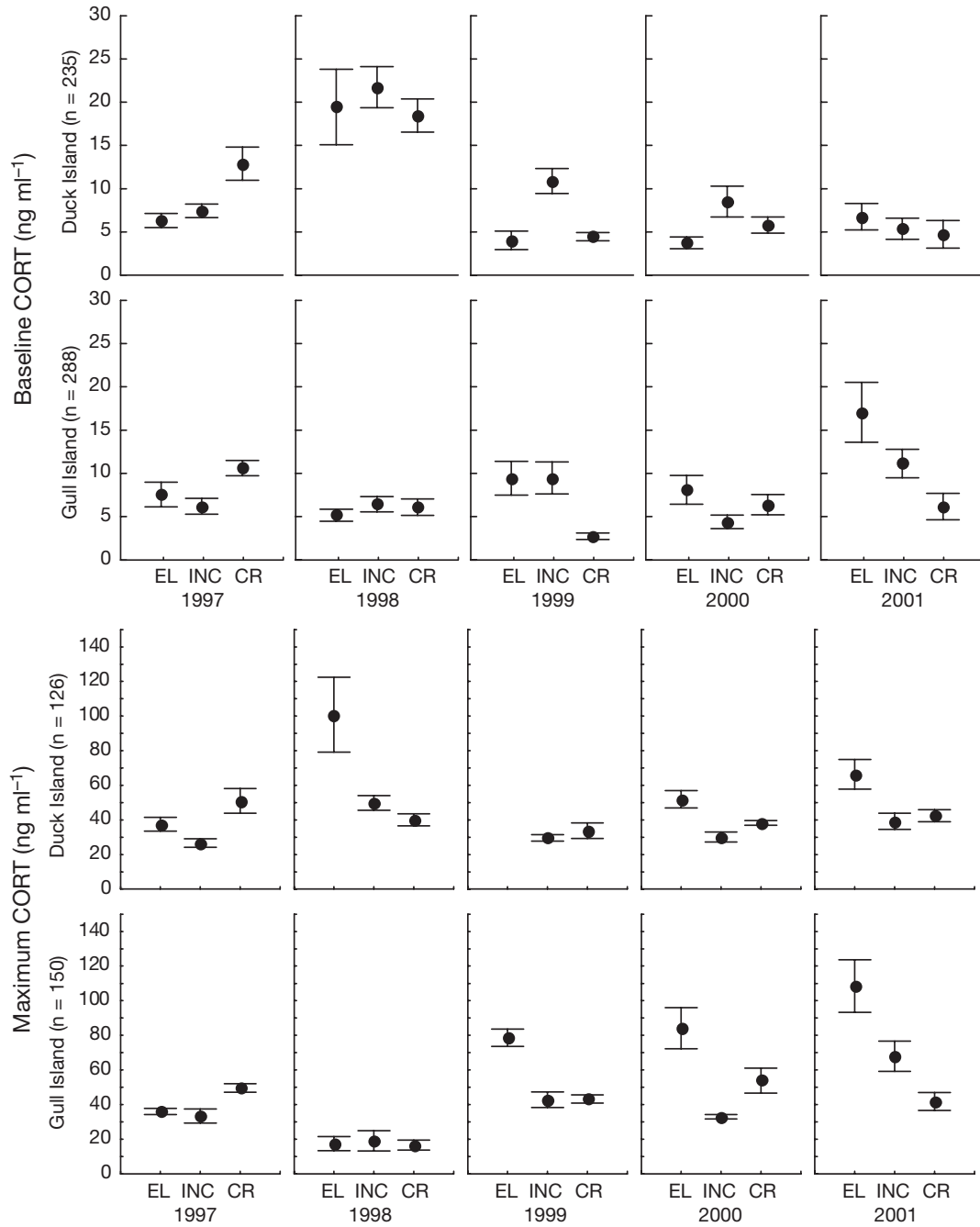
Fig. 1. *Uria aalge.* Inter-annual (1997 to 2001) and intra-seasonal dynamics of baseline and maximum corticosterone values (CORT; mean ± SE) in common murres breeding at Duck and Gull Islands, Cook Inlet, Alaska. EL: egg-laying; INC: incubation, CR: chick-rearing

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;

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

Factor	df effect	MS effect	df error	F	p	Bonferroni significance
Baseline CORT (ANOVA)						
Year	4	1.638	493	17.39	**< 0.00001**	**Yes**
Colony	1	0.249	493	2.65	0.10428	No
Stage	2	0.275	493	2.93	0.05475	No
Year × Colony	4	1.831	493	19.45	**< 0.00001**	**Yes**
Year × Stage	8	0.417	493	4.43	**0.00003**	**Yes**
Colony × Stage	2	0.477	493	5.07	0.00664	No
Colony × Year × Stage	8	0.145	493	1.54	0.13993	No
Baseline CORT—effect of food abundance (ANCOVA)						
Year	3	0.261	295	2.74	0.04382	No
Food (current 2 wk)	1	5.064	295	53.15	**< 0.00001**	**Yes**
Food (current mo)	1	1.099	295	11.53	**0.00077**	**Yes**
Food (previous mo)	1	1.115	295	11.70	**0.00071**	**Yes**
Maximum CORT (ANOVA)						
Year	4	0.505	266	13.60	**< 0.00001**	**Yes**
Colony	1	0.041	266	1.11	0.29394	No
Stage	2	0.626	200	21.34	**0.00001**	**Yes**
Year × Colony	4	0.894	266	24.07	**0.00001**	**Yes**
Year × Stage	6	0.193	200	6.59	**0.00001**	**Yes**
Colony × Stage	2	0.007	200	0.24	0.79020	No
Colony × Year × Stage	6	0.061	200	2.09	0.05658	No
Maximum CORT—effect of food abundance (ANCOVA)						
Year	3	0.277	115	6.98	**0.00025**	**Yes**
Stage	2	0.098	115	2.47	0.08927	No
Food (current 2 wk)	1	0.002	115	0.06	0.81509	No
Food (current mo)	1	0.039	115	0.99	0.32086	No
Food (previous mo)	1	0.794	115	20.02	**0.00001**	**Yes**

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).

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 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

| Variables	K[a]	ΔAIC_c[a]	SSE	W_i[a]	Ev. ratio
Baseline CORT (n = 271)					
F2W, FCM, FPM	5	0.00	0.097	0.879	1.0
F2W, stage	4	5.66	0.100	0.052	17.0
F2W, year, stage	5	8.07	0.100	0.016	56.5
F2W, stage, sex	5	8.71	0.101	0.011	78.0
F2W, colony, stage	5	8.75	0.101	0.011	79.3
F2W, FCM	4	9.61	0.102	0.007	122.2
F2W	3	10.10	0.103	0.006	156.4
F2W, FPM	4	10.75	0.102	0.004	216.3
F2W, year, colony, stage	6	11.08	0.101	0.003	254.7
F2W, year, stage, sex	6	11.17	0.101	0.003	266.3
Maximum CORT (n = 110)					
FPM, year, colony, stage	6	0.00	0.035	0.601	1.0
FPM, year, colony, stage, sex	7	0.86	0.034	0.391	1.5
FPM, year	4	10.31	0.039	0.003	173.2
FPM, year, colony	5	12.10	0.039	0.001	424.8
FPM, year, stage	5	12.39	0.039	0.001	491.2
FPM, year, sex	5	13.14	0.040	0.001	713.0
FPM, year, colony, sex	6	14.95	0.040	0.000	1763.3
FPM, year, stage, sex	6	15.41	0.040	0.000	2220.3
Year	3	18.17	0.043	0.000	8805.2
Body mass, year	4	19.41	0.043	0.000	16365.1
[a]Defined in 'Data analysis'					
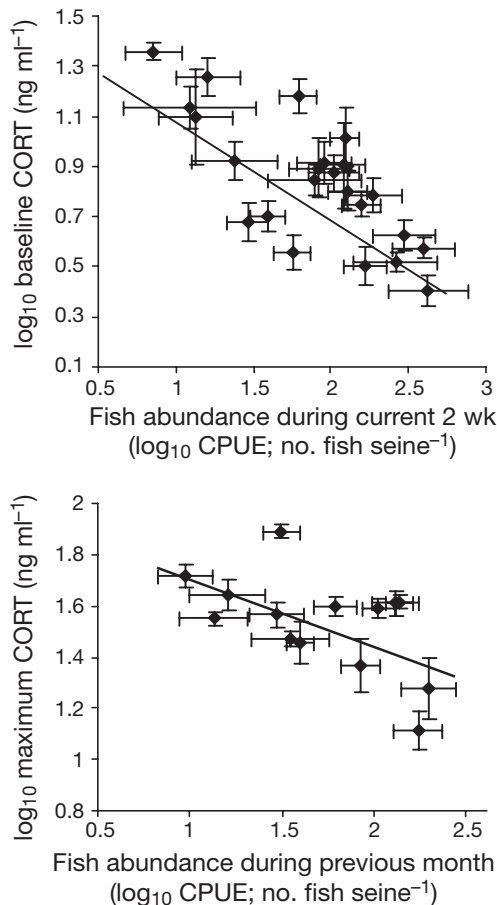
Fig. 2. *Uria aalge.* Relationships between corticosterone (CORT) and food abundance in common murres breeding on Duck and Gull Islands, from 1996 to 1999 (mean ± SE). Lines represent slopes of linear regression analyses of mean CORT levels and mean fish abundance during current 2 wk for baseline (R^2 = 0.56, $F_{1, 22}$ = 27.08; p < 0.0001, N = 23, both colonies and all 4 yr combined) and during previous month for maximum CORT (R^2 = 0.31, $F_{1,13}$ = 5.26; p = 0.040, N = 14, both colonies and all 4 yr combined). CPUE: catch per unit effort

Fig. 3. *Uria aalge.* Persistence of individuals at declining (Duck Island) and increasing (Gull Island) colonies of common murres breeding in Cook Inlet, Alaska, from 1997 to 2001, in relation to their baseline corticosterone value (CORT; mean ± SE). A significant difference between groups with different re-sighting histories is indicated by a change in lettering above the SE bars. Numbers below the SE bars represent sample sizes

CORT and persistence of individuals in the colony

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 birds that 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

Table 3. *Uria aalge.* Relationships between corticosterone (CORT) and reproductive performance (colony/year/stage-specific values) in common murres breeding on Duck and Gull Islands, from 1996 to 2001. Reported numbers are Spearman correlation coefficients and sample sizes (in parentheses); statistically significant relationships (p < 0.05) indicated in bold

Parameter	Egg-laying phenology	Hatching success	Fledging success	Productivity
Baseline CORT				
Egg-laying	0.69 (8)	**−0.73** (8)	**−0.87** (8)	**−0.76** (9)
Incubation	**0.78** (9)	**−0.82** (9)	**−0.80** (9)	**−0.80** (10)
Early chick-rearing	**0.83** (9)	**−0.79** (9)	**−0.82** (9)	**−0.79** (10)
Late chick-rearing	0.48 (8)	−0.34 (8)	−0.45 (8)	−0.37 (9)
Maximum CORT				
Egg-laying	0.39 (7)	−0.53 (7)	−0.61 (7)	−0.52 (8)
Incubation	0.59 (9)	**−0.78** (9)	**−0.83** (9)	−0.63 (10)
Early chick-rearing	0.42 (9)	**−0.77** (9)	**−0.72** (9)	**−0.67** (10)
Late chick-rearing	−0.26 (8)	−0.02 (8)	0.00 (8)	−0.02 (9)

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, Lanctot 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-

viduals. 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 maybe 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. Drovetski, 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 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.

LITERATURE CITED

Abookire AA, Piatt JF, Robards MD (2000) Nearshore fish distributions in an Alaskan estuary in relation to stratification, temperature and salinity. Estuar Coast Shelf Sci 51: 45–59

Aebischer NJ, Coulson JC (1990) Survival of the kittiwake in relation to sex, year, breeding experience and position in the colony. J Anim Ecol 59:1063–1071

Akana SF, Dallman MF, Bradbury MJ, Scribner KA, Strack AM, Walker CD (1992) Feedback and facilitation in the adrenocortical system—unmasking facilitation by partial inhibition of the glucocorticoid response to prior stress. Endocrinology 131:57–68

Anderson DR, Burnham KP, Thompson WL (2000) Null hypothesis testing: problems, prevalence, and an alternative. J Wildl Manag 64:912–923

Anderson PJ, Piatt JF (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar Ecol Prog Ser 189:117–123

Benowitz-Fredericks MZ, Kitaysky AS, Thompson CW (2006) Growth and resource allocation by common murre (*Uria aalge*) chicks in response to experimentally restricted diets. Auk 123:722–734

Birkhead TR, Nettleship DN (1982) The adaptive significance of egg size and laying date in thick-billed murres *Uria lomvia*. Ecology 63:300–306

Brown CR, Brown MB, Raouf SA, Smith LC, Wingfield JC (2005) Effects of endogenous steroid hormone levels on annual survival in cliff swallows. Ecology 86:1034–1046

Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York

Cailliet GM, Love MS, Ebeling AW (1986) Fishes: a field and laboratory manual on their structure, identification and natural history. Wadsworth, Belmont, CA

Cam E, Hines JE, Monnat J-Y, Nichols JD, Danchin E (1998) Are adult nonbreeders prudent parents? The kittiwake model. Ecology 79:2917–2930

Cam E, Cadiou B, Hines JE, Monnat J-Y (2002) Influence of behavioral tactics on recruitment and reproductive trajectory in the kittiwake. J Appl Stat 29:163–185

Clinchy M, Zanette L, Boonstra R, Wingfield JC, Smith JNM (2004) Balancing food and predator pressure induces chronic stress in songbirds. Proc R Soc Lond B 271:2473–2479

Cockrem JF (2004) Conservation and behavioral neuroendocrinology. Horm Behav 48:492–501

Cockrem JF, Silverin B (2002) Variation within and between birds in corticosterone responses of great tits (*Parus major*). Gen Comp Endocrinol 125:197–206

Crespin L, Harris M, Leberton J-D, Frederiksen M, Wanless S (2006) Recruitment to a seabird population depends on environmental factors and population size. J Anim Ecol 75:228–238

Dallman MF, Akana SF, Strack AM, Scribner KS, Pecoraro N, La Fleur SE, Houshyar H, Gomez F (2004) Chronic stress-induced effects of corticosterone on brain: direct and indirect, stress: current neuroendocrine and genetic approaches. Ann N Y Acad Sci 1018:141–150

Edwards AE (2004) Proximate and ultimate constraints on breeding in seabirds. PhD thesis, University of Washington, Seattle, WA

Frederiksen M, Wanless S, Harris MP, Rothery P, Wilson L (2004) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. J Appl Ecol 41:1129–1139

Golet GH, Schmutz JA, Irons DB, Estes JA (2004) Determinants of reproductive costs in the long-lived black-legged kittiwake: a multiyear experiment. Ecol Monogr 74:353–372

Hatch SA, Roberts BD, Fadley BS (1993) Adult survival of black-legged kittiwakes *Rissa tridactyla* in a Pacific colony. Ibis 135:247–254

Hunt GL, Byrd GV (1999) Marine bird populations and carrying capacity of the eastern Bering Sea. In: Loughlin TR, Otani K (eds) Dynamics of the Bering Sea. University of Alaska Sea Grant, Fairbanks, AK, p 631–650

Hunt GL Jr, Decker MB, Kitaysky AS (1996) Fluctuations in the Bering Sea ecosystem as reflected in the reproductive ecology and diets of kittiwakes on the Pribilof Islands, 1975 to 1991. In: Greenstreet SPR, Tasker ML (eds) Aquatic predators and their prey. Fishing News Books, Oxford, p 142–153

Kitaysky AS (1999) Metabolic and developmental responses of alcid chicks to experimental variation in food intake: functional significance of juvenile traits in varying environments. Physiol Zool 72:462–473

Kitaysky AS, Golubova EG (2000) Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids. J Anim Ecol 69:248–262

Kitaysky AS, Piatt JF, Wingfield JC, Romano M (1999a) The adrenocortical stress-response of black-legged kittiwake chicks in relation to dietary restrictions. J Comp Physiol B 169:303–310

Kitaysky AS, Wingfield JC, Piatt JF (1999b) Food availability, body condition and physiological stress response in breeding black-legged kittiwakes. Funct Ecol 13:577–584

Kitaysky AS, Hunt GL, Flint EN, Rubega MA, Decker MB (2000) Resource allocation in breeding seabirds: responses to fluctuations in their food supply. Mar Ecol Prog Ser 206:283–296

Kitaysky AS, Kitaiskaia EV, Wingfield JC, Piatt JF (2001a) Dietary restriction causes chronic elevation of corticosterone and enhances stress-response in red-legged kittiwake chicks. J Comp Physiol B 171:701–709

Kitaysky AS, Wingfield JC, Piatt JF (2001b) Corticosterone facilitates begging and affects resource allocation in the black-legged kittiwake. Behav Ecol 12:619–625

Kitaysky AS, Kitaiskaia EV, Piatt JF, Wingfield JC (2003) Benefits and costs of increased corticosterone secretion in seabird chicks. Horm Behav 43:140–149

Kitaysky AS, Romano MD, Piatt JF, Wingfield JC, Kikuchi M (2005) The adrenocortical response of tufted puffin chicks to nutritional stress. Horm Behav 47:609–619

Kitaysky AS, Kitaiskaia EV, Wingfield JC, Piatt JF (2006) A mechanistic link between chick diet and decline in seabirds? Proc R Soc Lond B 273:445–450

Lack D (1966) Population studies of birds. Clarendon Press, Oxford

Lanctot RB, Hatch SA, Gill VA, Eens M (2003) Are corticosterone levels a good indicator of food availability and reproductive performance in a kittiwake colony? Horm Behav 43:489–502

Lebrerton JD, Burnham KD, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: case studies and recent advances. Ecol

Monogr 62:67–118

Lloyd CS (1979) Factors affecting breeding of razorbills *Alca torda* on Skokholm. Ibis 121:165–176

Lormee H, Jouventin P, Trouve C, Chastel O (2003) Sex-specific patterns in baseline corticosterone and body condition changes in breeding red-footed boobies *Sula sula*. Ibis 145:212–219

Lynn SE, Breuner CW, Wingfield JC (2003) Short-term fasting affects locomotor activity, corticosterone, and corticosterone binding globulin in a migratory songbird. Horm Behav 43:150–157

Medrano JF, Aasen E, Sharrow L (1990) DNA extraction from nucleated red blood cells. Biotechniques 8:43

Merrick RL, Louphlin TR, Calkins DG (1987) Decline in abundance of the northern sealion, *Eumetopias jubatus*, in Alaska, 1956–86. Fish Bull (Wash DC) 85:351–365

Mougin JL, Jouanin C, Roux F (1997) Intermittent breeding in Cory's shearwater *Calonectris diomedia* of Selvagem Grande, North Atlantic. Ibis 139:40–44

Piatt JF, Anderson PJ (1996) Response of common murres to the Exxon Valdez oil spill and long-term changes on the Gulf of Alaska marine ecosystem. In: Rice SD, Spies RB, Wolfe DA, Wright BA (eds) Exxon Valdez Oil Spill Symp Proc. Am Fish Soc Symp 18: 720–773

Piatt JF (2002) Response of seabirds to fluctuations in forage fish density. Final report to Exxon Valdez Oil Spill Trustee Council (Restoration Project 00163M) and Minerals Management Service (Alaska OCS Region). Alaska Science Center, U.S. Geological Survey, Anchorage, AK

Piatt JF (2004) Survival of adult murres and kittiwakes in relation to forage fish abundance. Final report to Exxon Valdez Oil Spill Restoration Project (Restoration Project 00338). U.S. Geological Survey, Anchorage, AK

Pravosudov VV, Kitaysky AS (2006) Effects of nutritional restrictions during post-hatching development on adrenocortical function in western scrub-jays (*Aphelocoma californica*). Gen Comp Endocrinol 145:25–31

Pravosudov VV, Kitaysky AS, Wingfield JC, Clayton NS (2001) Long-term unpredictable foraging conditions and physiological stress response in mountain chickadees (*Poecile gambeli*). Gen Comp Endocrinol 123:324–331

Raouf SA, Smith LC, Brown MB, Wingfield JC, Brown CR (2006) Glucocorticoid hormone levels increase with group size and parasite load in cliff swallows. Anim Behav 71: 39–48

Regehr HM, Montevecchi WA (1997) Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: indirect effects of fisheries activities and implications for indicator species. Mar Ecol Prog Ser 155:249–260

Robards MD, Piatt JF, Kettle AB, Abookire AA (1999) Temporal and geographic variation in fish communities of lower Cook Inlet, Alaska. Fish Bull (Wash DC) 97:962–977

Robards MD, Rose GA, Piatt JF (2002) Growth and abundance of Pacific sand lance, *Ammodytes hexapterus*, under differing oceanographic regimes. Environ Biol Fish 64: 429–441

Romero LM (2002) Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. Gen Comp Endocrinol 128:1–24

Romero LM (2004) Physiological stress in ecology: lessons from biomedical research. Trends Ecol Evol 19:249–255

Romero LM, Wikelski M (2000) Corticosterone levels predict survival probabilities of Galapagos marine iguanas during El Niño events. Proc Natl Acad Sci USA 98:7366–7370

Romero LM, Reed JM (2005) Collecting baseline corticosterone samples in the field: is under 3 min good

enough? Comp Biochem Physiol A 140:73–79

Romero LM, Ramenofsky M, Wingfield JC (1997) Season and migration alters the corticosterone response to capture and handling in an Arctic migrant, the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). Comp Biochem Physiol 116:171–177

Sandvik H, Erikstad KE, Barrett R, Yoccoz NG (2005) The effect of climate on adult survival in five species of North Atlantic seabirds. J Anim Ecol 74:817–831

Sapolsky RM, Romero ML, Munck AU (2000) How do glucocorticoids influence stress responses? integrative, permissive, suppressive, stimulatory, and preparation actions. Endocr Rev 21:55–89

Shea RE, Ricklefs RE (1995) An experimental test of the idea that food supply limits growth rate in tropical seabirds. Am Nat 125:116–122

Shea RE, Ricklefs RE (1996) Temporal variation in growth performance in six species of tropical, pelagic seabirds. J Anim Ecol 65:29–42

Sonsthagen SA, Talbot SL, White CM (2004) Gene flow and genetic characterization of northern goshawks breeding in Utah. Condor 106:826–836

Thompson PM, Ollason JC (2001) Lagged effects of ocean climate change on fulmar population dynamics. Nature 413:417–420

Wanless S, Harris MP, Redman P, Speakman JR (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. Mar Ecol Prog Ser 189:117–123

Williams GC (1966) Natural selection, the costs of reproduction and a refinement of Lack's principle. Am Nat 100: 687–692

Wingfield JC (1994) Modulation of the adrenocortical response to stress in birds. In: Davey KG, Peter RE, Tobe SS (eds) Perspectives in comparative endocrinology. National Research Council of Canada, Ottawa, p 520–528

Wingfield JC, Kitaysky AS (2002) Endocrine responses to unpredictable environmental events: stress or anti-stress hormones? Integr Comp Biol 42:600–609

Wingfield JC, Bruener C, Jacobs J (1997) Corticosterone and behavioral responses to unpredictable events. In: Harvey S, Etches RJ (eds) Perspectives in avian endocrinology. Society for Endocrinology, Bristol, p 267–278

Zador SG, Piatt JF (1999) Time-budgets of common murres at a declining and increasing colony in Alaska. Condor 101:149–152

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

Dan P. Robinette*, Julie Howar, William J. Sydeman, Nadav Nur

PRBO Conservation Science, Marine Ecology Division, 3820 Cypress Drive #11, Petaluma, California 94954, USA

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 icthyplankton 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 sec-

ondary 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
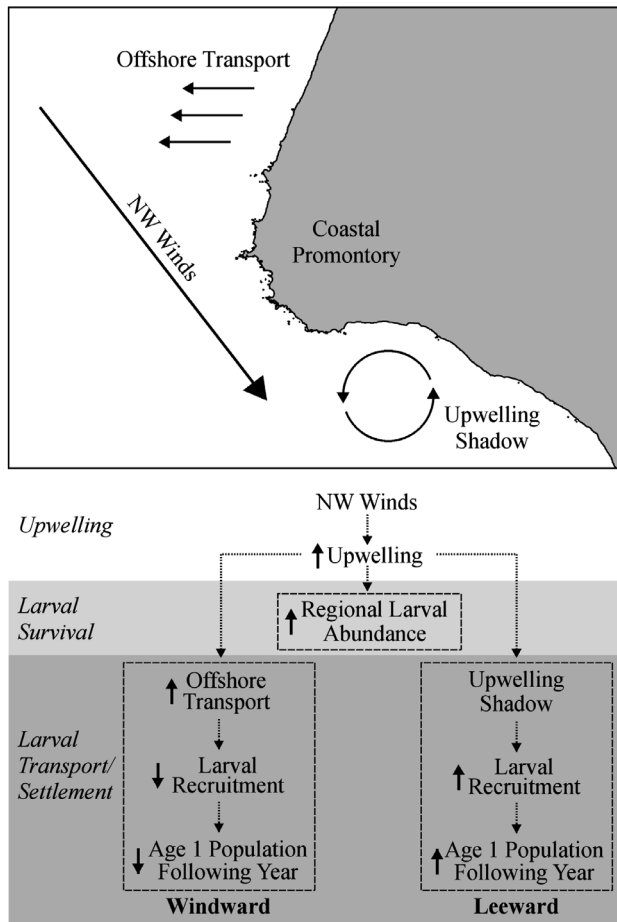
Fig. 1. Theoretical diagram showing the cascading effects of upwelling winds on demersal fish recruitment to windward and leeward habitats around a coastal promontory in Central California

be increased at windward sites and reduced at leeward sites when prior-year upwelling is 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,
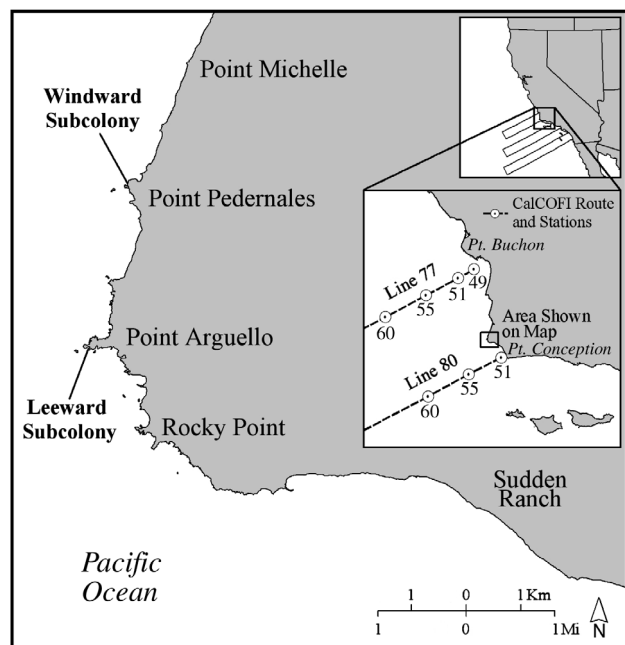

Fig. 2. Map of the Point Arguello Promontory showing the Point Pedernales (windward) and Point Arguello (leeward) sub-colonies. The larger inset map shows nearshore sampling stations along California Cooperative Oceanic Fisheries Investigations (CalCOFI) Lines 77 and 80. The entire CalCOFI survey route is shown in the smaller inset map

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^x to diet in yr^{x+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 Cal-COFI transect impacts. We estimated separate slopes for windward and leeward sites for the respective variable of interest (larval abundance or upwelling)

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

Prey taxon	2000	2001	2002	2004	2005
Sanddab (*Citharichthys* sp.)	23.73	57.50	29.11	60.42	43.95
Anchovy (*Engraulis mordax*)	0.00	1.25	0.00	2.08	3.24
Smelt (Family Osmeridae)	0.00	0.00	6.33	0.00	0.00
Squid (*Loligo* sp.)	0.00	1.25	0.00	0.00	0.00
Rockfish (*Sebastes* sp.)	1.69	0.00	5.70	0.00	4.42
Saury (*Cololabis saira*)	0.00	0.00	0.00	0.00	1.18
Octopus (*Octopus* sp.)	6.78	5.00	9.49	0.00	1.18
Sculpin (Family Cottidae)	15.25	7.50	17.09	14.58	2.95
Cuskeel (Family Ophidiidae)	0.00	1.25	0.00	2.08	1.47
Kelpfish (Family Clinidae)	1.69	0.00	0.00	2.08	2.95
Greenling (*Hexagrammos* sp.)	0.00	1.25	1.27	0.00	3.24
Shrimp (*Crangon* sp.)	0.00	0.00	3.16	6.25	12.68
Blenny (*Hypsoblennius* sp.)	0.00	0.00	0.63	2.08	1.18
Lingcod (*Ophiodon elongatus*)	1.69	2.50	6.33	0.00	0.29
Sardine (*Sardinops sagax*)	0.00	0.00	0.00	2.08	0.00
Midshipman (*Porichthys* sp.)	20.34	18.75	11.39	4.17	10.62
Surfperch (Family Embiotocidae)	0.00	0.00	1.27	0.00	0.00
Gunnel (Family Pholididae)	3.39	1.25	1.27	4.17	2.65
Prickleback (Family Stichaeidae)	15.25	0.00	6.96	0.00	4.13
Sandcrab (*Blepharipoda occidentalis*)	5.08	1.25	0.00	0.00	2.06
Poacher (Family Agonidae)	1.69	1.25	0.00	0.00	0.00
Combfish (*Zaniolepis* sp.)	3.39	0.00	0.00	0.00	1.47
n	59	80	158	48	338
Diversity (*H'*)	0.90	0.63	0.93	0.62	0.89

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 ± 7.34); 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 Pederanles forage windward of the promontory.

Table 2. *Cepphus columba.* Diet composition (% total observations yr^{-1}) and diet diversity (*H'*, Shannon-Wiener index) of pigeon guillemots breeding at the Point Arguello (leeward) sub-colony in 2001 to 2005

Prey taxon	2001	2002	2003	2004	2005
Sanddab (*Citharichthys* sp.)	64.04	53.06	46.75	41.45	46.13
Anchovy (*Engraulis mordax*)	0.44	0.00	0.41	15.65	5.99
Smelt (Family Osmeridae)	0.00	9.18	0.00	7.83	0.00
Squid (*Loligo* sp.)	0.44	1.02	0.00	2.61	0.70
Rockfish (*Sebastes* sp.)	1.32	1.02	7.32	3.77	3.17
Saury (*Cololabis saira*)	0.00	0.00	0.00	0.29	0.35
Sablefish (*Anoplopoma fimbria*)	0.44	0.00	0.00	0.00	0.00
Octopus (*Octopus* sp.)	8.77	15.31	16.67	0.00	0.70
Sculpin (Family Cottidae)	1.32	0.00	10.57	2.03	0.00
Cuskeel (Family Ophidiidae)	0.00	1.02	0.00	2.61	1.41
Kelpfish (Family Clinidae)	0.00	0.00	0.41	3.19	0.70
Greenling (*Hexagrammos* sp.)	0.00	0.00	0.41	0.29	0.70
Shrimp (*Crangon* sp.)	1.75	1.02	0.81	6.09	27.82
Blenny (*Hypsoblennius* sp.)	0.44	0.00	0.00	0.29	1.06
Lingcod (*Ophiodon elongatus*)	0.00	0.00	0.41	0.00	2.46
Sardine (*Sardinops sagax*)	0.44	0.00	0.00	0.87	0.35
Midshipman (*Porichthys* sp.)	11.40	8.16	10.16	4.06	4.93
Surfperch (Family Embiotocidae)	0.44	0.00	0.81	3.19	0.00
Gunnel (Family Pholididae)	1.75	1.02	1.63	1.45	0.00
Prickleback (Family Stichaeidae)	4.82	9.18	0.81	0.29	1.76
Sandcrab (*Blepharipoda occidentalis*)	0.00	0.00	0.00	0.00	0.70
Poacher (Family Agonidae)	1.32	0.00	2.44	2.32	0.00
Combfish (*Zaniolepis* sp.)	0.88	0.00	0.41	1.74	1.06
n	228	98	246	345	284
Diversity (*H'*)	0.60	0.65	0.74	0.91	0.73

Upwelling, regional larval abundance and guillemot diet

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).
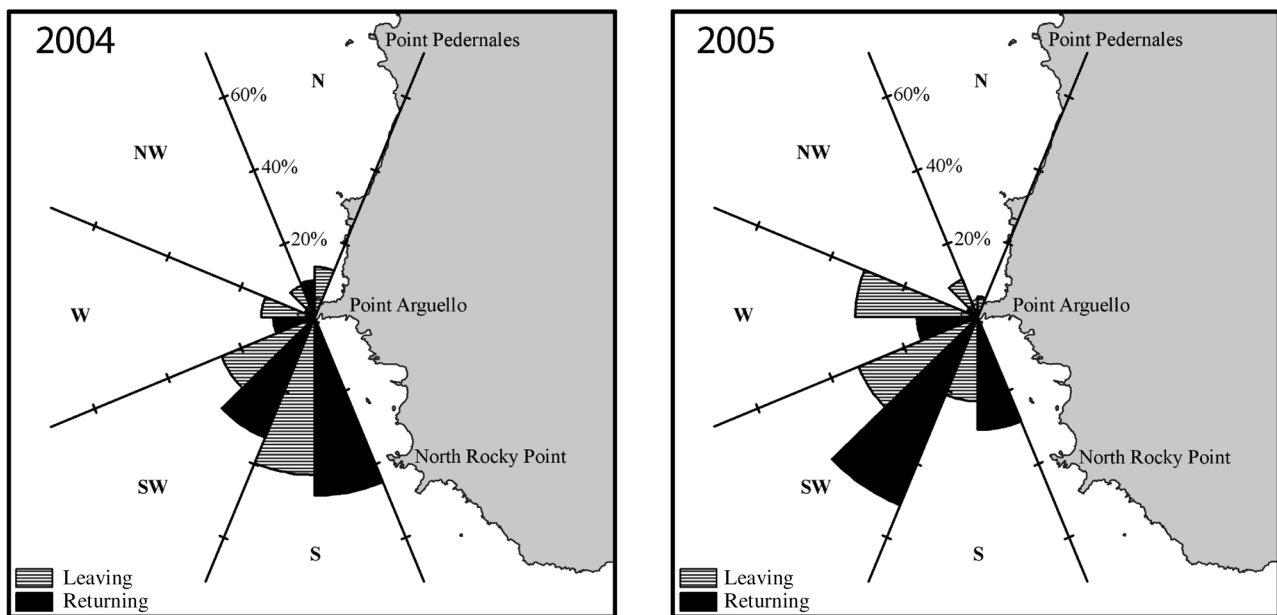

Fig. 3. *Cepphus columba.* Percent of total guillemots observed leaving and returning in each direction during foraging bouts from Point Arguello (leeward) in 2004 and 2005
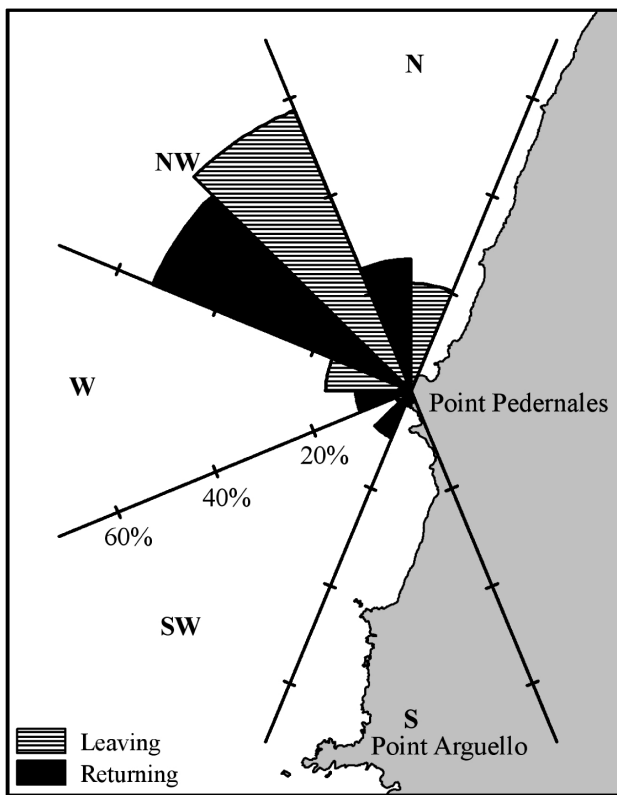
Fig. 4. *Cepphus columba*. Percent of total guillemots observed leaving and returning in each direction during foraging bouts from Point Pedernales (windward) in 2005

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.

Fig. 5. *Citharichthys* sp. Scatter plot and regression line of spring to fall larval sanddab abundance versus spring to fall upwelling variability

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 3. *Citharichthys* sp. Optimal predictive models of sanddab larval abundance versus upwelling intensity and variability using Mallows' C_p criterion for each of 3 time periods (spring to summer, fall, and spring to fall). Each model used 0, 1, or 2 upwelling variables and included California Cooperative Oceanic Fisheries Investigations (CalCOFI) transect effects; *k*: total number of parameters in the model, includes 1 for transect effect. Standardized regression coefficients (beta) are shown. **Bold:** model with the overall best fit

Optimal predictive model	Independent variable	Beta	p
Spring–Summer, $k = 2$, $R^2 = 0.347$	Spring–Summer upwelling variability	−0.588	0.057
Fall, $k = 3$, $R^2 = 0.798$	Spring–Summer upwelling variability	0.800	0.001
	Fall upwelling variability	−0.328	0.073
Spring–Fall, $k = 3$, $R^2 = 0.845$	**Spring–Summer upwelling variability**	**−0.940**	**<0.001**
	Fall upwelling intensity	**0.441**	**0.017**

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

Factor	Coefficient	SE	t	p
Location	−3.072	0.434	−7.08	0.001
Larval abundance	0.144	0.017	8.28	<0.001
Upwelling variability				
Windward site	0.069	0.006	11.27	<0.001
Leeward site	0.031	0.006	5.13	0.004

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

Factor	Coefficient	SE	t	p
Location	0.496	0.233	2.13	0.087
Upwelling variability	0.066	0.010	5.76	0.002
Larval abundance				
Windward site	0.112	0.032	3.47	0.018
Leeward site	0.224	0.037	6.00	0.002

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
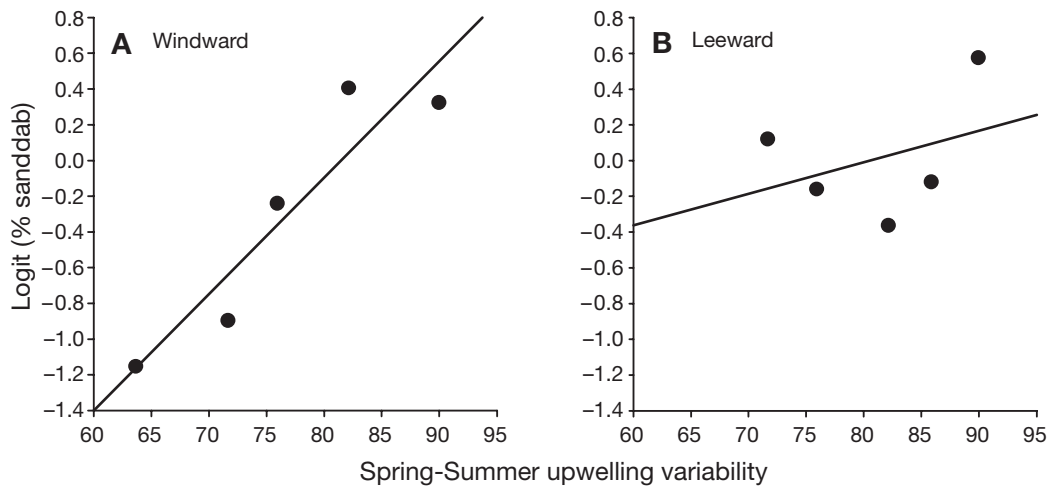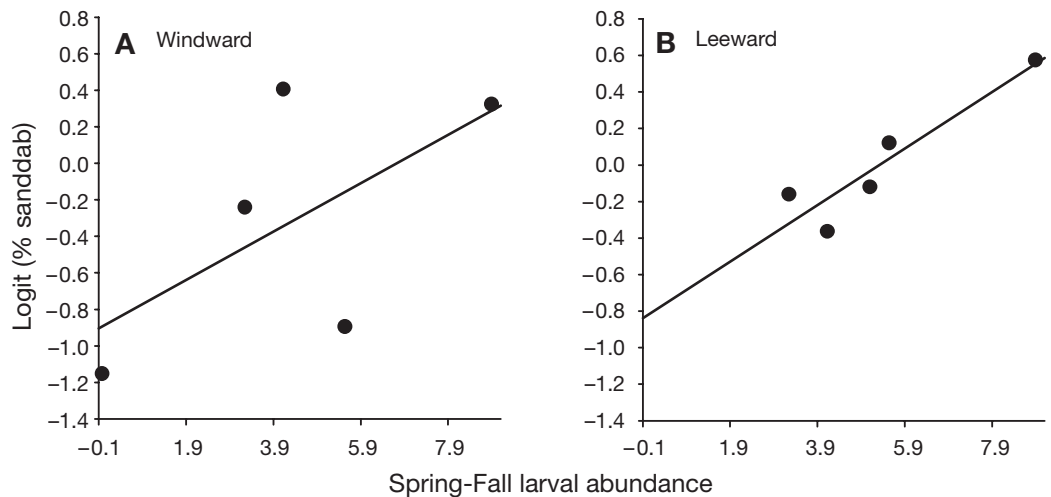

Fig. 7. *Citharichthys* sp. Scatter plots of logit-transformed percent sanddab in the guillemot *Cepphus columba* diet versus spring to fall larval abundance at the: (A) windward and (B) leeward sub-colonies. Values plotted are residuals from the linear model presented in Table 5

expect 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 mid-shelf, 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.

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

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.

LITERATURE CITED

Abraham CL, Sydeman WJ (2006) Prey-switching by Cassin's auklet *Ptychoramphus aleuticus* reveals seasonal climate-related cycles of *Euphausia pacifica* and *Thysanoessa spinifera*. Mar Ecol Prog Ser 313:271–283

Anderson DW, Gress F (1984) Brown pelicans and the anchovy fishery off southern California. In: Nettleship DN, Sanger GA, Springer PF (eds) Marine birds: their feeding ecology and commercial fisheries relationships. Canadian Wildlife Service Special Publication, Dartmouth, Nova Scotia

Brower JE, Zar JH, von Ende CN (1998) Field and laboratory methods for general ecology. McGraw-Hill, Boston, MA

Cairns DK (1992) Bridging the gap between ornithology and fisheries science: use of seabird data in stock assessment models. Condor 94:811–824

Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. Annu Rev Ecol Evol Syst 27:477–500

Cudaback CN, Washburn L, Dever E (2005) Subtidal inner-shelf circulation near Point Conception, California. J Geophys Res 110:C10007

Cury P, Roy C (1989) Optimal environmental window and pelagic fish recruitment succession in upwelling areas. Can J Fish Aquat Sci 46(4):670–680

Dever EP (2004) Objective maps of near-surface flow states near Point Conception, California. J Phys Oceanogr 34:444–461

Dong C, Oey L (2005) Sensitivity of coastal currents near Point Conception to forcing by three different winds: ECMWF, COAMPS, and blended SSM/I-ECMWF-Buoy winds. J Phys Oceanogr 35:1229–1244

Ewins PJ (1993) Pigeon guillemot (*Cepphus columba*). In: Poole A, Gill F (eds) The birds of North America, No. 49. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC

Follett WI, Ainley DG (1976) Fishes collected by pigeon guillemots, *Cepphus columba* (Pallas), nesting on Southeast Farallon Island, California. Calif Fish Game 62:28–31

Golet GH, Kuletz KJ, Roby DD, Irons DB (2000) Adult prey choice affects chick growth and reproductive success in pigeon guillemots. Auk 117(1):82–91

Graham WM, Largier JL (1997) Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. Cont Shelf Res 17(5):509–532

Hatch SA, Sanger GA (1992) Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. Mar Ecol Prog Ser 80:1–14

Hickey BM (1979) The California Current System: hypotheses and facts. Prog Oceanogr 12:259–284

Jenkins GP, Black KP (1994) Temporal variability in settlement of a coastal fish (*Sillaginodes punctata*) determined by low-frequency hydrodynamics. Limnol Oceanogr 39(7):1744–1754

Kutner MH, Nachtsheim CJ, Neter J, Li W (2005) Applied linear statistical models. McGraw-Hill Irwin, New York

Levin PS (1996) Recruitment in a temperate demersal fish: Does larval supply matter? Limnol Oceanogr 41(4):672–679

Litzow MA, Piatt JF, Abookire AA, Prichard AK, Robards MD (2000) Monitoring temporal and spatial variability in sandeel (*Ammodytes hexapterus*) abundance with pigeon guillemot (*Cepphus columba*) diets. ICES J Mar Sci 57:976–986

Mallows CL (1973) Some comments on C_p. Technometrics 15:661–675

Miller AK, Sydeman WJ (2004) Rockfish response to low-frequency ocean climate change as revealed by the diet of a marine bird over multiple time scales. Mar Ecol Prog Ser 281:207–216

Mills KL, Laidig T, Ralston S, Sydeman WJ (2007) Diets of top predators indicate pelagic juvenile rockfish (*Sebastes* spp.) abundance in the California Current System. Fish Oceanogr 16(3):273–283

Monaghan P (1996) Relevance of the behavior of seabirds to the conservation of marine environments. Oikos 77:227–237

Montevecchi WA, Myers RA (1995) Prey harvests of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales. Mar Ecol Prog Ser 117:1–9

Montevecchi WA, Myers RA (1996) Dietary changes of seabirds indicate shifts in pelagic food webs. Sarsia 80:313–322

Nur N, Jones SL, Geupel GR (1999) Statistical guide to data analysis of avian monitoring programs. Biological Technical Publication BTP-R6001-1999, USDI Fish and Wildlife Service, Washington, DC

Ohashi K, Wang D (2004) Circulation in the Santa Maria Basin, California, during 1998. J Geophys Res 109:C11012

Ohman MD, Smith PE (1995) A comparison of zooplankton sampling methods in the CalCOFI time series. Calif Coop Ocean Fish Investig Rep 36:153–158

Rackowski JP, Pikitch EK (1989) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest)—Pacific and speckled sanddabs. US Fish and Wildlife Service Biological Report 82(11.107). US Army Corps of Engineers, TR EL-82-4, Waterways Experiment Station, Vicksburg, MS

Sakuma KM, Larson RJ (1995) Distribution of pelagic metamorphic-stage sanddabs *Citharichthys sordidus* and *Citharichthys stigmaeus* within areas of upwelling off Central California. Fish Bull 93(3):516–529

Sakuma KM, Ralston S (1995) Distributional patterns of late larval groundfish off Central California in relation to hydrographic features during 1992 and 1993. Calif Coop Ocean Fish Investig Rep 36:179–192

STATA Corp (2005) STATA statistical software: Release 8.2. STATA Corporation, College Station, TX

Sunada JS, Yamashita IS, Kelly PR, Gress F (1981) The brown pelican as a sampling instrument of age group structure in the northern anchovy population. Calif Coop Ocean Fish Investig Rep 22:65–68

Trainer VL, Adams NG, Bill BD, Stehr CM, Wekell JC (2000) Domoic acid production near California coastal upwelling zones, June 1998. Limnol Oceanogr 45(8):1818–1833

Wing SR, Largier JL, Botsford LW, Quinn JF (1995) Settlement and transport of benthic invertebrates in an intermittent upwelling region. Limnol Oceanogr 40(2):316–329

Wing SR, Botsford LW, Ralston SV, Largier JL (1998) Meroplanktonic distribution and circulation in a coastal retention zone of the northern California upwelling system. Limnol Oceanogr 43(7):1710–1721

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

Ann M. A. Harding[1], John F. Piatt[2,*], Joel A. Schmutz[2]

[1]Environmental Science Department, Alaska Pacific University, 4101 University Drive, Anchorage, Alaska 99508, USA
[2]US Geological Survey, Alaska Science Center, 1011 East Tudor Road, Anchorage, Alaska 99503, USA

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 & Montevecchi 2003).

Time and energy demands associated with reproduction are generally thought to be at 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 produc-

tivity; 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**. Model-averaged fits to the data for the non-linear relationship are shown in Fig. 1

Relationships Food density x-axis		Predicted models evaluated			Values from non-linear relationships	
Colony attendance y-axis		Non-linear	Null	Linear:positive	Food threshold (g m^{-3})	Attendance plateau (bird-min h^{-1})
Incubation	ΔAICc value	1.32	**0.00**	1.78	0.033	75.20
	AICc weight	0.27	**0.52**	0.21		
	r^2	0.35	**0.0**	0.10		
Chick-rearing	ΔAICc value	**0.00**	8.80	1.85	0.058	72.13
	AICc weight	**0.65**	0.01	0.28		
	r^2	**0.71**	0.00	0.49		

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 con-
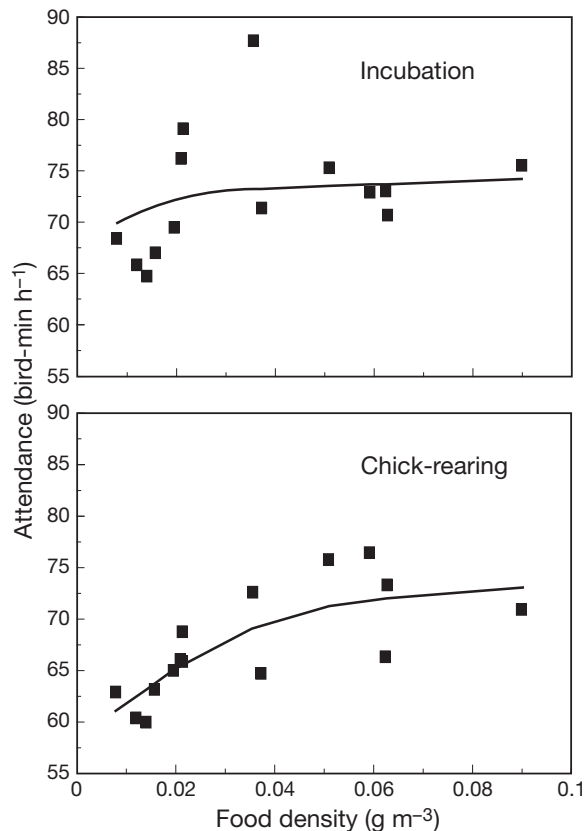

Fig. 1. *Uria aalge.* Model-averaged fit of the non-linear relationship between attendance during incubation and chick-rearing versus local prey density. Fitted values for model-average based on Akaike information criterion weights

stant 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 (ΔAICc = 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 (ΔAICc > 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).

LITERATURE CITED

Abookire AA, Piatt JF (2005) Oceanographic conditions structure forage fish into lipid-rich and lipid-poor communities in lower Cook Inlet, Alaska, USA. Mar Ecol Prog Ser 287: 229–240

Benvenuti S, Dall'Antonia L, Falk F (2002) Diving behaviour differs between incubating and brooding Brunnich's guillemots, *Uria lomvia.* Polar Biol 25:474–478

Burger AE, Piatt JF (1990) Flexible time budgets in breeding common murres: buffers against variable prey abundance. Stud Avian Biol 14:71–83

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York

Cairns DK (1987) Seabirds as monitors of marine food supplies. Biol Oceanogr 5:261–271

Croll DA, Gastin AJ, Noble DG (1991) Adaptive loss of mass in thick-billed murres. Condor 93:496–502

Davoren GK, Montevecchi WA (2003) Consequences of foraging trip duration on provisioning behavior and fledging condition of common murres *Uria aalge.* J Avian Biol 34: 44–53

Durant JM, Anker-Nilssen T, Stenseth NC (2003) Trophic interactions under climate fluctuations: the Atlantic puffin as an example. Proc R Soc Lond B 270:1471–2954

Falk K, Benvenuti S, Dall'Antonia L, Gilchrist G, Kampp K (2002) Foraging behaviour of thick-billed murres breeding in different sectors of the North Water polynya: an intercolony comparison. Mar Ecol Prog Ser 231:293–302

Frederiksen M, Harris, MP, Daunt F, Rothery P, Wanless S (2004) Scale-dependent climate signals drive breeding phenology of three seabird species. Global Change Biol 10:1214–1221

Gaston AJ (1985) Energy invested in reproduction by thick-billed murres (*Uria lomvia*). Auk 102:447–458

Gaston AJ, Nettleship DN (1982) Factors determining seasonal changes in attendance at colonies of the thick-billed murre (*Uria lomvia*). Auk 99:468–473

Gauthier S, Horne JK (2004) Acoustic characteristics of forage fish species in the Gulf of Alaska and Bering Sea based on Kirchhoff-approximation models. Can J Fish Aquat Sci 61:1839–1850

Golet GH, Schmutz JA, Irons DB, Estes JA (2004) Determinants of reproductive costs in the long-lived black-legged kittiwake: a multiyear experiment. Ecol Monogr 74: 353–372

Harding AMA, Piatt JF, Schmutz JA, Shultz M, Van Pelt TI, Kettle AB, Speckmann SG (2007) Prey density and the behavioural flexibility of a marine predator: the common guillemot (*Uria aalge*). Ecology 88:2024–2033

Hare SR, Mantua NJ (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog Oceanogr 47: 103–145

Harris MP, Wanless S (1988) The breeding biology of guillemots (*Uria aalge*) on the Isle of May over a six year period. Ibis 130:172–192

Harris MP, Wanless S, Rothery P (1986) Counts of breeding and nonbreeding guillemots (*Uria aalge*) at a colony during the chick rearing period. Seabird 9:43–46

Hassell MP, May RM (1974) Aggregation of predators and insect parasites and its effect on stability. J Anim Ecol 43:567–594

Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can Entomol 91:293–320

Jansen JK, Russel RW, Meyer WR (2002) Seasonal shifts in the provisioning behavior of chinstrap penguins (*Pygoscelis antarctica*). Oecologia 131:306–318

Johannesson KA, Mitson RB (1983) Fisheries acoustics: a practical manual for aquatic biomass estimation. FAO Fish Tech Pap 240:1–249

Jones IL, Rowe S, Carr SM, Fraser G, Taylor P (2002) Different patterns of parental effort during chick-rearing by female and male thick-billed murres (*Uria lomvia*) at a low-arctic colony. Auk 119:1064–1074

Monaghan P, Walton P, Wanless S, Uttley JD, Burns MD (1994) Effects of prey abundance on the foraging behavior, diving efficiency and time allocation of breeding guillemots (*Uria aalge*). Ibis 136:214–222

Philips RA, Caldow RWG, Furness RW (1996) The influence of food availability on the breeding effort and reproductive success of Arctic skuas (*Stercorarius parasiticus*). Ibis 138:410–419

Piatt JF, Anderson P (1996) Response of common murres to the Exxon Valdez oil spill and long-term changes in the Gulf of Alaska marine ecosystem. Am Fish Soc Symp 18:720–737

Piatt JF, Harding AMA (2007) Population ecology of seabirds in Cook Inlet. In: Spies R (ed) Long-term ecological change in the northern Gulf of Alaska. Elsevier, Amsterdam, p 335–352

Ricklefs RE (1983) Some considerations on the reproductive energetics of pelagic seabirds. Stud Avian Biol 8:84–94

Rose GA, Leggett WC (1988) Hydroacoustic signal classification of fish schools by species. Can J Fish Aquat Sci 45:597–604

Shaffer SA, Costa DP, Weimerskirch H (2003) Foraging effort in relation to the constraints of reproduction in free-living albatross. Funct Ecol 17:66–74

Speckman SG (2004) Characterizing fish schools in relation to the marine environment and their use by seabirds in lower Cook Inlet, Alaska. PhD thesis, University of Washington, Seattle

Speckman SG, Piatt JF, Minte-Vera CV, Parrish JK (2005) Parallel structure among environmental gradients and three trophic levels in a subarctic estuary. Prog Oceanogr 66:25–65

Suddaby RM, Ratcliffe N (1997) The effects of fluctuating food availability on breeding Arctic terns (*Sterna paradisaia*). Auk 114:524–530

Thomas GL, Kirsch J, Thorne RE (2002) *Ex-situ* target strength measurements of Pacific herring and Pacific sand lance. North Am J Fish Manage 22:1136–1145

Toms JD, Lesperance ML (2003) Piecewise regression: a tool for identifying ecological thresholds. Ecology 84:2034–2041

Uttley JD, Walton P, Monaghan P, Austin G (1994) The effects of food abundance on breeding performance and adult time budgets of guillemots (*Uria aalge*). Ibis 136:205–215

Zador SG, Piatt JF (1999) Time-budgets of common murres at a declining and increasing colony in Alaska. Condor 101:149–152

Beached birds and physical forcing in the California Current System

**Julia K. Parrish[1],*, Nicholas Bond[2], Hannah Nevins[3], Nathan Mantua[1,2],
Robert Loeffel[4], William T. Peterson[5], James T. Harvey[3]**

[1]School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, Washington 98195-5020, USA
[2]Joint Institute for the Study of the Atmosphere and Ocean, University of Washington, Seattle, Washington 98195, USA
[3]Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, California 95039, USA
[4]9626 SE Cedar St., South Beach, Oregon 97366, USA
[5]Northwest Fisheries Science Center, NOAA National Marine Fisheries Service, Newport, Oregon 97366, USA

ABSTRACT: Seabirds have often been proposed as environmental indicators. Beached bird data may provide an additional data source and such data is efficacious because it can reliably be collected by volunteers. In addition to anthropogenic factors, such as oil spills, changes in the ocean-atmosphere can affect carcass beaching rate in 3 non-exclusive ways: (1) direct mortality following storms, (2) mortality via bottom-up food web processes, and (3) increase in carcass delivery due to shifts in surface water movement. We used data from 3 volunteer-based beached bird data sets collected within the California Current System (CCS) to (1) examine the level of response to anomalous ocean conditions in 2005 and (2) explore the degree to which long-term beaching patterns could be explained by one or more of our proposed mechanisms. In 2005, anomalous die-offs of Cassin's auklet *Ptychoramphus aleuticus* and the rhinoceros auklet *Cerorhinca monocerata* occurred in the winter in Monterey. By spring, anomalous die-offs of Brandt's cormorant *Phalacrocorax pencillatus* and the common murre *Uria aalge* occurred throughout the CCS. Over the longer term, increases in beaching were associated with changes in the timing and intensity of upwelling and, secondarily, with zonal winds aloft—a potential proxy of shifts in pelagic community composition. These results suggest that a bottom-up food web mechanism best explains seabird beaching, at least in the spring. Correlations of local measures of storminess to seabird beaching rates were weak to non-existent. Correlations were much stronger at the California site (8 yr) and weaker to non-existent at the Oregon site (26 yr). Collectively, these data suggest that relationships between ocean physics and beached bird response may be site specific and/or may reflect choices live birds make vis-à-vis non-breeding distribution.

KEY WORDS: Upwelling · Seabird · Common murre · Brandt's cormorant · Cassin's auklet · Rhinoceros auklet

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 & Green-

wood 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
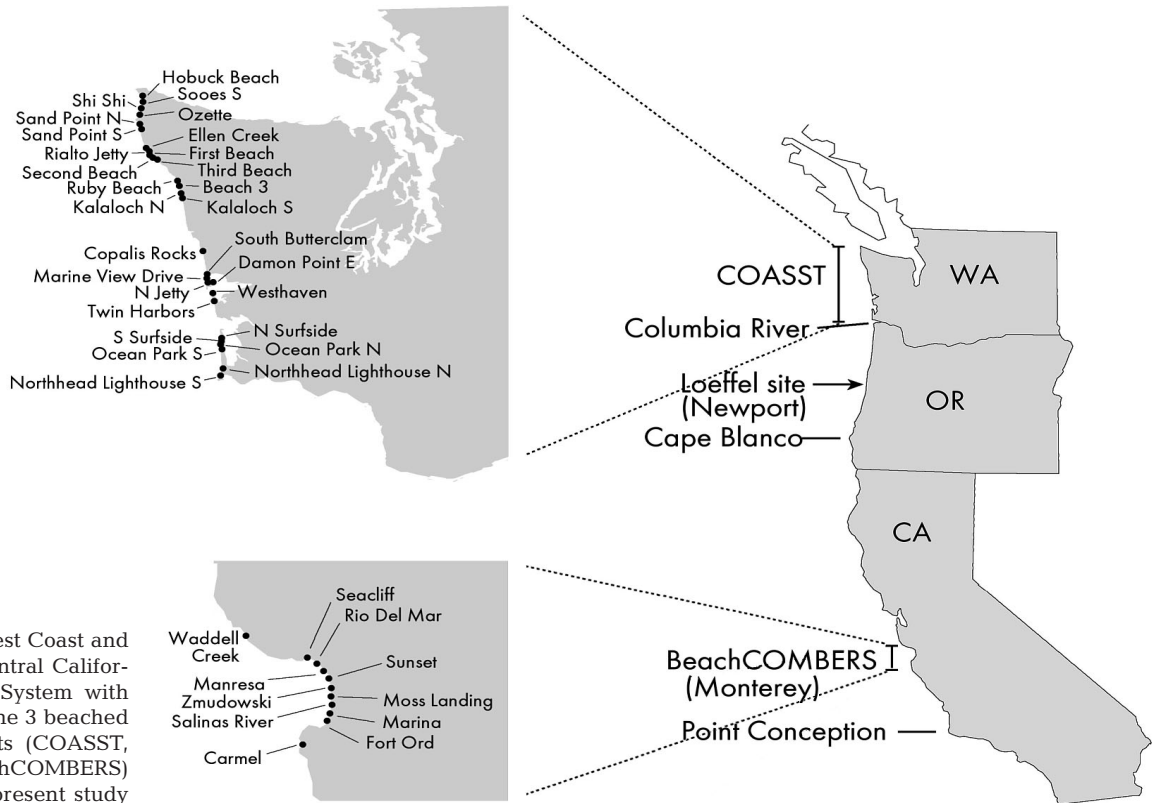
Fig. 1. US West Coast and north and central California Current System with locations of the 3 beached bird data sets (COASST, Loeffel, BeachCOMBERS) used in the present study

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 under-representation 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 pro-

tocol 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 & Thoreson 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 monocerata* 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 pencillatus* 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 down-

welling 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 (ω) 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 ($r \approx 0.7$ 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 $m^2\ s^{-2}$) 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 $10\ m^2\ s^{-2}$. 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 ($m^2\ s^{-2}$), the maximum event intensity (cumulative $m^2\ s^{-2}$ 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*

mimus, *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 pencillatus* 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^{-1}). 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
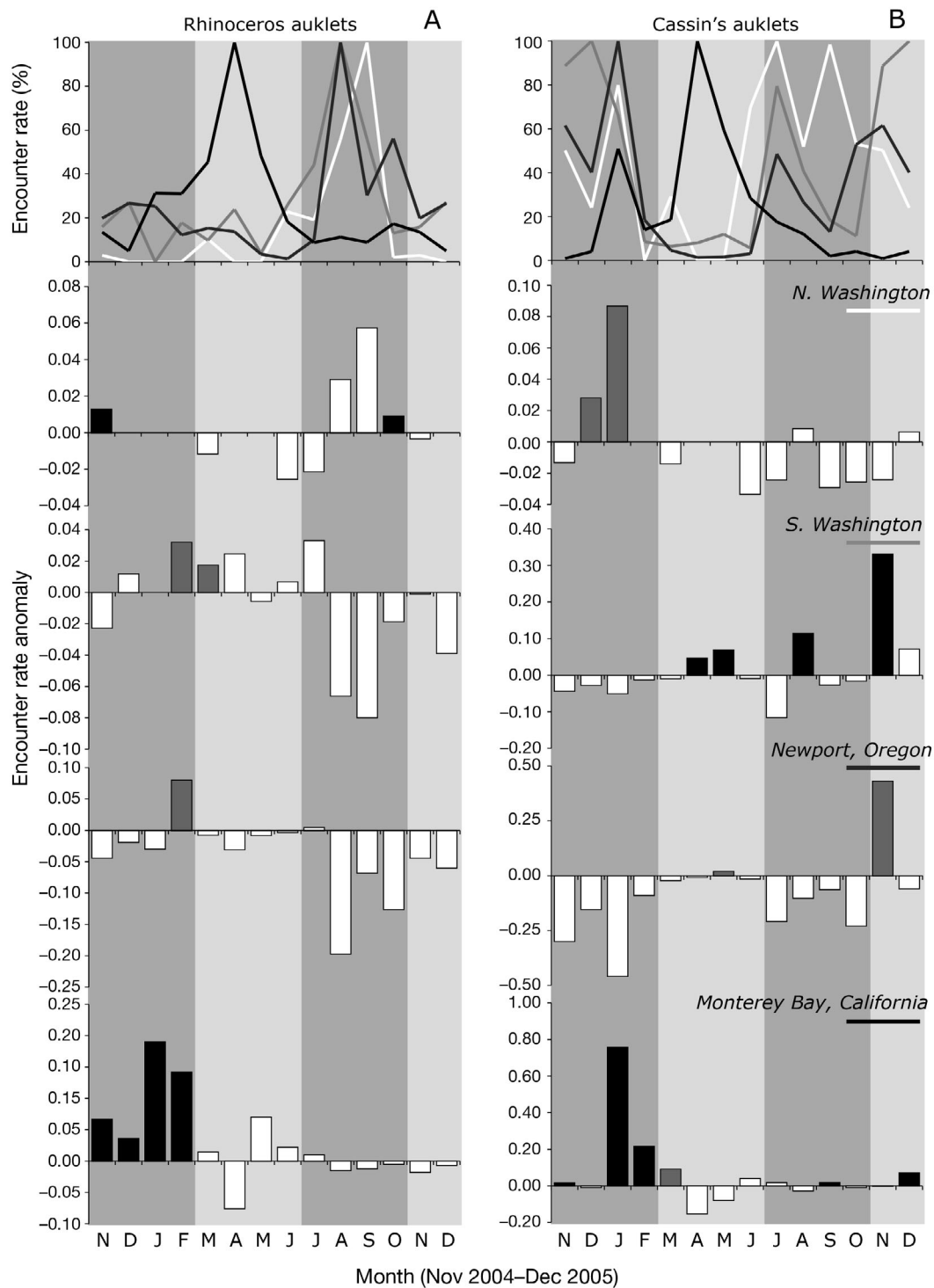
Fig. 2. (Above and facing page.) Encounter rates of (A) rhinoceros auklets, (B) Cassin's auklets, (C) common murres, and (D) Brandt's cormorants across the 4 sampling locations. Top row of panels: the average monthly encounter rate (a proxy for deposition) over the history of each program, standardized 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)
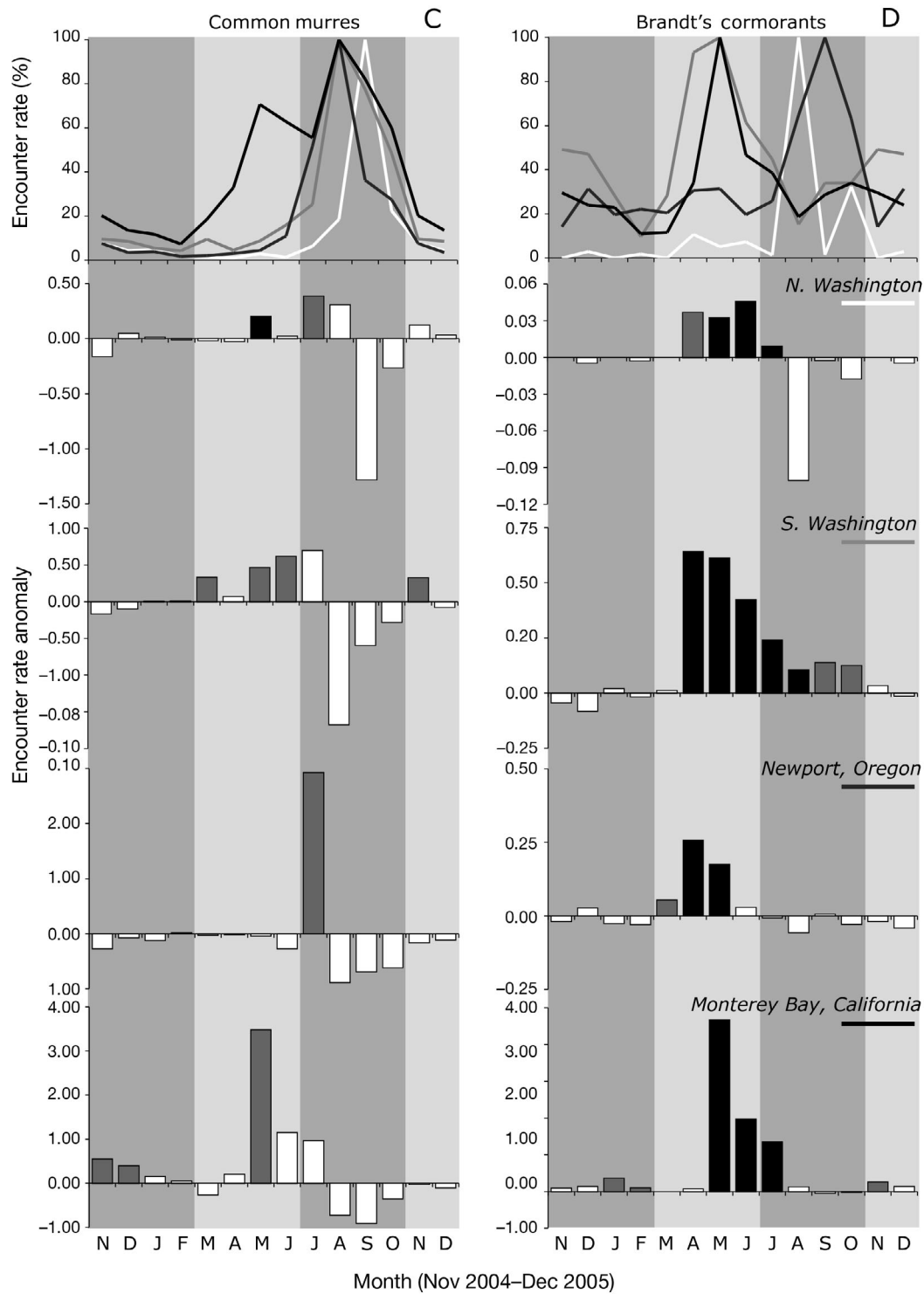
Fig. 2 (continued)

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

Table 1. Comparison of 2005 seasonal beaching rates versus program average values (1-sample, 2-sided *t*-tests). Negative, significant *t*-values (indicating higher than expected beaching) are **bold**. Positive, significant *t*-values (indicating lower than expected beaching) are ***bold and italicized***. Sample sizes (n), in years, are listed following each location. COMU: common murre *Uria aalge*; BRAC: Brandt's cormorant *Phalacrocorax pencillatus*; RHAU: rhinoceros auklet *Cerorhinca monocerata*; CAAU: Cassin's auklet *Ptychoramphus aleuticus*; winter: November to February; spring–summer: March to June; post-breeding: July to October; n.s.: not significant

	COMU		BRAC		RHAU		CAAU	
	t	p	*t*	p	*t*	p	*t*	p
North coast, WA (n = 5)								
Winter	1.852	n.s.	1.633	n.s.	−3.000	n.s.	−2.379	n.s.
Spring–Summer	**−3.707**	**<0.05**	**−3.920**	**<0.05**	1.471	n.s.	1.615	n.s.
Post-breeding	0.659	n.s.	1.235	n.s.	−0.751	n.s.	1.513	n.s.
South coast, WA (n = 5)								
Fall–Winter	1.283	n.s.	1.539	n.s.	−0.145	n.s.	0.509	n.s.
Spring–Summer	**−3.600**	**<0.05**	**−3.989**	**<0.05**	−1.355	n.s.	**−3.823**	**<0.05**
Post-breeding	1.442	n.s.	**−3.984**	**<0.02**	1.652	n.s.	0.585	n.s.
Newport, OR (n = 25, 26)								
Winter	*2.895*	*<0.01*	*2.328*	*<0.05*	0.448	n.s.	1.888	n.s.
Spring–Summer	2.049	n.s.	**−19.641**	**<0.0001**	*2.163*	*<0.05*	*2.090*	*<0.05*
Post-breeding	−0.723	n.s.	1.999	n.s.	*3.778*	*<0.001*	1.918	n.s.
Monterey, CA (n = 8)								
Winter	**−5.088**	**<0.002**	**−3.951**	**<0.01**	**−6.838**	**<0.001**	**−6.998**	**<0.001)**
Spring–Summer	**−3.366**	**<0.01**	**−6.931**	**<0.001**	−0.142	n.s.	0.310	n.s.
Post-breeding	0.728	n.s.	**−5.985**	**0.001**	1.529	n.s.	0.061	n.s.

experienced only scattered anomalously high months. By spring, beaching of the auklet species had either returned to normal values, or values were actually significantly less than expected (Oregon; Fig. 2, Table 1).

Common murre and Brandt's cormorant beaching was somewhat elevated during the winter, but only in California (Fig. 2C,D, Table 1). In the northern CCS, beaching rates were either normal (Washington) or actually significantly lower than expected during the winter (Oregon; Fig. 2, Table 1). However, by spring both of these species were washing up in significant numbers throughout their breeding range (Fig. 2, Table 1). 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 versus the long-term mean, $t = -8.466$, p <0.0001; Fig. 2C). By the post-breeding season, mortality rates had returned to normal mean values, and individual months fell well below normal peak values.

By far, the strongest and longest spring mortality anomaly came from Brandt's cormorants (Fig. 2D, Table 1). All 4 locations registered significant increases in the carcasses of these cormorants during spring to summer, irrespective of whether peak mortalities were expected (southern Washington, California) or not (northern Washington, Oregon; Fig. 2D, top panel). Unseasonably high beaching continued through the beginning of the post-breeding season in southern Washington and California (Fig. 2D, Table 1).

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

Table 2. Correlation coefficients (R^2) between cumulative encounter rates (birds km^{-1}) during the winter (November to February), and a range of proxies of regional and local winter conditions. Relationships in a direction other than expected given hypotheses (see 'Results, Exploring bio-physical linkages, Winter') are in *italics*. Sample size (n), in yr, is listed following each location. For local buoy wind data, Monterey sample size was 7 (1999 to 2005). For Newport, sample size was 12 (1992 to 1996, 1999 to 2005) due to missing data months in all other inclusive years. See Table 1 for taxonomic names

| | Zonal winds | Vertical velocity | Upwelling index | Buoy data | | | | |
				Duration mean (d)	Onshore wind (d)	Number of storms	Intensity mean ($m^2 s^{-2}$)	Intensity max. ($m^2 s^{-2}$)
Monterey, CA (n = 8)								
Common murres	0.202	0.432	0.237	*0.024*	0.098	*0.018*	0.033	0.000
Brandt's cormorants	0.544	0.140	0.041	0.080	0.004	*0.388*	*0.005*	0.094
Rhinoceros auklets	0.388	*0.001*	*0.018*	*0.197*	0.379	0.001	0.082	*0.165*
Newport, OR (n = 25)								
Common murres	0.038	*0.103*	0.071	*0.080*	*0.095*	0.035	*0.058*	*0.044*
Brandt's cormorants	*0.024*	0.001	*0.051*	0.049	*0.005*	0.000	0.016	0.001
Rhinoceros auklets	*0.106*	0.032	*0.003*	0.013	0.048	0.148	0.016	0.149
Cassin's auklets	0.142	*0.040*	*0.021*	*0.056*	*0.072*	0.012	*0.044*	*0.066*

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
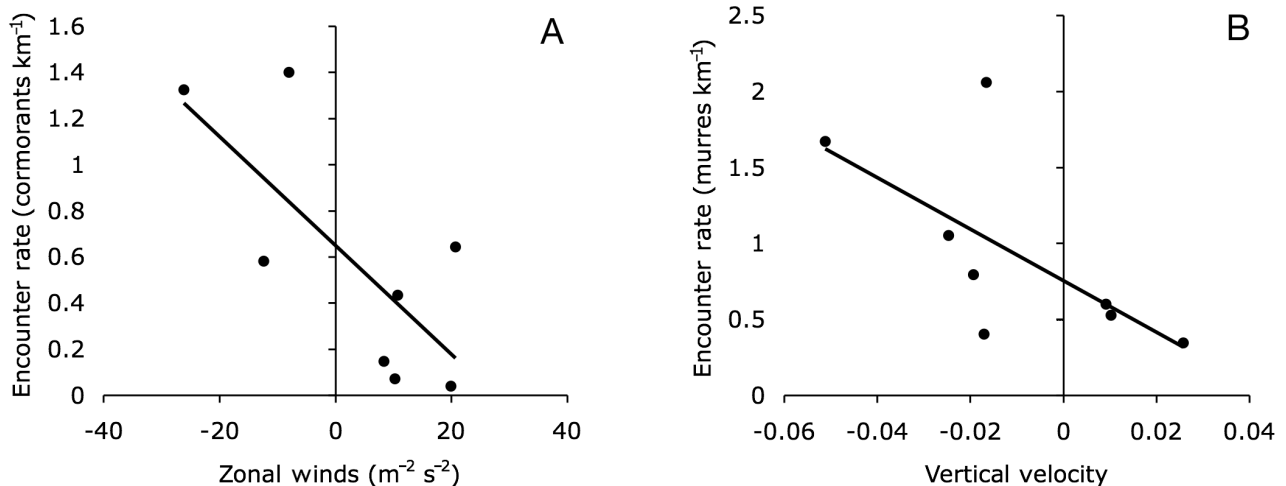

Fig. 3. Encounter rates of (A) Brandt's cormorants as a function of winter (November to February) zonal winds at 300 hPa (where birds = −0.0236 zonal winds + 0.650) and (B) common murres as a function of winter (November to February) vertical velocity (where birds = −16.94 vertical velocity + 0.755), both within the Monterey, CA, site

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 m² 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.

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 ($y = cx^b$) 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

	Spring transition (day of the year)	Upwelling index			Copepod index	
		MA	MAM	MAMJ	MA	MAM
Monterey, CA (n = 8)						
Common murres	0.112	0.162*	0.656*	0.635*		
Brandt's cormorants	0.568	0.275*	0.710*	0.692*		
Newport, OR (n = 26)						
Common murres	*0.002*	0.078	0.036	0.021		
Brandt's cormorants	0.232	0.044	0.115	0.122		
Newport, OR (n = 8; 9 for copepod index)						
Common murres	*0*	*0.050*	*0.036*	*0.139*	0.138	0.176
Brandt's cormorants	0.638	0.023	0.185	0.326	0.061	0.384

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 cor-

morants. 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-
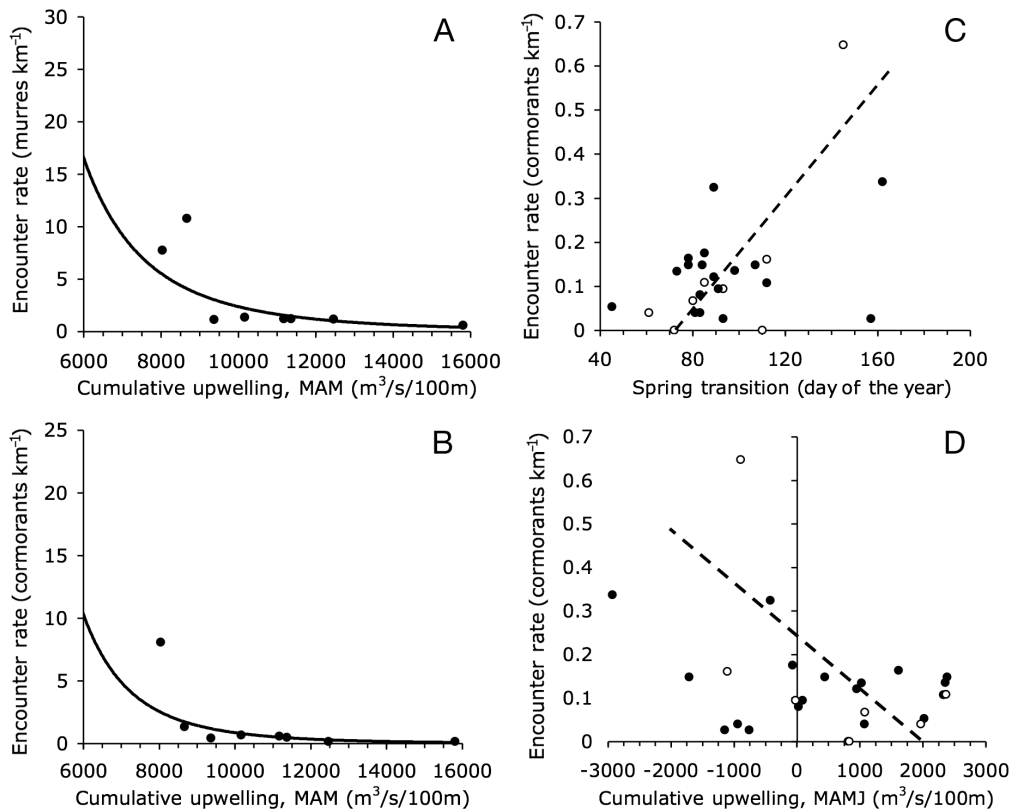
Fig. 4. Spring to summer (MAM: Mar to May, MAMJ: Mar to Jun) encounter rates of local breeders versus spring upwelling intensity (UW) and onset (ST). (A) Common murres in Monterey (birds = [4E + 15] × UW⁻³·⁷⁹⁶⁴), (B) Brandt's cormorants in Monterey (birds = [2E + 19] × UW⁻⁴·⁸³⁶⁶), (C) Brandt's cormorants 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
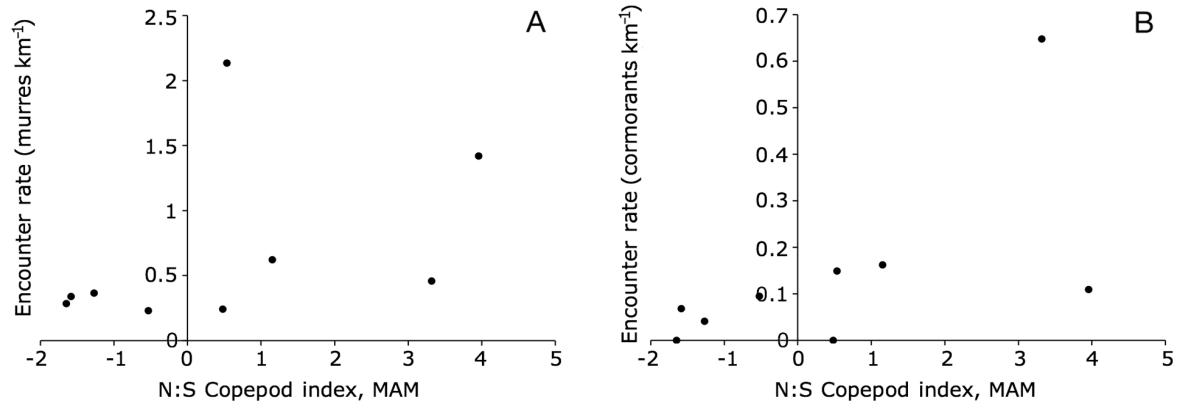
Fig. 5. Spring to summer (MAM: Mar to May) encounter rates of local breeders versus index of northern (negative) versus southern (positive) copepod community, 1997 to 2005. (A) Common murres in Newport and (B) Brandt's cormorants in Newport

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 cormorants. 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, Fig. 4). 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 pencillatus* 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 (*Ptychorhamphus 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 telescoping 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.

LITERATURE CITED

Ainley DG, Jones RE, Stallcup R, Long DJ and others (1993) Beached marine birds and mammals of the North American west coast: a revised guide to their census and identification, with supplemental keys to beached sea turtles and sharks. National Oceanic and Atmospheric Administration, San Francisco, CA

Ainley DG, Sydeman WJ, Norton J (1995) Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. Mar Ecol Prog Ser 118:69–79

Ainley DG, Nettleship DN, Carter HR, Storey AE (2002) Common murre (*Uria aalge*). In: Poole A, Gill F (eds) The birds of North America, No. 666. The Birds of North America, Philadelphia, PA

Anderson PJ, Piatt JF (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar Ecol Prog Ser 189:117–123

Barber RT, Chavez FP (1983) Biological consequences of El Niño. Science 222:1203–1210

Barth JA, Menge BA, Lubchenco J, Chan F and others (2007) Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California Current. Proc Natl Acad Sci USA 104:3719–3724

Bayer RD, Lowe RW, Loeffel RE (1991) Persistent summer mortalities of common murres along the Oregon central coast. Condor 93:516–525

Bertram DF, Harfenist A, Smith BD (2005) Ocean climate and El Niño impacts on survival of Cassin's auklets from upwelling and downwelling domains of British Columbia. Can J Fish Aquat Sci 62:2841–2853

Briggs KT, Tyler WB, Lewis DB, Carlson DR (1987) Bird communities at sea off California: 1975–1983. Stud Avian Biol 11:1–79

Brodeur RD, Ralston S, Emmett RL, Trudel M, Auth TD, Phillips AJ (2006) Anomalous pelagic nekton abundance, distribution, and apparent recruitment in the northern California Current in 2004 and 2005. Geophys Res Lett 33:L22S08

Camphuysen KCJ, Wright PJ, Leopold M, Hüppop O, Reid JB (1999) A review of the causes, and consequences at the population level, of mass mortalities of seabirds ICES Coop Res Rep 232:51–62

Duffy DC, Arntz WE, Serpa HT, Boersma PD, Norton RL (1988) A comparison of the effects of El Niño and the Southern Oscillation on birds in Peru and the Atlantic Ocean. In: Ouellet H (ed) Acta XIX Congress on International Ornithology (1986), Vol II. University of Ottawa Press, Ottawa, p 1740–1758

Finney SK, Wanless S, Harris MP (1999) The effect of weather conditions on the feeding behaviour of a diving bird, the common guillemot, *Uria aalge*. J Avian Biol 30:23–30

Flint P, Fowler AC (1998) A drift experiment to assess the influence of wind on recovery or oiled seabirds on St Paul Island, Alaska. Mar Pollut Bull 36:165–166

Forney KA, Benson SR, Cameron GA (2001) Central California gillnet effort and bycatch of sensitive species, 1990–1998. In: Melvin EF, Parrish JK (eds) Seabird bycatch: trends, roadblocks, and solutions. AK-SG-01-01, University of Alaska Sea Grant, Anchorage, AK, p 141–160

Furness RW, Greenwood JJD (1993) Birds as monitors of environmental change. Chapman & Hall, London

Furness RW, Camphuysen KCJ (1997) Seabirds as monitors of the marine environment. ICES J Mar Sci 54:726–737

Gaston AJ, Dechesne SBC (1996) Rhinoceros auklet (*Cerorhinca monocerata*). In: Poole A, Gill F (eds) The birds of North America, No. 212. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC

Gleason KL (2006) United States. In: Shein KA (ed) State of the climate in 2005. Bull Am Meteorol Soc 87:62–66

Granadeiro JP, Silva MA (1993) Beached bird surveys in Portugal 1991–92 and relationship between weather and density of corpses. Sula 7:1–8

Granadeiro JP, Silva MA, Fernandes C, Reis A (1997) Beached bird surveys in Portugal 1990–1996. Ardeola 44:9–17

Hass T, Parrish JK (2002) Beached birds: a COASST field guide. Wavefall Press, Seattle, WA

Hickey BM (1989) Patterns and processes of shelf and slope circulation. In: Landry MR, Hickey BM (eds) Coastal oceanography of Washington and Oregon. Elsevier Science, Amsterdam, p 41–115

Hickey BM, Banas NS (2003) Oceanography of the US Pacific Northwest coastal ocean and estuaries with application to coastal ecology. Estuaries 26:1010–1031

Huyer A (1983) Coastal upwelling in the California Current System. Prog Oceanogr 12:259–284

Kistler R (2001) The NCEP-NCAR 50-year reanalysis: monthly means CD-ROM and documentation. Bull Am Meteorol Soc 82:247–267

Kosro PM, Peterson WT, Hickey BM, Shearman RK, Pierce SD (2006) Physical versus biological spring transition: 2005. Geophys Res Lett 33:L22S03

MacFadyen A, Hickey BM, Foreman MCG (2005) Transport of surface waters from the Juan de Fuca eddy region to the Washington coast. Cont Shelf Res 25:2008–2021

Mackas DL, Peterson WT, Ohman MD, Lavaniegos BE (2006) Zooplankton anomalies in the California Current system before and during the warm ocean conditions of 2005. Geophys Res Lett 33:L22S07

Manuwal DA, Thoresen AC (1993) Cassin's auklet (*Ptychoramphus aleuticus*). In: Poole A, Gill F (eds) The birds of North America, No. 50. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC

Mueter FJ, Ware DM, Peterman RM (2002) Spatial correlation patterns in coastal environmental variables and survival rates of Pacific salmon in the Northeast Pacific Ocean. Fish Oceanogr 11:205–218

Newton I (2006) Can conditions experienced during migration limit the population levels of birds? J Ornithol 147:146–166

Norris JR (2000) Interannual and interdecadal variability in the storm track, cloudiness and sea surface temperature over the summertime North Pacific. J Clim 13:422–430

Peterson WT, Keister JE (2003) Interannual variability in copepod community composition at a coastal station in the northern California Current: a multivariate approach. Deep-Sea Res II 50:2499–2517

Roemmich D, McGowan J (1995) Climatic warming and the decline of zooplankton in the California Current. Science 267:1324–1326

Scholin CA, Gulland F, Douchette GJ, Benson S and others (2000) Mortality of sea lions along the Central California coast linked to a toxic diatom bloom. Nature 403:80–84

Schreiber EA (2002) Climate and weather effects on seabirds. In: Schreiber EA, Burger J (eds) Biology of marine birds. CRC Press, New York, p 179–215

Schwing FB, O'Farrell M, Steger JM, Baltz K (1996) Coastal upwelling indices, west coast of North America, 1946–1995. NOAA Tech Mem NOAA 231:1–32

Schwing FB, Bond NA, Bograd SJ, Mitchell T, Alexander MA, Mantua N (2006) Delayed coastal upwelling along the U.S. west coast in 2005: a historical perspective. Geophys Res Lett 33:L22S01

Strub PT, Allen JS, Huyer A, Smith RL (1987) Large-scale structure of the spring transition in the coastal ocean off western North America. J Geophys Res C 92:1527–1544

Sydeman WJ, Bradley RW, Warzybok P, Abraham CL and others (2006) Planktivorous auklet *Ptychoramphus aleuticus* responses to the anomaly of 2005 in the California Current. Geophys Res Lett 33:L22S09

Veit RR, Pyle P, McGowan JA (1996) Ocean warming and long-term change in pelagic bird abundance within the California current system. Mar Ecol Prog Ser 139:11–18

Wallace EAH, Wallace GE (1998) Brandt's cormorant (*Phalacrocorax penicillatus*). In: Poole A, Gill F (eds) The birds of North America, No. 362. The Birds of North America, Philadelphia, PA

Wiese FK, Robertson GJ (2004) Assesing seabird mortality from chronic oil discharges at sea. J Wildl Manag 68:627–638

Wiese FK (2003) Sinking rates of dead birds: improving estimates of seabird mortality due to oiling. Mar Ornithol 31:65–70

Wiese FK, Ryan PC (2003) The extent of chronic marine oil pollution in southeastern Newfoundland waters assessed through beached bird surveys 1984–1999. Mar Pollut Bull 46:1090–1101

Wilson UW (1991) Response of three seabird species to El Niño events and other warm water episodes on the Washington coast, 1979–1990. Condor 93:853–858

Hot oceanography: planktivorous seabirds reveal ecosystem responses to warming of the Bering Sea

Alan M. Springer[1],*, G. Vernon Byrd[2], Sara J. Iverson[1,3]

[1]**Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska 99775-7220, USA**

[2]**Alaska Maritime National Wildlife Refuge, US Fish and Wildlife Service, 95 Sterling Highway, Suite 1, Homer, Alaska 99603, USA**

[3]**Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada**

ABSTRACT: The Bering Sea has experienced dramatic warming in this century that has altered elements of the ecosystem, including the structure and productivity of the zooplankton community on the continental shelf, and the extent to which waters and associated plankton of oceanic origin have intruded onto the shelf. We documented temporal and spatial scales of these changes by monitoring diets of least auklets *Aethia pusilla* on the Pribilof Islands—least auklets are planktivores that specialize on the large calanoid copepods *Neocalanus* spp. from the basin and *Calanus marshallae* from the shelf. Diets were estimated in the summers of 1996 to 2006 by enumerating prey in regurgitated meals brought to chicks by adults, and by fatty acid analyses of live biopsy samples of adipose tissue from adult birds in 2003 and 2004, which provided additional insight. In the unusually warm 2000s, *Neocalanus* spp. apparently were excluded from regions of the outer shelf, where they typically occur in cooler years, and, concurrently, *C. marshallae* was depressed over a large region of the shelf because of chronic failures of spring cohorts to survive. Both changes were associated with anomalously high water temperatures over the middle shelf. The information provided by least auklets greatly improves our understanding of the consequences of environmental change and supplies clues about how communities and ecosystem processes respond to physical forcing. Continued warming of the magnitude seen in recent years could become a cause for concern for auklets and other planktivores in the eastern Bering Sea if it alters prey availability in ways detrimental to their populations.

KEY WORDS: Bering Sea · Climate change · Seabird · Auklet · Diet · Copepod · Oceanography

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 & Piatt 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
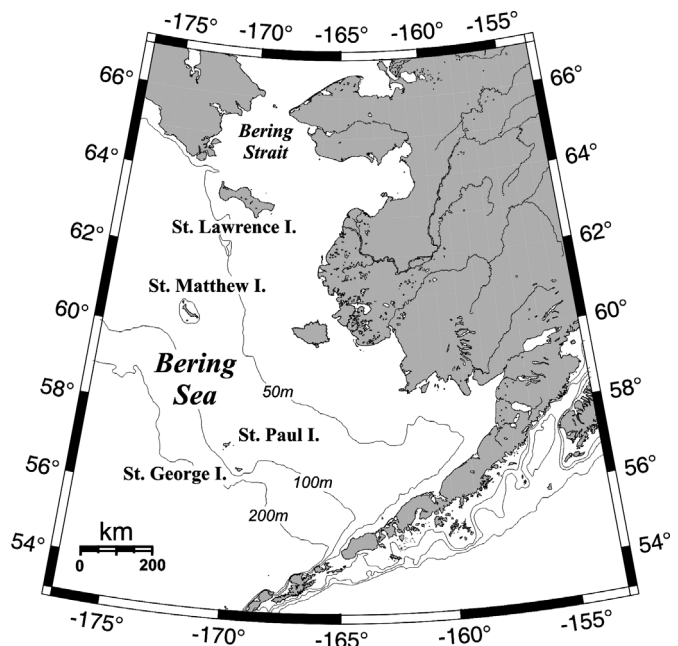
Fig. 1. Pribilof Islands and other locations discussed in the text

Table 1. *Aethia pusilla*. Sample sizes and dates when diet samples were collected at the Pribilof Islands. Asterisks denote samples for fatty acids; all others are regurgitations

	June Date/Interval	n	Early July Date/Interval	n	Mid-July Date/Interval	n	Late July Date/Interval	n	Early August Date/Interval	n
St. George I.										
1996					Jul 21	20				
1997					Jul 21	21	Jul 31	14		
1998					Jul 19	4	Jul 30	12		
1999									Aug 2	14
2000							Jul 25	15	Aug 6–7	20
2001							Jul 24–30	15		
2002					Jul 17	13	Jul 27–28	18		
2003			Jun 29–Jul 3	14	Jul 11	11	Jul 29–Aug 1	22		
2004			Jun 30–Jul 6	11			Jul 25–27	8		
2005			Jul 1–4	20	Jul 12–23	15	Jul 23–Aug 1	17		
2006					Jul 6–22	19				
St. Paul I.										
1996					~Jul 14	15				
1997					Jul 18–21	10	Jul 22–31	7		
1998					Jul 18–24	7	Jul 27–29	8		
1999										
2000					Jul 17–22	43	Jul 24–30	52	Aug 1–10	26
2001							Jul 24–31	12	Aug 1–9	15
2002									Aug 2	7
2003			Jul 7	12	Jul 12–19	13	Jul 24–31	12		
2003*	Jun 2–12	10			Jul 12–15	16				
2004			Jun 30–Jul 13	67	Jul 19–23	38	Jul 25–31	10		
2004*	Jun 1–11	25					Jul 25–29	17		
2005			Jul 5–7	3	Jul 21	2				
2006					Jul 12–17	13				

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

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 2. *Aethia pusilla*. Composition of least auklet diets at the Pribilof Islands from 1996 to 2006. Values are composition of regurgitations as a percentage of total mass of prey

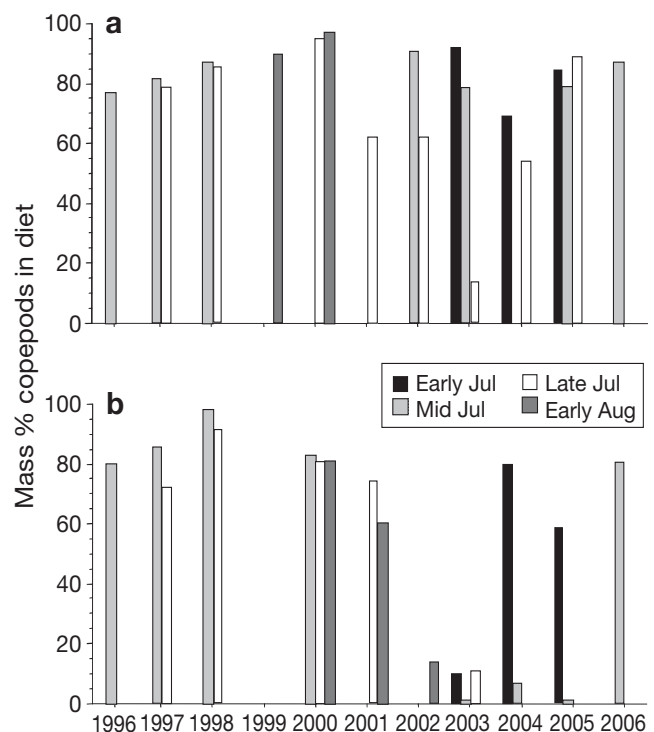| Year	Interval	Neocalanus cristatus Mean	SE	N. plumchrus/ flemingeri Mean	SE	Calanus marshallae Mean	SE	Hyperiid amphipods Mean	SE	Euphausiids Mean	SE	Juvenile crabs Mean	SE	Juvenile shrimp Mean	SE	Other invertebrates Mean	SE	Larval fish Mean	SE
St. George I.																			
1996	Mid-July	41	5.7	36	4.7	0		0.32	0.25	13	3.1	0.6	0.4	6.9	1.9	0.07	0.03	2.4	2.4
1997	Mid-July	0.68	0.31	71	4.9	10	3.3	0.08	0.08	12	2.7	4.1	2.2	2.4	0.52	0.07	0.04	0	
	Late July	1.1	0.62	42	6	35	6.3	0		17	4.8	0.77	0.42	0.87	0.53	0.33	0.13	0.2	0.11
1998	Mid-July	0		87	7.5	0		1.8	1.1	1.4	1.4	3.6	3.1	1.3	1.3	0.8	0.8	4	4
	Late July	2.5	0.94	84	3.2	0.3	0.19	0		3.6	2.1	3.5	1.8	6.2	2.7	0.42	0.1	0	
1999	Early August	1.5	1.2	47	4.7	41	3.3	0.92	0.92	8.0	6.1	0.83	0.31	0		0.17	0.1	0	
2000	Late July	93	1.3	0.72	0.2	0.49	0.31	0.26	0.17	4.7	1.1	0.51	0.24	0.3	0.3	0		0	
	Early August	90	2.9	1.5	0.53	5.5	2.4	0.22	0.09	1.3	0.36	0.19	0.13	0.91	0.43	0.03	0.02	0	
2001	Late July	3.4	1.5	2.9	1.7	57	8.3	0.92	0.64	24	8.7	0.04	0.04	8	3.9	4.1	2	0	
2002	Mid-July	21	5.2	71	7.3	0		4.0	2.8	2.2	0.78	1.4	0.72	1.3	0.57	0.26	0.26	0	
	Late July	14	6.3	41	6.9	7.1	1.9	11	3.6	14	6.8	7.8	2.1	3.7	1.2	1.1	1.1	2.8	2.8
2003	Early July	17	5.8	75	8.7	0		2.1	1.1	2.6	1.1	1.9	0.84	1.9	0.92	0		0	
	Mid-July	33	7.2	46	8.1	0		5.8	3.0	11	8.6	1.2	0.53	3	1.5	0		0	
	Late July	4.0	2.0	6.8	4.2	3.4	1.4	6.4	2.3	66	6	13	3.9	0.26	0.26	0.59	0.55	0	
2004	Early July	0		69	6.3	0		0		31	6.3	0.02	0.01	0		0		2.9	2.9
	Late July	54	14	0		0		0.9	0.80	45	13	0.32	0.2	0		0		0	
2005	Early July	9.6	3.7	75	4.3	0.34	0.18	0.27	0.20	12	3.2	1.4	0.39	1.3	0.69	0.05	0.03	0	
	Mid-July	36	7.4	43	8.0	0		2.4	1.6	19	5.3	0.61	0.35	0.48	0.48	0.04	0.02	0	
	Late July	30	5.3	58	5.7	0		0.92	0.45	5.4	2.4	0.45	0.31	3.7	1.6	0.2	0.01	0	
2006	Mid-July	44	8.2	43	8.7	0		0		6.7	4.7	1.8	0.95	3	1.7	0.1	0.1	1.2	1.2
St. Paul I.																			
1996	Mid-July	19	10	61	10	0.29	0.23	0		17	7	1.7	1.2	0.82	0.82	0		0	
1997	Mid-July	2.7	1.3	57	14	26	10	0.03	0.03	9.1	4.3	1.5	0.71	3.5	3	0.56	0.37	0.04	0.02
	Late July	0		3.5	2	68	12	0		26	14	2.5	1.5	0		0.02	0.02	0	
1998	Mid-July	1.6	0.99	93	2.8	3.1	1.4	0		0		0.91	0.72	1.1	0.71	0.06	0.04	0.58	0.42
	Late July	2.2	0.97	88	2.8	1.4	0.77	0.13	0.10	0.31	0.28	1.3	0.44	3.8	2.1	0.09	0.06	2.6	1.9
2000	Mid-July	12	3.2	13	3.5	58	4.9	0.27	0.10	11	2.6	3.4	0.83	1.6	0.47	0.28	0.25	0	
	Late July	15	2.9	26	4.5	40	4.5	1.2	1.2	11	2.5	3.4	0.7	2.4	0.52	0.01	0.01	0	
	Early August	11	3.8	34	6.7	36	6.1	4.9	1.6	8.8	3.4	4.2	1.2	1.9	0.78	0.001	0.001	0	
2001	Late July	0.20	0.20	0.51	0.34	74	6.1	1.9	0.99	17	6.2	5.7	3.2	0.8	0.46	0		0	
	Early August	0		0		60	6.0	5.4	3.6	31	6.1	1.9	0.92	1.4	0.93	0		0	
2002	Early August	14	14	0		0		20	7.2	61	13	4.4	3.8	0		0		0	
2003	Early July	6.1	4.6	0.69	0.69	3.8	3.8	50	9.1	2.7	1.4	19	7.6	14	6	0.3	0.3	2.8	2.2
	Mid-July	0.29	0.29	0		0.19	0.19	26	7.7	44	11	22	7.4	2.1	2.1	0		4.4	3.6
	Late July	11	7.1	0		0.24	0.21	12	3.4	10	2.8	68	7.8	0.24	2.4	0		0.42	0.42
2004	Early July	1.7	0.43	78	2.8	0		0.13	0.08	6.4	1.4	8.6	2	5.6	1.5	0.22	0.05	0	
	Mid-July	0.03	0.03	5.7	2.9	1.5	1.1	5.3	3.2	48	6.5	30	5.9	2.1	1.2	0.28	0.23	5.2	2.2
	Late July	0		0		0		0.68	0.68	27	12	70	12	0.11	0.11	0.03	0.03	2.9	2.9
2005	Early July	0		0		59	15	1.2	0.17	28	14	9.9	3.1	1.7	0.17	0.7	0.6	0	
	Mid-July	0		0		0.62	0.62	0		99	0.6	0		0		0		0	
2006	Mid-July	54	9.9	27	10	2.6	1.2	0.15	0.15	0		15	4.9	0		0.66	0.42	0	

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 mono-unsaturated 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 Dalsgarrd 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.
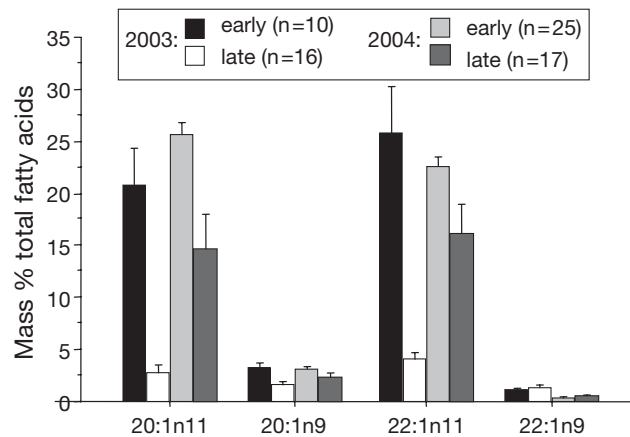

Fig. 3. *Aethia pusilla.* Characteristic copepod fatty acid biomarkers (mean ± SE) measured in adipose tissue biopsies obtained from adult least auklets in June (early) and July (late) of 2003 and 2004 on St. Paul I.

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* in late July 2001, the only interval (of 20 intervals in 11 yr in our study) when *C. marshallae* was dominant at St. George I., although it was of about equal importance as *Neocalanus* at times in 1997 and 1999. *C. marshallae* was apparently much more profitable than *Neocalanus* 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 1985, 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.
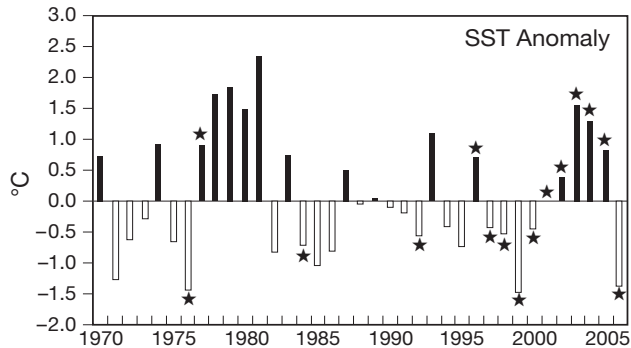
Fig. 4. May sea surface temperature (SST) anomalies in the southeastern Bering Sea (mean temp. = 2.38°C). ★: diet samples obtained at St. Paul I. SST data available at: http://www.beringclimate.noaa.gov/data/index.php

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-

standing 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.

LITERATURE CITED

Anderson PJ, Piatt JF (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar Ecol Prog Ser 189:117–123

Bedard J (1969) Feeding of the least, crested and parakeet auklets on St. Lawrence Island, Alaska. Can J Zool 47: 1025–1050

Benowitz-Fredericks ZM, Shultz MT, Kitaysky AS (2008) Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in two years. Deep-Sea Res II (in press)

Bradstreet MSW (1985) Chapter IV. Feeding studies. In: Johnson SR (ed) Population estimation, productivity, and food habits of nesting seabirds at Cape Peirce and the Pribilof Islands, Bering Sea, Alaska. Report by LGL Ecological Research Associates, Inc., to Minerals Management Service, Anchorage, AK, p 257–306

Coachman LK (1986) Circulation, water masses, and fluxes on the southeastern Bering Sea shelf. Cont Shelf Res 5: 23–108

Coachman LK, Charnell RL (1979) On lateral water mass interaction—a case study, Bristol Bay, Alaska. J Phys Oceanogr 9:278–297

Cooney RT (1981) Bering Sea zooplankton and micronekton communities with emphasis on annual production. In: Hood DW, Calder JA (eds) The eastern Bering Sea shelf: oceanography and resources, Vol 2. NOAA, Juneau, AK, p 947–974

Coyle KO, Pinchuk AL, Eisner LB, Napp JM (2008) Zooplankton species composition, abundance and biomass on the eastern Bering Sea shelf during summer: the potential role of water column stability and nutrients in structuring the zooplankton community. Deep-Sea Res II (in press)

Dalsgaard J, St John M, Kattner G, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46:225–340

Dragoo DD, Byrd GV, Irons DB (2006) Breeding status, population trends, and diets of seabirds in Alaska, 2003. US Fish and Wildlife Service Report AMNWR 04/15, Homer, AK

Ebbesmeyer CC, Cayan DR, McLain FH, Peterson DH, Redmond KT (1991) 1976 step in the Pacific climate: forty environmental changes between 1968–1975 and 1977–1985. In: Betancourt JL, Tharp VL (eds) Proc 7th Ann Pacific Climate Workshop Interagency Ecol Stud Prog, Tech Rep 26. California Dept. of Water Resources, Sacramento, CA, p 129–141

Flint MV, Golovkin AN (2002) How do planktivorous least auklets (*Aethia pusilla*) use foraging habitats around breeding colonies? Adaptation to mesoscale distribution of zooplankton. Oceanology (Suppl) 42(1):114–121

Francis RC, Hare SR (1994) Decadal-scale regime shifts in the large marine ecosystems of the north-east Pacific: a case for historical science. Fish Oceanogr 3(4):279–291

Gall AE, Roby DD, Irons DB, Rose IC (2006) Differential response in chick survival to diet in least and crested auklets. Mar Ecol Prog Ser 308:279–291

Grebmeier JM, Overland JE, Moore SE, Farley EV and others (2006) A major ecosystem shift in the northern Bering Sea. Science 311:1461–1464

Hare SR, Mantua NJ (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog Oceanogr 47:103–146

Hunt GL Jr, Harrison NM (1990) Foraging habitat and prey taken by least auklets at King Island, Alaska. Mar Ecol Prog Ser 65:141–150

Hunt GL Jr, Mayer B, Rodstrom W, Squibb R (1978) Reproductive ecology, foods and foraging areas of seabirds nesting on the Pribilof Islands. Environ Assess Alask Cont Shelf 1:570–775

Hunt GL Jr, Burgesson B, Sanger GA (1981) Feeding ecology of seabirds of the eastern Bering Sea. In: Hood DW, Calder JA (eds) The eastern Bering Sea shelf: oceanography and resources, Vol 2. NOAA, Juneau, AK, p 629–648

IPCC (Intergovernmental Panel on Climate Change) (2007) Climate change 2007: the physical science basis. IPCC Secretariat, Geneva

Iverson RL, Coachman LK, Cooney RT, English TS and others (1979) Ecological significance of fronts in the southeastern Bering Sea. In: Livingston RJ (ed) Ecological processes in coastal and marine systems. Plenum Press, New York, p 437–466

Iverson SJ, Springer AM, Kitaysky AS (2007) Seabirds as indicators of food web structure and ecosystem variability: qualitative and quantitative diet analyses using fatty acids. Mar Ecol Prog Ser 352:235–244

Jones IL (1993) Least auklet (*Aethia pusilla*). In: Poole A, Gill F (eds) The birds of North America, No. 69. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC

Jones IL, Williams JC (2007) On the meaning of annual variation in auklet (*Aethia* spp.) demographic parameters and chick diet. Abstract of presentation at the Alaska Marine Science Symposium, Jaunary 2007, Anchorage, AK. Available at www.alaskamarinescience.org

Kitaysky AS, Piatt JF, Wingfield JC (2007) Stress hormones link food availability and population processes in seabirds. Mar Ecol Prog Ser 352:245–258

Obst BS, Russell RW, Hunt GL Jr, Eppley ZA, Harrison NM (1995) Foraging radii and energetics of least auklets (*Aethia pusilla*) breeding on three Bering Sea islands. Physiol Zool 68:647–672

Overland JE, Wang M (2007) Future climate of the North Pacific Ocean. EOS Trans Am Geophys Union 88:178–182

Roby DD, Brink KL (1986) Breeding biology of Least Auklets on the Pribilof Islands, Alaska. Condor 88:336–346

Sambrotto RN, Niebauer HJ, Goering JJ, Iverson RL (1986) Relationships among vertical mixing, nitrate uptake, and phytoplankton growth during the spring bloom in the southeast Bering Sea middle shelf. Cont Shelf Res 5: 161–198

Smith SL, Vidal J (1984) Spatial and temporal effects of salinity, temperature and chlorophyll on the communities of zooplankton in the southeastern Bering Sea. J Mar Res 42:221–257

Smith SL, Vidal J (1986) Variations in the distribution, abundance, and development of copepods in the southeastern Bering Sea in 1980 and 1981. Cont Shelf Res 5:215–240

Springer AM, Roseneau DG (1985) Copepod-based food webs: auklets and oceanography in the Bering Sea. Mar Ecol Prog Ser 21:229–237

Springer AM, Roseneau DG, Lloyd DS, McRoy CP, Murphy EC (1986) Seabird responses to fluctuating prey abundance in the eastern Bering Sea. Mar Ecol Prog Ser 32: 1–12

Springer AM, McRoy CP, Flint MV (1996) The Bering Sea Green Belt: shelf edge processes and ecosystem production. Fish Oceanogr 5:205–223

Stabeno PJ, Bond NA, Salo SA (2007) On the recent warming of the eastern Bering Sea shelf. Deep Sea Res II 54: 2599–2618

Stabeno PJ, Mordy C, Righi D, Salo SA (2008) An examination of the physical forcing around the Pribilof Islands, 2004. Deep-Sea Res II (in press)

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

Scott H. Newman[1,2,4,5,*]**, Aleksei Chmura**[2]**, Kathy Converse**[3]**, A. Marm Kilpatrick**[2]**,**
Nikkita Patel[2]**, Emily Lammers**[1]**, Peter Daszak**[2]

[1]**Wildlife Trust, 460 West 34th Street, New York, New York 10001, USA**
[2]**Consortium for Conservation Medicine, 460 West 34th Street, New York, New York 10001, USA**
[3]**USGS National Wildlife Health Center, 6006 Schroeder Road, Madison, Wisconsin 53711, USA**

[4]*Present address:* **Food and Agriculture Organization of the United Nations (FAO), Infectious Disease Group, Emergency**
Centre for Transboundary Animal Diseases (ECTAD), Animal Health Service, Viale delle Terme di Caracalla, Rome 00100, Italy
[5]*Present address:* **Wildlife Conservation Society, Field Veterinary Program, 2300 Southern Boulevard, Bronx, New York 10460, USA**

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, includ-ing avian cholera (*Pasteurella multocida*), chlamydiosis (*Chalmydia psittici*), and salmonellosis (*Sal-monella* 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 conserva-tion 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 in-fectious 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 & Cunning-ham 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 di-rectly linked to anthropogenic environmental changes

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 pub-

lic. 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

Table 1. General causes of aquatic bird mortality events (number and percentage) for each of the 23 bird families, according to data from 2 USGS databases, Epizoo and Diagnostic. Specific causes of mortality were grouped into 6 categories of mortality events— anthropogenic: fishing net entrapment, gunshot, powerline collision, and trauma (vehicle, collisions, or unknown source); environmental: biotoxin, weather, natural biology-depredated or intra- or con-specific trauma, emaciation/starvation; infectious: bacterial, viral, parasitic, fungal, undiagnosed bacterial or viral; pathology with no etiology: undiagnosed, but histological lesions in tissue samples; toxicosis: heavy metal, nutritional (selenium or salt), oil (petroleum and non-petroleum), pesticide (carbamate, organophosphate, organochlorine), poison (cyanide, calcium nitrate, strychinine), undetermined poison; undetermined: no diagnosis

Family	Number and percentage of mortality events per family												
	Anthropogenic		Environmental		Infectious		Pathology with no etiology		Toxicosis		Undetermined		Total numbers
	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	(n)
Anatidae	9	4	62	26	105	45	13	6	25	11	21	9	235
Gaviidae	16	12	34	25	22	16	29	21	22	16	15	11	138
Diomedeidae	2	10	1	5	1	5	13	65	1	5	2	10	20
Procellariidae	15	21	14	20	2	3	29	41	5	7	5	7	70
Hydrobatidae	1	20	3	60	0	0	0	0	1	20	0	0	5
Phaethontidae	0	0	0	0	0	0	3	100	0	0	0	0	3
Sulidae	3	8	13	33	12	31	6	15	1	3	4	10	39
Pelecanidae	24	7	169	47	64	18	27	8	19	5	53	15	356
Phalacrocoracidae	15	6	87	35	88	35	30	12	6	2	26	10	252
Anhingidae	0	0	0	0	0	0	0	0	1	100	0	0	1
Fregatidae	1	33	0	0	0	0	0	0	0	0	2	67	3
Ardeidae	24	5	228	45	98	19	67	13	45	9	45	9	507
Threskiornithidae	3	4	53	73	5	7	6	8	4	5	2	3	73
Ciconiidae	2	67	0	0	0	0	0	0	1	33	0	0	3
Phoenicopteridae	0	0	1	50	0	0	0	0	1	50	0	0	2
Charadriidae	20	10	83	43	27	14	51	26	6	3	7	4	194
Haematopodidae	0	0	0	0	1	100	0	0	0	0	0	0	1
Recurvirostridae	2	2	80	75	15	14	3	3	1	1	5	5	106
Scolopacidae	5	1	435	80	38	7	15	3	23	4	31	6	547
Laridae	36	4	450	45	233	23	83	8	86	9	114	11	1002
Stercorariidae	0	0	1	33	0	0	0	0	1	33	1	33	3
Alcidae	2	3	26	45	3	5	8	14	9	16	10	17	58
Cinclidae	0	0	0	0	0	0	1	100	0	0	0	0	1
Total													3619

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.
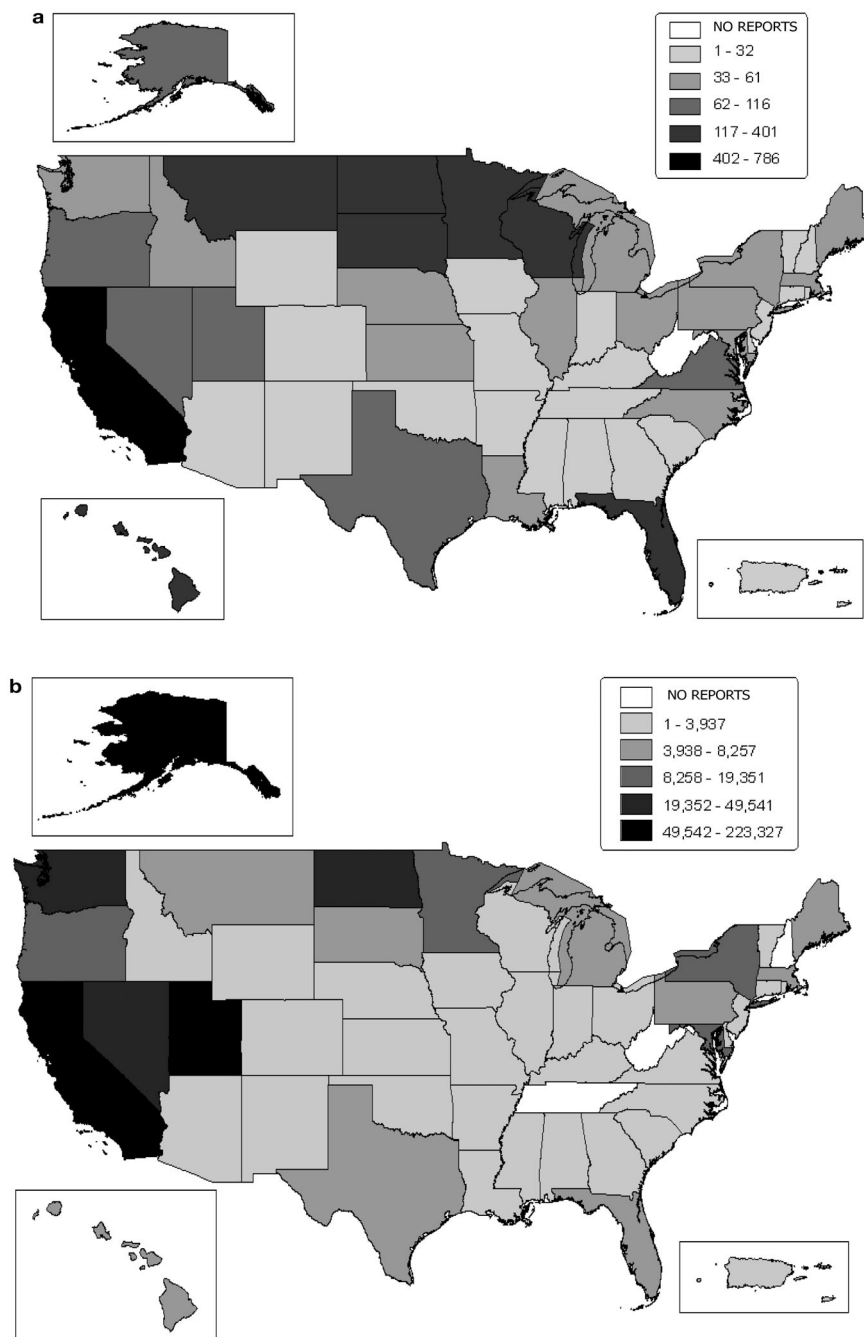
Fig. 1. Number of aquatic bird (a) mortality events and (b) deaths reported in the US (per state) and Puerto Rico between 1971 and 2005. Note: no mortality events were reported from West Virginia; only 2 and 3 mortality events were recorded, respectively, for Tennessee and New Hampshire, which reported no dead birds from mortality events

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.

Table 2. Specific causes of aquatic bird mortality events and aquatic bird deaths based on species habitat use (pelagic/offshore, nearshore/coastal, and freshwater). Note: no totals listed here. A sum of each row for each major category (mortality events or dead aquatic birds) will not equal the respective totals, since many birds utilize >1 habitat group, and thus were counted within each

Disease category	Mortality events			Dead aquatic birds		
	Pelagic/Offshore	Nearshore/Coastal	Freshwater	Pelagic/Offshore	Nearshore/Coastal	Freshwater
Anthropogenic						
Gunshot	3[a]	25	24	1009	1107	1099
Net entrapment	1	16	14	_[b]	1467	1367
Powerline collision	0	18	20	0	98	100
Trauma	20	99	90	788	1426	1386
Environmental						
Biotoxin	9	1377	1468	27	139823	341376
Natural biology	1	14	14	8	1006	1006
Emaciation/Starvation	63	176	130	79168	85195	9909
Weather	1	49	50	1	9388	9220
Infectious						
Bacterial	3	418	419	1	47987	43123
Bacterial or viral	1	5	3	350	3	3
Fungal	9	89	79	334	9029	8689
Parasites	4	70	65	12	1574	1448
Viral	0	113	114	0	66432	66434
Pathology with no etiology						
Pathology	58	338	315	398	22175	22032
Toxicosis						
Heavy metal	0	30	29	0	115	114
Nutritional	0	13	13	0	32	32
Oil	16	63	54	11595	13141	1571
Pesticide	0	61	61	0	2022	2022
Poison	1	24	26	1	574	575
Undetermined	2	53	54	27	1766	1766
Undetermined						
Open	27	327	303	11136	15521	8398

[a]Of these 3 events, 1 lists 1000 Fulmar killed in Grey's Harbor on the coast of Washington state on 6 Dec 1995
[b]No dead birds reported despite a mortality event being reported

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 *Chalmydia psittici*, 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
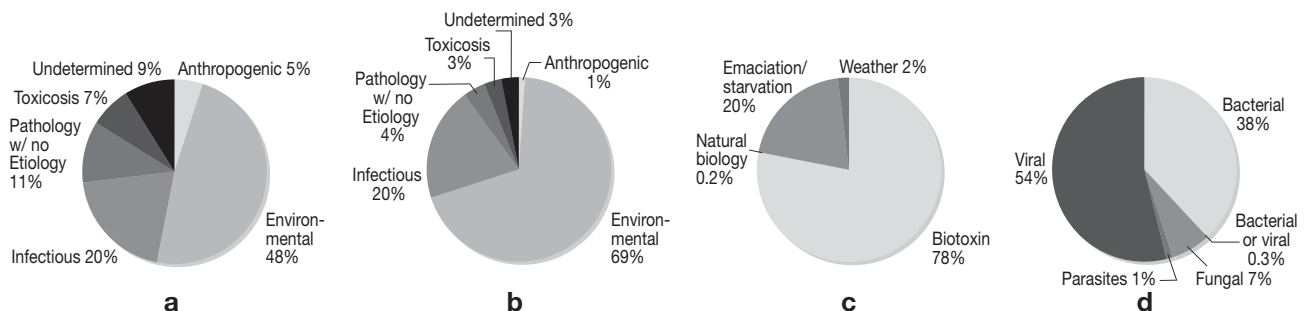

Fig. 2. Specific and general causes of aquatic bird deaths from 1971 to 2005. (a) Cause of death per mortality event shown in percent of 3619 aquatic bird mortality events. (b) Cause of death per bird of 633 708 aquatic birds. (c) Specific cause of death per bird of 441 045 aquatic bird mortalities due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

Aspergillus fumigatus) and parasitic diseases (*Acantho-cephala* spp., *Eustrongylides* spp., *Leyogonimus* spp., *Acanthobdella* spp. and *Coccidia*).

Aquatic bird mortality attributable to anthropogenic interactions accounted for 5% (180) of the mortality events or 1% (5580) 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 dead birds; and incidents of undetermined origin accounted for 9% (343) 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
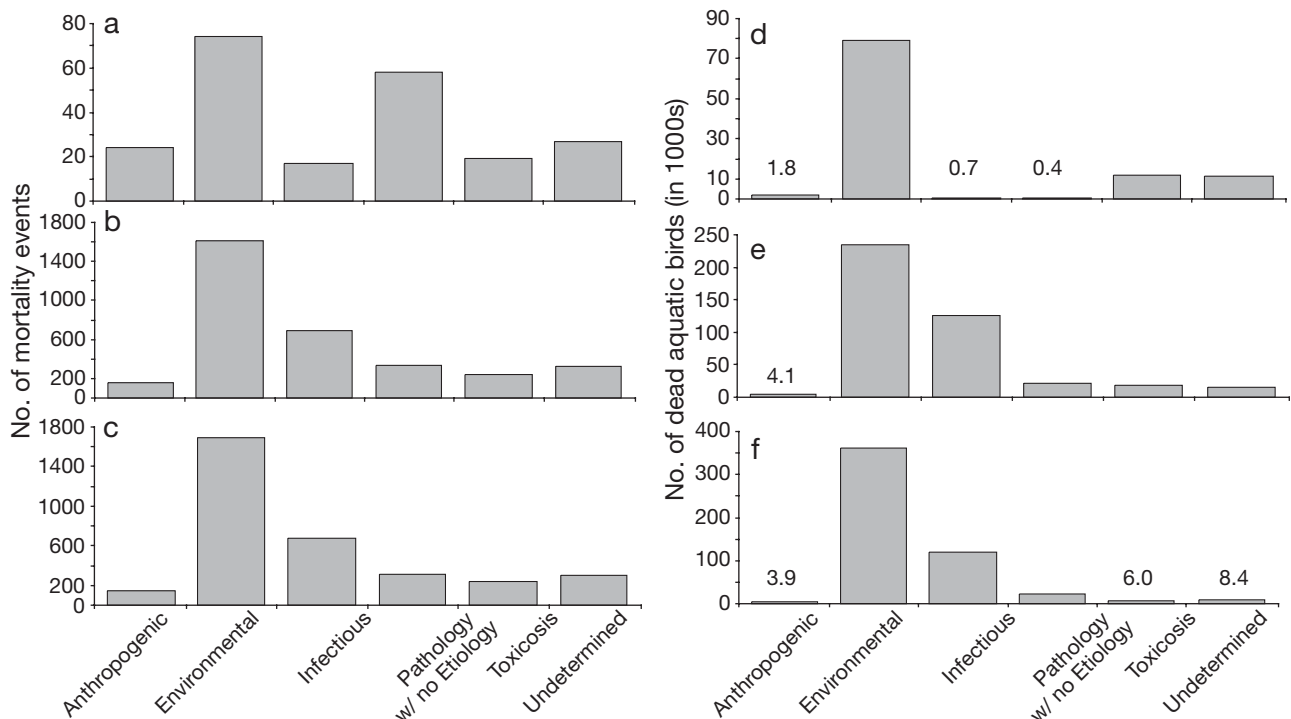

Fig. 3. Bar graphs showing the numbers according to each general category for aquatic bird mortality events (a,b,c), and for numbers of dead aquatic birds (d,e,f). Mortality events for (a) pelagic/offshore bird species, (b) nearshore/coastal bird species, (c) freshwater bird species. Dead aquatic birds (in 1000s) for (d) pelagic/offshore bird species, (e) nearshore/coastal bird species, (f) freshwater bird species

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

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

5 yr period ending in:	Anthropogenic	Environmental	Infectious	Pathology with no etiology	Toxicosis	Undetermined	Total number
Number of mortality events							
Pre-1971	2	20	11	0	1	11	45
1975	0.2 ± 0.2	1.8 ± 0.8	3.8 ± 2.5	0	1.8 ± 1.0	0.2 ± 0.2	39
1980	0	17.2 ± 9.4	6.6 ± 3.1	0	1.6 ± 1.0	2.4 ± 0.9	139
1985	0.8 ± 0.6	36.6 ± 8.5	11.2 ± 1.7	2 ± 1.0	7.2 ± 2.1	9.2 ± 1.7	335
1990	5.2 ± 1.9	53.6 ± 8.5	16.8 ± 4.4	4.6 ± 1.2	18.6 ± 4.8	12.8 ± 1.9	558
1995	7 ± 2.7	78.2 ± 6.3	30.2 ± 7.0	6.4 ± 0.4	9.6 ± 1.9	20.4 ± 2.4	759
2000	0.8 ± 0.2	93.6 ± 5.6	28.6 ± 3.5	4 ± 1.3	4 ± 1.9	9.8 ± 1.3	704
2005	2 ± 0.3	51.4 ± 15.6	29.6 ± 8.1	2.2 ± 0.9	4.8 ± 0.6	11.6 ± 4.6	508
						Total	3087
Number of dead birds							
Pre-1971	4	13 015	4482	0	0[a]	35	17 536
1975	0[a]	828 ± 501	38 ± 36	0	2 ± 2	2 ± 2	4355
1980	0	2381 ± 782	110 ± 74	0	91 ± 90	23 ± 8	13027
1985	1 ± 1	7879 ± 6179	1043 ± 753	19 ± 18	73 ± 48	1473 ± 936	52440
1990	360 ± 213	5051 ± 1864	1966 ± 1079	66 ± 61	2098 ± 1832	1370 ± 333	54554
1995	406 ± 228	13053 ± 9589	6822 ± 4165	342 ± 179	1181 ± 800	816 ± 333	113101
2000	190 ± 190	49444 ± 41166	1764 ± 506	18 ± 12	13 ± 4	112 ± 83	257707
2005	57 ± 38	6526 ± 3349	11595 ± 4967	120 ± 109	80 ± 42	409 ± 306	93941
						Total	606661

[a]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

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

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.

LITERATURE CITED

Ainley DG, Boekelheide RJ (1990) Seabirds of the Farallon Islands. Stanford University Press, Stanford, CA

Berger L, Speare R, Daszak P, Green DE and others (1998) Chytridiomycosis causes amphibian mortality associated with population declines in the rainforests of Australia and Central America. Proc Natl Acad Sci 95:9031–9036

Bodkin JL, Jameson RJ (1991) Patterns of seabird and marine mammal carcass deposition along the central California coast, 1980–1986. Can J Zool 69:1149–1155

Bourne WRP (1976) The mass mortality of common murres and guillemots in the Irish Sea in 1969. J Wildl Manage 40:789–792

Burger J, Gochfeld M (2004) Marine birds as sentinels of environmental pollution. Ecohealth 1(3):263–274

Camphuysen CJ, Heubeck M (2001) Marine oil pollution and beached bird surveys: the development of a sensitive monitoring instrument. Environ Pollut 112:443–461

Carter HR (2003) Oil and California's seabirds: an overview. Mar Ornithol 31:1–7

Converse KA, Kidd GA (2001) Duck plague epizootics in the United States, 1967–1995. J Wildl Dis 37:347–357

Daoust PY, Conboy G, McBurney S, Burgess N (1998) Interactive mortality factors in common loons from Maritime Canada. J Wildl Dis 34:524–531

Daszak P, Cunningham AA (1999) Extinction by infection. Trends Ecol Evolut 14:279

Daszak P, Cunningham AA, Hyatt AD (2001) Anthropogenic environmental change and the emergence of infectious diseases in wildlife. Acta Trop 78(2):103–116

Dobson A, Foufopoulos J (2001) Emerging infectious pathogens of wildlife. Philos Trans R Soc Lond B 356(1411): 1001–1012

Domingo M, Ferrer L, Pumarola M, Marco A, Plana J, Kennedy S, McAliskey M, Rima BK (1990) Morbillivirus in dolphins. Nature 348:21

Estes JA, Tinker MT, Williams TM, Doak DF (1998) Killer whale predation on sea otters linking oceanic and near-shore ecosystems. Science 282(5388): 473–476

Ford RG, Page GW, Carter HR (1987) Estimating mortality of seabirds from oil spills. In: Proc 1987 Oil Spill Conference. American Petroleum Institute, Washington, DC, p 547–551

Ford RG, Himes Boor GK, Reed NA (2004) Background oiling rate and historic beached bird deposition rate study. Final report to the US Fish and Wildife Service, Oregon Fish and Wildlife Office, Corvallis, OR

Friend M, McLean RG, Dein FJ (2001) Disease emergence in birds: challenges for the twenty-first century. Auk 118: 290–303

Hampton S, Zafonte M (2007) Exploring factors influencing beached bird collection during the Luckenback 2001– 2002 oil spill. Mar Ornithol 34:109–113

Harvell CD, Kim K, Burkholder JM, Colwell RR and others (1999) Emerging marine diseases—climate links and anthropogenic factors. Science 285(5433):1505–1510

Harvell CD, Mitchell CE, Ward JR, Altizer S, Dobson AP, Ostfeld RS, Samuel MD (2002) Climate warming and disease risks for terrestrial and marine biota. Science 296: 2158–2162

Lederberg J, Shope RE, Oakes SCJ (1992) Emerging infections: microbial threats to health in the United States. Institute of Medicine, National Academy Press, Washington, DC

Lyles AM, Dobson AP (1993) Infectious-disease and intensive management—population-dynamics, threatened hosts, and their parasites. J Zoo Wildl Med 24:315–326

Muzzafar SB, Jones IL (2004) Parasites and diseases of auks (Alcidae) of the world and their ecology—a review. Mar Ornithol 32: 121–146

Newman SH, Ziccardi MH, Berkner AB, Holcomb J, Clumpner C, Mazet JKA (2003) A historical perspective on oil spill response in California. Mar Ornithol 31:59–64

Newman SH, Harris RJ, Tseng FS (2006) Beach surveys past, present, and future: Toward a global surveillance network for stranded seabirds. Mar Ornithol 34: 87–90

Piatt JF, Anderson P (1996) Response of common murres to the Exxon Valdez oil spill and long-term changes in the Gulf of Alaska marine ecosystem. In: Rice SD, Spies RB, Wolfe DA, Wright BA (eds) Proc Exxon Valdez Oil Spill Symp. Am Fish Soc Symp 18:720–737

Piatt JF, Ford RG (1996) How many seabirds were killed by the Exxon Valdez oil spill? In: Rice SD, Spies RB, Wolfe

DA, Wright BA (eds) Proc Exxon Valdez Oil Spill Symp. Am Fish Soc Symp 18:712–719

Piatt JF, Van Pelt TI (1997) Mass-mortality of guillemots (*Uria aalge*) in the Gulf of Alaska in 1993. Mar Pollut Bull 34(8):656–662

Piatt JF, Litzow MA, Prichard AK, Roby DD (2002) Response of pigeon guillemots to variable abundance of high-lipid and low-lipid prey. Oecologia 132: 286–295

Reece RL (1989) Avian pathogens: their biology and methods of spread. In: Cooper JE (ed) Diseases and threatened birds. Technical Publication No. 10, International Council for Bird Preservation, Cambridge, p 1–23

Rocke TE, Friend M (1999) Botulism. In: Friend M, Franson JC (eds) Field manual of wildlife diseases—general field procedures and diseases of birds. Information and Technology Report 1999–2001, US Dept. of the Interior, US Geological Survey, Washington, DC, p 271–281

Schrag SJ, Wiener P (1995) Emerging infectious disease: What are the relative roles of ecology and evolution? Trends Ecol Evolut 10(8):319–324

Sherman BH, Epstein PR (2001) Past anomalies as a diagnostic tool for evaluating multiple marine ecological disturbances: applying the North American prototype to the Baltic Sea ecosystem. Human Ecol Risk Asses (7(5): 1519-1510

Smolinski MS, Hamburg MA, Lederberg J (2003) Microbial threats to health: emergence, detection, and response. The National Academies Press, Washington, DC

Stone R (2000) Canine virus blamed in Caspian seal deaths. Science 289:2017–2018

Sydeman WJ, McLaren EB, Pyle P (1994) ENSO 1992 and ENSO 1993: biological consequences and seabird population regulation in the California Current. Pac Seabirds 21:50

Warner RE (1968) The role of introduced disease in the extinction of the endemic Hawaiian avifauna. Condor 70: 101–120

Williams EH Jr, Bunkley-Williams L, Lopez-Irizarry I (1992) Die-off of brown pelicans in Puerto Rico and the United States Virgin Islands. Am Birds 46(5):1106–1108

Williams EH Jr, Bunkley-Williams L, Peters EC, Pinto-Rodriguez B and others (1994) An epizootic of cutaneous fibropapillomas in green turtles (*Chelonia mydas*) of the Caribbean: Part of a panzootic? J Aquat Anim Health 6: 70–78