



Seabirds as Indicators of Marine Ecosystems: A Brief History

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The Premise

We can observe seabirds at sea and study them at their colonies with relative ease, and so quantify many aspects of seabird behavior and biology. Because seabirds forage over a wide range of marine habitats, they serve as sensitive and cost-effective indicators of the health and status of marine ecosystems.

Background

Understanding ecosystem variability at multiple temporal and spatial scales has become a central focus in marine community ecology, population biology, and applied fisheries science. Quantifying ecosystem variability is important in the adaptive management of marine resources, although few fisheries are currently managed from a perspective of ecosystem variability (Botsford et al. 1997). In the U.S. EEZ, environmental variation has been shown to affect the spawning rates, survival, and biomass of many key stocks of commercial interest such as salmonids, groundfish, and crabs (Hare and Mantua 2000). Interannual to interdecadal environmental variation also affects forage fish (Anderson and Piatt 1999) and zooplankton (Brodeur et al. 1996) communities. As the fisheries dependent upon these stocks also fluctuate in relation to ecosystem change, it is important to detect ecosystem change in “near real time” or, if possible, to predict oncoming fluctuations. The significance of this need is clear. Some fisheries have become economically extinct due, in part, to unfavorable ecosystem conditions, such as California’s Pacific sardine. For this stock, large harvests in the 1940s and 1950s coupled with a generally “poor climate” for this species at that time (Chavez et al. 2003) drove the stock to economic extinction. Today, the fishery for Pacific sardine is one of few fisheries in the North Pacific managed from an ecosystem perspective, with harvest guidelines set by stock-ocean temperature relationships.

Ideally, establishing a system to detect ecosystem fluctuations in real time is a key first step in implementing ecosystem-based fisheries management. However, obtaining the right information at the right time and place about both physical and biological change is a daunting task. Intuitively, one might assume that physical data is more important to acquire in real time than biological data, but extensive analyses of time series data suggest otherwise: Physical data are more erratic and often confusing over the short term compared to biological data, which tends to fluctuate less on annual time scales (Hare and Mantua 2000). Alaska has an extensive coastline, characterized by highly variable physical and biological conditions. Plans for extensive ocean observing systems, such as the Alaska Ocean Observing System (AOOS), will aid in this effort, but may not provide sufficient resolution or depth of information on the variation of lower and middle trophic level organisms (i.e., the prey base) that drives fisheries stock fluctuations. Furthermore, marine species respond differently to ecosystem variability, thereby affecting community structure and ecological interactions differently (Anderson and Piatt 1999). Thus, while

warming temperatures in the Gulf of Alaska favored an increase in gadids and flatfish, a variety of forage fish and pandalid shrimp species virtually disappeared. At the basin scale, favorable conditions for salmon in Alaska are inversely matched by poor conditions in the California Current (Francis and Hare 1998). In marine birds, subtropical species increased while subarctic ones decreased during a warming phase in the southern California Bight (Hyrenbach and Veit 2003). Zooplankton communities in the Gulf of Alaska also demonstrate similar patterns of response, with out-of-phase fluctuations in species abundance (Brodeur et al. 1996). *Thus, there is great need to develop multi-species, multi-region, and multi-trophic level approaches to quantify marine ecosystem fluctuations and to use this information in fisheries management. Seabirds— and seabird communities— can contribute to this approach, offering unique insights into ecosystem status and change. .*

Present state of knowledge for seabirds as indicators

Global fisheries landings are currently 80 million metric tons, 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 and health of marine ecosystems. For this purpose, seabirds offer many advantages. They are highly visible animals in an ecosystem in which most other plants and animals are completely hidden under water. They are easily observed flying above the sea surface, or foraging in flocks in productive hotspots. At colonies, large numbers gather annually to reproduce, and so it is often possible to census and monitor trends for a significant fraction of populations. Furthermore, some species are easy to observe and capture at colonies, allowing us to measure a wide variety of demographic, behavioral and physiological parameters. It is therefore not surprising that seabirds have often been identified as useful indicators of the health and status of marine ecosystems (Furness and Camphuysen 1997, Montevecchi 2002). Like other marine disciplines, however, marine ornithology has evolved rapidly in recent decades, and the ways in which seabirds may act as indicators have grown with the science (Table 1). Today, technological advances have greatly expanded our ability to study seabirds and their ecology, offering ever more complex insights into the function of marine systems. Seabirds *are* useful indicators, but a greater level of sophistication is required to know *exactly* what it is they indicate at any one time and place, and how to interpret variability in seabird parameters over different temporal and spatial scales.

The earliest recognition of seabirds as potential indicators came from studies where dramatic breeding failures or declines in seabird populations accompanied major crashes in fish populations (Table 1). For example, the reproductive failure and decline of Peruvian guano birds (booby, pelican, cormorant) in association with over-exploitation and collapse of the anchoveta (*Engraulis ringens*) fishery during the 1950s and 1960s has been well documented (Shaffer 1970, Duffy 1983). Similarly, Cape Gannet (*Sula capensis*) populations in southern Africa plummeted following a fishery-induced collapse of pilchard (*Sardinops ocellata*) during the 1960s (Crawford and Shelton 1978). Similar events have occurred regularly to the present time, for example, reproductive failures of Atlantic Puffins (*Fratercula arctica*) heralded the collapse of herring (*Clupea harengus*) stocks off Norway during the 1970s (Anker-Nilssen et al. 1997), the near-instantaneous crash of Common Murre (*Uria aalge*) populations in the Barents Sea during the 1980s signaled the collapse of capelin (*Mallotus villosus*) in the Barents Sea (Vader et al. 1990), and widespread failures in breeding of Black-legged Kittiwakes (*Rissa tridactyla*) in the North Sea during the late 1980s (Harris and Wanless 1990) presaged changing environmental conditions and a collapse of sand eel (*Ammodytes* spp.) stocks that has been confirmed in recent years by a dramatic and wide-spread decline in reproductive success of several seabird species in the North Sea (RSPB 2004).

While colony work was beginning to yield insights into ecosystem functioning, data gathered at sea was also beginning to reveal patterns in marine systems. Following the early pioneer (but largely opportunistic) work of investigators like Murphy, Kuroda and Wynne-Edwards, pelagic investigations during the 1950s though 1970s became more systematic and regional coverage became extensive enough to begin relating seabird distribution and abundance to major oceanographic features such as continental shelves, currents and water masses (Shuntov 1972, King 1974, Brown et al. 1975, Gould et al. 1982, Ainley and Boekelheide 1983).

During the 1970s and early 1980s, seabird studies began to focus on seabird-fisheries interactions in more quantitative ways. Time series of seabird diet composition began to suggest status and trends in local prey stocks (e.g., Harris and Hislop 1978, Anderson et al. 1980)— although few spatially concurrent data sets on birds and fish were available to test concordance. During this period, following the serial depletion of traditional groundfish stocks, industrial scale fisheries on forage species began in earnest (“fishing down food webs”; Pauly et al. 1998), and concern mounted for the impact of fisheries on marine predators (Furness 1982). Quantitative models of prey harvest by seabirds were initiated in many regions, all generally revealing that seabird populations are significant consumers of secondary production in marine systems, on a par with marine mammals and human fisheries (Wiens and Scott 1975, Furness 1978,

Table 1. Development over time in the use of seabirds as indicators in marine ecosystems.

Years	Developments in using seabirds as indicators
1950s-1970s	Seabird populations and productivity linked to major fluctuations in fish stocks. Pelagic distribution described in relation to major oceanographic features.
1970s-1980s	Diet composition linked to changes in fish communities, impacted by fisheries. Modeling of seabird demands for fish, and community impacts on ecosystems. At sea distribution and abundance correlated with oceanographic features such as fronts, upwelling zones, currents and prey.
1980s-1990s	Focus on greater variety of demographic, behavioral and physiological parameters. Better tools and technologies to measure parameters at colonies and at sea. More rigorous examination of seabird-fisheries interactions. Examination and testing of scale effects in seabird ecology. Quantitative assessments of aggregative predator-prey behavior at sea
1990s-2000s	Increasing time series on oceanography, fish, fisheries and seabirds. Quantitative measures of functional relationships between seabirds and prey, and testing of hypotheses about seabirds as indicators. Bio-geographic integration of pelagic seabird data with oceanography, plankton and fish ecology. Increasing recognition of the importance of climate effects on annual, decadal and longer time scales for birds at sea and on colonies.

Livingston 1993). These models also pointed to gaps in understanding, and called for new studies to gather data on a wider variety of biological parameters. At the same time, studies of seabirds at sea grew more sophisticated, especially when marine ornithologists collaborated with other marine scientists on multi-disciplinary fisheries and oceanography cruises. The complexity of pelagic habitat began to be revealed, and the predictable association of individual seabird species or feeding guilds with particular marine features, such as fronts, upwelling zones, current boundaries, prey aggregations, etc., was observed commonly in many regions (e.g., Brown 1980, Schneider 1982, Ainley et al. 1984, Hunt et al. 1987, Piatt 1987). Soon, ornithologists were telling oceanographers when physical boundaries had been

crossed on transects, simply from the presence or absence of indicator species of seabirds at the sea surface.

The concept of seabirds as indicators was well established by the early 1980s (e.g., Nettleship et al. 1984, Croxall et al. 1988) and efforts for the next two decades focused on gathering data on a wider variety of demographic, behavioral and physiological parameters (Figure 1). At sea, questions related to the acquisition of prey (Springer et al. 1984, Burger and Piatt 1990, Hatch and Sanger 1992, Uttley et al. 1994, Barrett and Krasnov 1996, Springer et al. 1996, Gaston et al. 2003). How effective were seabirds as samplers, how far did they travel, how deep did they dive, what species did they consume or deliver to chicks, and how quickly could they acquire it? How did all these parameters relate to the local abundance of prey? Were birds able to buffer against fluctuations in food availability by adjusting foraging effort and use of discretionary time?

Once delivered to the colony, questions focused on how prey were assimilated and how this translated into demographic parameters of biology (e.g., Harris and Wanless 1988, Monaghan et al. 1989, Murphy et al. 1991, Hamer et al. 1993, Hunt et al. 1996, Irons 1996, Phillips et al. 1996, Bryant et al. 1999, Croxall et al. 1999, Kitaysky et al. 2000, Barrett 2002, Gill et al. 2003). On what basis was clutch size determined? What controlled the timing of laying, and therefore the subsequent breeding season? Chick growth varied among years and in apparent relation to food delivery rate, but what about laying, hatching and fledging success? Growth of chicks and breeding success could be highly variable, but how much of it was due to factors besides food, such as brooding and adult attendance, siblicide, air temperature,

precipitation, predation or pollution; all acting at different stages in the breeding cycle?

A variety of technological advances allowed us to better address these questions by allowing us to measure time budgets (time-activity recorders, e.g., Cairns et al. 1990), foraging effort (time-depth recorders, e.g., Croll et al. 1992), energy expenditure (doubly-labeled water, Gabrielson et al. 1987), stress levels (corticosteroid hormone concentrations, Kitaysky et al. 1999), diet trends (stable isotope and fatty acid analyses, e.g., Hobson et al. 1994) and a number of other parameters which provide insight into how seabirds respond to changes in their environments. Taking advantage of the ability to measure fish and plankton abundance remotely and continuously with hydro-acoustic sonar equipment, concurrent studies of seabirds and forage fish allowed investigators to examine aggregative predator-prey

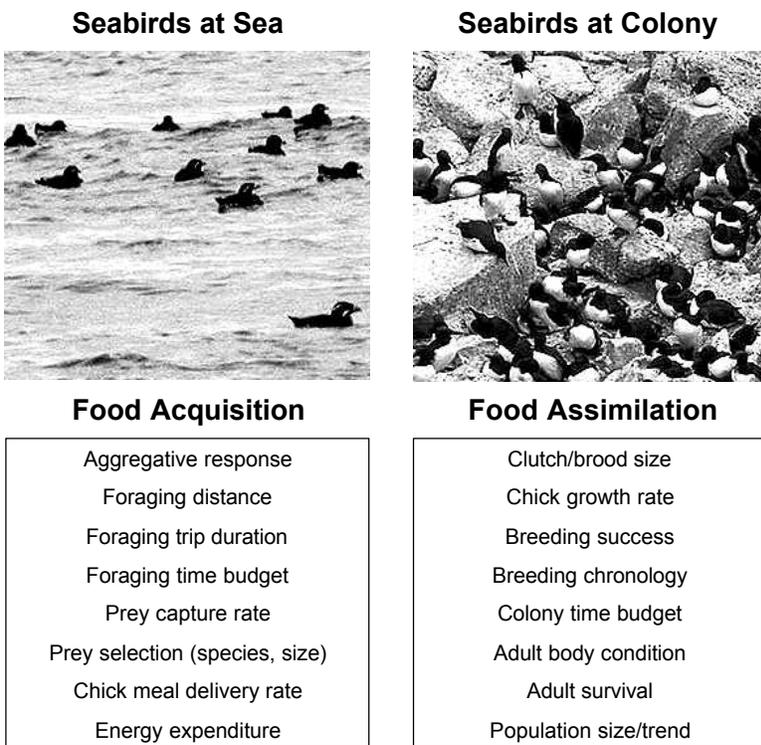


Figure 1. Range of demographic, physiological and behavioral parameters commonly studied in seabirds and which may serve as sensitive indicators of change in their marine environment

relationships as never before (Piatt 1990, Hunt et al. 1990, Erikstad et al. 1990). Not only were seabirds often found in strongly correlated associations with prey, the form of responses was usually non-linear, and the importance of encountering prey densities above minimum threshold values was increasingly

recognized as a critical factor influencing the likelihood of finding birds at sea (Mehlum et al. 1999). The converse was also usually true: Large aggregations of seabirds at sea are reliable indicators that dense concentrations of prey are nearby (Piatt 1990, Fauchald and Erikstad 2002).

The importance of scale became increasingly obvious while looking for spatial patterns in pelagic distribution data (Schneider and Piatt 1986, Schneider 1993). 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 or decadal time periods, and to the influence of ocean basins and current regimes at the largest spatial scales (Hunt and Schneider 1987). Scale effects are important to consider as we search for patterns because those patterns may be otherwise overlooked. For example, the aggregative response of murres to prey schools and the strength of their correlation is strongly scale-dependent and non-linear (Piatt 1990, Mehlum et al. 1999). The spatial distribution of murres can be described by a hierarchical patch structure that reflects the distribution of its main prey, whereby small-scale patches are nested within patches at larger scales (Fauchald and Erikstad 2000). This may help explain why prey harvest by seabirds can reflect fisheries landing on multiple spatial and temporal scales (Montevecchi and Myers 1995). Ultimately, scale is important as we search for concordance in demographic trends across basin-wide scales (Ainley et al. 1994) and the effects of climate variation on local populations (Parish and Zador 2003).

One of the most important outcomes of work in the 1980s was the development of specific hypotheses about using seabirds as indicators (Cairns 1987). Cairns hypothesized that many responses of seabirds to fluctuations in prey abundance would likely be non-linear (Figure 2), and further, that

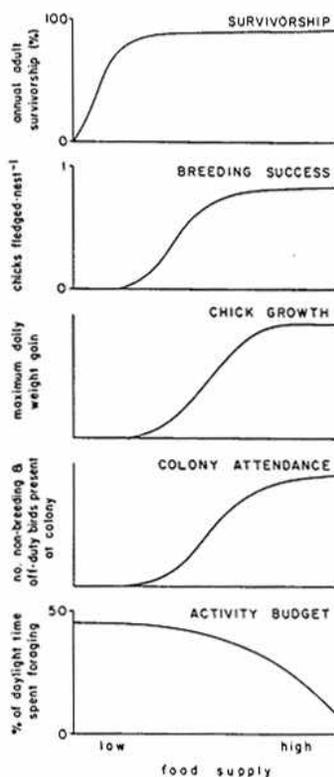


Figure 2. Hypothesized relationship between various seabird parameters and food supply (from Cairns 1987)

different parameters such as growth rates, breeding success or survival would have different thresholds to prey density because of a variety of buffering mechanisms. During the 1990s and 2000s, marine ornithologists continued their collection of detailed data on a variety of species throughout the world's oceans. This has permitted us to examine functional relationships between seabirds and prey, and test some of Cairns' specific hypotheses about seabirds as indicators (e.g., Phillips et al. 1996, Furness and Camphuysen 1997, Klomp and Furness 1992, Piatt 2002, Litzow and Piatt 2003).

Perhaps the most intriguing use of seabird data in recent years has been in the study of climate change and regime shifts in marine ecosystems. A pivotal paper by Aebischer et al. (1990) revealed a remarkable parallelism in long-term trends across four 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 (in this case breeding phenology, clutch size and chick production by kittiwakes) are accurate indicators of ecosystem status and change.

In the North Pacific, seabirds provided early indication that a major shift in the biological regime of the Gulf of Alaska (GOA) had occurred in the late 1970s. Widespread reproductive failures in kittiwakes, and population declines in several species of marine birds and mammals were observed during the 1980s and early 1990s in the GOA, but the cause of these demographic changes remained obscure. Mounting evidence suggested that a major change in climatic and oceanographic regimes had occurred during the late 1970s (Kerr 1992). Then analysis of a 30-year time series of small-mesh trawl catches at a site along the Alaska Peninsula suggested

that marine fish communities had also changed rapidly in the late 1970s, marked especially by the disappearance of pelagic forage species such as Pandalid shrimp and capelin. Contemporaneous changes in diet composition of five abundant seabirds in the GOA, from diets dominated by high-energy capelin to low-energy pollock (*Theragra chalcogramma*), pointed a finger at climate change as the ultimate cause of demographic changes in seabird populations (Piatt and Anderson 1996). Eventually an hypothesis emerged to explain how decadal-scale changes in atmospheric forcing in the Aleutians affected current flow and water temperatures, primary and secondary production, fish stocks and higher trophic levels in the NE Pacific (Francis et al. 1998). Effects of this 'regime shift' on fish populations were later confirmed to have occurred throughout the GOA (Anderson and Piatt 1999). It is notable that biological changes observed during regime shifts appear more predictable and stable from year to year than the underlying physical variables (Hare and Mantua 2000).

An emerging paradigm of the new millennium is the over-arching importance of climate and global warming on marine bird populations. 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 diet and reproductive output of 11 species of seabirds in the southern California Current reflect low-frequency climate change (Sydeman et al. 2001). Indeed, seabird diets can reveal the influence of climate at many time scales, including annual, multi-annual (e.g., ENSO frequency), decadal and centurial scales (Miller and Sydeman 2004, Montevecchi and Myers 1997). It appears that annual variability of within-year timing of seasonal temperature cycles and corresponding timing of zooplankton blooms may have a pronounced effect on productivity of marine fish and birds, owing to match-mismatch effects (Anderson and Piatt 1999, Bertram et al. 2001, Abraham and Sydeman 2004). Besides 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, Barber and Chavez 1983), demographic parameters like production, survival and population trend can be strongly correlated with proxies for climate change such as air temperature (Croxall et al. 2002), sea surface temperature (Gjerdrum et al. 2003), the Southern Oscillation Index (Ainley et al. 1995), the North Pacific Index (Jones et al. 2002), and the North Atlantic Oscillation (Thompson and Ollason 2001).

Although more limited owing to logistic constraints, a number of long-term data sets on seabirds at sea also reveal patterns of climate variability. Because some species show strong affinities for particular water masses or particular features (such as fronts, current boundaries, etc.), changes in the abundance or relative distribution of these species are especially revealing. For example, there is a rapid invasion by warm-water species of marine waters in southern California during strong ENSO events (Ainley et al. 1995). Over the longer term, some species (especially Sooty Shearwaters *Puffinus griseus*) in this region have declined dramatically as water temperatures have increased, and this trend is reflected in bird surveys off central California and Washington (Veit et al. 1997). Over the long term, the avifauna off southern California shifted from a 'high-productivity' community typical of eastern boundary upwelling systems, to a 'low-productivity' assemblage similar to those inhabiting subtropical gyres (Hyrenbach and Veit 2003). During a 30-year period off the Washington coast, the seabird community has reflected influences of ENSO events and decadal temperature changes in the coincident waxing and waning of several species (Wahl and Tweit 2000).

Issues in the Future

As summarized above, marine ornithologists have suggested that seabirds are useful indicators of variation in marine ecosystems, change in lower trophic-level prey organisms, and fluctuations in the physical environment. However, marine ornithologists have generally provided more qualitative than quantitative indices, and they have neglected to effectively highlight their work in the realm of fisheries science and conservation (Cairns 1992). In few cases have functional (possibly predictive) relationships between seabird indicators and ecosystem properties been developed. Often because of 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 regression equations would be most valuable in a management context. Previous work

has also failed to address the “shape” of these correlations: linear, non-linear, or “threshold” (step-function). 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). Finally, while marine ornithologists have demonstrated that seabirds can be used as monitors and in some cases samplers of marine ecosystems, they have generally failed to develop specific applications, especially in fisheries management (but see, for example, Hatch and Sanger (1992) who attempted to develop pollock recruitment indices from puffin chick diets in the Gulf of Alaska).