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Global Seabird Response to Forage Fish Depletion—One-Third for the Birds

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Determining the form of key predator-prey relationships is critical for understanding marine ecosystem dynamics. Using a comprehensive global database, we quantified the effect of fluctuations in food abundance on seabird breeding success. We identified a threshold in prey (fish and krill, termed “forage fish”) abundance below which seabirds experience consistently reduced and more variable productivity. This response was common to all seven ecosystems and 14 bird species examined within the Atlantic, Pacific, and Southern Oceans. The threshold approximated one-third of the maximum prey biomass observed in long-term studies. This provides an indicator of the minimal forage fish biomass needed to sustain seabird productivity over the long term.

Public and scientific appreciation for the role of top predators in marine ecosystems has grown considerably, yet many upper trophic level (ULT) species, including seabirds, marine mammals, and large predatory fish, remain depleted owing to human activities (1–4). Fisheries impacts include direct mortality of exploited species and the more subtle effects of altering trophic pathways and the functioning of marine ecosystems (5). Specifically, fisheries for lower trophic level (LTL) species, primarily small coastal pelagic fish (e.g., anchovies and sardines), euphausiid crustaceans (krill), and squid (hereafter referred to as “forage fish”), threaten the future sustainability of UTL predators in marine ecosystems (6, 7). An increasing global demand for protein and marine oils contributes pressure to catch more LTL species (8). Thus, fisheries for LTL species are likely to increase even though the consequences of such activity remain largely unknown at the ecosystem level. It remains challenging, however, to assess fishing impacts on food webs because numerical relationships between predators and prey are often unknown, even for commercially valuable fish (9, 10). Ecosystem models and ecosystem-based fisheries management, for which maintaining future gains (11). Impacts of LTL fisheries on the sustainability of UTL species need to be considered in marine management frameworks (12). In this regard, the recovery of forage fish species is critical for the sustainability of marine ecosystems and the conservation of other valuable species at risk (13).

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Supporting Online Material

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Materials and Methods

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References and Notes

11. Materials and methods are available as supporting material on Science Online.

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predator populations is an objective (2, 11, 12), will remain controversial until these relationships are more fully quantified.

To improve our understanding of the effects of LTL fisheries on marine ecosystems, more information on predator-prey relationships across a range of species and ecosystems is required (6). Seabirds are conspicuous members of marine ecosystems globally. Many aspects of seabird ecology have been measured consistently for decades, encompassing ecosystem change at multiple scales (13). Substantial long-term data sets on seabird breeding success have been compiled for many taxa in several marine ecosystems around the world (14–16), but for relatively few has independent information on prey availability been obtained concurrently. For those where prey data are available, temporal covariance in predators and their prey suggests that seabirds can be used as indicators of forage fish population fluctuations (7, 16, 17). Here, we used data collected contemporaneously over multiple decades from seabirds and forage fish to test the hypothesis that the form of the numerical response between seabird breeding success and forage fish abundance is consistent across species and ecosystems. We used data from seabird species that have strong dietary dependencies on forage fish prey and where the time series for both the predator and the prey have high spatial and temporal congruence. We compiled data from 19 time series covering seven marine ecosystems, nine sites, and 14 seabird species and their major prey (Fig. 1 and table S1). The data set included 438 data points spanning 15 to 47 colony-years per breeding site (table S1). The abundance of principal prey for each seabird species was estimated independently of the data collected from the birds, usually as part of population assessments conducted in support of fisheries management (table S1).

To examine empirical relationships between seabird breeding success and prey abundance, we used nonparametric statistical methods that facilitate nonlinear modeling by making no a priori assumptions about the form of the relationships (generalized additive models, or GAMs). Initially, each time series (seabird breeding success and prey abundance) was normalized by expressing the measurements as the number of standard deviations from the mean; this enables robust comparisons across species and ecosystems. Once the numerical relationship was established, we used a change-point analysis (sequential tests that find the most likely point at which the slope of breeding success changes in relation to prey abundance) to identify thresholds within nonlinear relationships (18) (Fig. 2A). A bootstrap analysis was used to calculate confidence intervals of the threshold, and the variance in seabird breeding success was calculated for each prey abundance class. Last, a selection of a priori parametric models ranging from linear, sigmoid, asymptotic, to hierarchical (table S2) was fitted to the general relationship. The most parsimonious model was then used to fit the relationship between seabird breeding success and forage fish population size for each ecosystem (pooling all species) and each seabird species (pooling all ecosystems).

Seabird breeding success showed a nonlinear response to changes in prey abundance (Fig. 2A). The threshold at which breeding success began to decline from the asymptote was not significantly different from the long-term mean of prey abundance (range –0.30 and +0.13, standard deviation of the mean, Fig. 2A). The threshold was 34.6% (95% confidence interval 31 to 39%), or approximately one-third of the maximum observed prey abundance. The coefficient of variation between the different thresholds among species and ecosystems was 28% (table S1). All time series were of sufficient duration to identify the threshold (detection is possible after 13 years of observation, fig. S1) and the maximum biomass (detection is possible after 11 years, fig. S2). Variance in breeding success increased significantly (∆F test, F < 10^-6) below the threshold of prey abundance (Fig. 2B). Fitting parametric models to individual responses showed a similar inflection point and similar asymptotic values across ecosystems and species (Figs. 2, C and D, and 3), indicating that the functional form was a general feature of the seabird–forage fish relationship.

The asymptotic form of the relationship between seabird breeding success and forage fish abundance has been reported previously (15, 16, 19–24), but the common scaling across species and ecosystems and the consistency of threshold values are new observations. The global pattern shows a threshold below which the numerical response declines strongly as food abundance decreases and above which it reaches a plateau and does not change even as food abundance increases. This pattern is apparently robust to the varying life-history strategies, habitat preferences, and population sizes of the seabird species considered. Nonetheless, we acknowledge that a range of factors may interact to weaken or possibly accentuate the relationship between seabird breeding performance and prey species abundance. Alternative drivers of change in breeding success include changes in habitat characteristics or predation pressures, or complex intercolony dynamics. Predators may also show more or less capacity to switch to alternative prey items, which may buffer productivity against declines in any single prey species (25).

Periods of consistently high or low breeding success, or occasional complete breeding failures, are normal in seabirds, and most species are adapted to fleeting anomalous environmental conditions. However, chronic food scarcity, as potentially defined by prey abundance below the threshold described here for seabirds, will compromise long-term breeding success, and this may affect the trajectory of their populations.

Fig. 1. Map of the distribution of seabird and prey species considered in our analysis.
Fig. 2. (A) Relationship between normalized annual breeding success of seabirds and normalized prey abundance. Each data point from all the time series was plotted with the predictions of a generalized additive model (GAM) (solid line). The gray area represents the 95% confidence interval of the fitted GAM. The threshold in the nonlinear relationship (black solid vertical line) and its 95% confidence interval (black dashed vertical lines) were detected from a change-point analysis. (B) Change in variance across the range of normalized food abundance ranging from −1.5 to 2 standard deviations in eight classes. Variance below the threshold was 1.8 times higher than above it. (C and D) Similar relationships were present when data were pooled (C) for species within ecosystems and (D) for species pooled among ecosystems using the best-fitting asymptotic model (table S2). The Arctic Tern (not shown) model fit was not significant (table S1). The colors in (A) and (C) represent the data set for each ecosystem and in (D) for each seabird species.

Fig. 3. Relationship between normalized annual breeding success of pooled seabird species and normalized prey abundance for the seven different ecosystems using the most parsimonious asymptotic model (table S2).
Mouse B-Type Lamins Are Required for Proper Organogenesis But Not by Embryonic Stem Cells

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B-type lamins, the major components of the nuclear lamina, are believed to be essential for cell proliferation and survival. We found that mouse embryonic stem cells (ESCs) do not need any lamins for self-renewal and pluripotency. Although genome-wide lamin-B binding profiles correlate with reduced gene expression, such binding is not directly required for gene silencing in ESCs or trophectoderm cells. However, B-type lamins are required for proper organogenesis. Defects in spindle orientation in neural progenitor cells and migration of neurons probably cause brain disorganizations found in lamin-B null mice. Thus, our studies not only disprove several Defects in spindle orientation in neural progenitor cells and migration of neurons probably cause B-type lamins, the major components of the nuclear lamina, are believed to be essential for organogenesis. Although a number of human diseases referred to as laminopathies (2), although the disease mechanism remains unclear. A-type lamins are expressed only in a subset of differentiated cells and are not essential for basic cell functions (3–4). By contrast, at least one B-type lamin is found in any given cell type. Because numerous functions, including transcriptional regulation, DNA replication, and regulation of mitotic spindles, have been assigned to B-type lamins, they are thought to be essential for basic cell proliferation and survival (1, 5–8).

References and Notes


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Supporting Online Material

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Materials and Methods

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Data and Codes

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