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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**

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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 biological data, which tend to fluctuate less on annual time scales (Hare & Mantua 2000). Even so, biological time-series may also be confusing when coexisting marine species respond differently to ecosystem variability. For example, while warming temperatures in the Gulf of Alaska following the 1976 to 1977 regime shift favored an increase in gadoids and flatfish, a variety of forage fish and pandalid shrimp species virtually disappeared (Anderson & Piatt 1999). Zooplankton communities in the Gulf of Alaska also demonstrated similar patterns of response (Francis et al. 1998). At the basin scale, favorable conditions for salmon in Alaska following the regime shift were matched inversely by poor conditions in the California Current (Francis et al. 1998). In marine birds, subtropical species increased, while subarctic ones decreased during a warming phase in the southern California Bight. Clearly, no single index can tell the whole story accurately. Multi-species, multi-region, and multi-trophic level approaches are needed to quantify fluctuations in marine ecosystem processes and in the distribution and abundance of its inhabitants, to determine critical parameter thresholds and to use this information in management and marine conservation.

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

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

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

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

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

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

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

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

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

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

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

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

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

- There are two types of indicators: (1) seabirds as 'sentinels' or 'bio-monitors' of ecosystem change (e.g. contaminant load indicates pollution) and (2) seabirds as quantitative indicators of specific ecosystem components, such as the abundance of a forage fish species. The latter requires detailed knowledge of the functional response of the seabird parameter under investigation to changes in prey density around a colony.
- In some cases, seabird parameters may be predictive. This could be important for managing fisheries, where knowledge of seabird responses to ecosystem variability may be used to forecast changes in fish stocks.
- Seabirds are not needed to indicate atmospheric and ocean climate changes *per se* (this can be done directly with satellites and other automated devices such as moorings), but they provide timely and accurate information on the ecological consequences of climate changes that are not as easily or rapidly detected using other organisms. In some cases, biological parameters provide a more reliable indication of ecosystem shifts than physical parameters because they tend to fluctuate less on a year-to-year basis.

- Spatial scale is critical. Variation in seabird response parameters generally reflects meso-scale variability in the environment, e.g. the success of breeding colonies may reflect fluctuations in local prey stocks before, or in addition to, reflecting broad-scale regional variability.
- Different seabird parameters indicate change over a wide range of temporal scales. Population size and trends provide information on ecosystem variability on the scale of years to decades, due to deferred reproduction. In contrast, annual reproductive performance provides information on a monthly scale from the initiation of egg-laying through chick-rearing each year, providing information on shorter term ecosystem variability.
- Multivariate (multi-species, multi-parameter) indices may integrate complex ecological relationships into a single parameter that is easier to evaluate for its ecological significance (and yield concepts that are easier to communicate to the public and managers). However, univariate indices are needed to calculate and interpret multivariate indices and to interpret individual biological functions (e.g. breeding success).
- Relationships between measurable components of seabird biology and prey resources take many forms. Some non-linear functions (e.g. sigmoid curves) indicate where thresholds occur in seabird–prey relationships. Binary (on–off; good or bad foraging) relationships are powerful, especially when considered over large spatial scales. Linear relationships are best for prediction, but rare.

In addition to attending the symposium and workshop, we invited participants to contribute papers to this special Theme Section of *Marine Ecology Progress Series*. The 10 papers presented here address many of the important questions posed to participants in the symposium. Frederiksen et al. and 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.

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