Effects of variation in the abundance and distribution of prey on the foraging success of central place foragers

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Summary

1. Seabirds and pinnipeds are vulnerable to reductions in prey availability, especially during the breeding season when spatial constraints limit their adaptive capacity. There are growing concerns about the effects of fisheries on prey availability in regions where large commercial fisheries target forage fish.

2. For breeding seabirds and pinnipeds, prey availability depends on a combination of abundance, accessibility, patchiness and distance from the colony. An understanding of the aspects of prey availability that determine foraging success is essential for the design of effective management responses.

3. We used a mechanistic individual-based foraging model based on observed data for two seabird species, the Peruvian Booby Sula variegata and Guanay Cormorant Phalacrocorax bougainvilliorum, to simulate the foraging patterns of seabirds feeding on schooling fish. We ran the model over simulated prey fields representing eight possible combinations of high or low prey abundance, shallow or deep prey, and broadly distributed or spatially concentrated prey.

4. The results highlight the importance of the accessibility of prey. Depth distribution was the primary factor determining modelled foraging success for both species, followed by abundance, and then spatial configuration.

5. Synthesis and applications. The individual-based foraging model provides a spatially explicit framework for assessing the effects of fisheries on the foraging success of seabirds and other central place foragers, and for evaluating the potential effectiveness of marine-protected areas and other fisheries management strategies for safeguarding central place foragers in dynamic ecosystems. Our analysis indicates that broad-scale fisheries management strategies that maintain forage fish above critical biomass levels are essential, but may need to be supplemented by targeted actions, such as time–area closures, when environmental conditions lead to low prey abundance or reduce prey accessibility for seabirds or pinnipeds of conservation concern. The individual-based foraging model is adaptable and could be reconfigured for application to other species and systems.

Key-words: Guanay Cormorant, Humboldt Current System, marine spatial planning, Peruvian Booby, Phalacrocorax bougainvilliorum, predator–prey interactions, prey availability, seabird competition with fisheries, Sula variegata

Introduction

Understanding relationships between predators and the abundance and distribution of their prey is essential for ecosystem-based approaches to management (Sainsbury, Punt & Smith 2000). Seabirds, pinnipeds and other central place foragers (CPF) are vulnerable to localized depletion and broad-scale shifts in the spatial distribution of their prey because they must return to a specific location between foraging trips (Orians & Pearson 1979). Seabirds...
are able to maintain provisioning rates and breeding success to some extent by compensating for reduced prey availability through increased foraging effort (Piatt et al. 2007), for example, increasing trip durations and traveling farther from the colony (e.g., Kitaysky et al. 2000). However, they are often operating close to time and energy constraints during the breeding season (Ashmole 1963; Piatt et al. 2007). When foraging conditions are poor, adults may abandon breeding efforts to avoid jeopardizing their own survival and future reproductive success (Stearns 1992; Croll et al. 2006). Severe reductions in breeding success and population declines in several species of seabirds have been attributed to reduced prey availability during oceanographic anomalies (Crawford & Jahncke 1999; Thayer & Sydeman 2007). Natural variability in oceanographic conditions is a major driver of forage fish abundance (Chavez et al. 2003), but there are also growing concerns about competition with fisheries, especially in regions where large commercial fisheries target forage fish that are also important for seabirds (e.g., Cury et al. 2011; Smith et al. 2011; Bertrand et al. 2012).

The design of effective conservation strategies for species threatened by reduced prey availability depends on how foraging success, and ultimately population dynamics, is affected by variation in prey availability and how this can be mitigated through management. Prey availability is generally correlated with abundance, but other factors also influence the ability of predators to acquire prey (Cairns 1987). For CPFs, prey availability can be defined in terms of abundance, accessibility and distance from the colony or central place (Boyd 1999). A further aspect of prey availability is the patchiness or spatial concentration of prey — prey may be clustered in a few large patches or aggregations or widely dispersed in many small patches (e.g. Davoren 2000). Some aspects of prey availability are more susceptible to management action than others. In particular, there is generally greater scope to influence the abundance of forage fish than their spatial distribution (see Discussion).

Empirical studies provide valuable insights into the effects of prey availability on proxies for the seabird or pinniped foraging success (e.g. body mass, breeding success and adult survival; Reid et al. 2005; Piatt et al. 2007). However, empirical studies have generally focused on prey abundance because of the challenges of separating the effects of different aspects of prey availability, which are often confounded in short-term data sets. Long-term data sets with contemporaneous data on predator and prey are required to disaggregate aspects of prey availability using correlation-based analysis. However, few such data sets are available and most rely on data from fisheries or stock assessments rather than data that describe prey availability to CPFs (e.g. Cury et al. 2011). Unfortunately, differences in the sampling strategies of seabirds and fisheries often frustrate efforts to match seabird responses with fisheries data (Hunt, Piatt & Eriksen 1991), and stock assessment outputs typically do not provide information on the distribution of forage fish at spatial scales relevant to CPFs. A new research approach that does not depend on long-term data sets is urgently required.

Our research goal was to strengthen understanding of the effects of variation in prey abundance and distribution on the foraging success of seabirds and other CPFs. Our primary hypothesis was that seabird foraging success depends on the depth distribution and spatial configuration of prey as well as prey abundance (i.e. we expected seabird foraging success to decline when prey is less abundant and/or deeper in the water column). We developed an alternative research approach to address the limitations of empirical studies based on a mechanistic individual-based foraging model (IBFM) of CPFs foraging on patchy prey (Boyd et al. 2016), informed by observed data on the movement and foraging patterns of seabirds feeding on schooling fish. A major advantage of this approach was that observed data on the abundance, depth distribution and spatial configuration of prey from 2 years with contrasting foraging conditions could be disaggregated and recombined in simulated prey fields that isolated changes in different aspects of prey availability. Using the mechanistic IBFM, it was possible to simulate seabird foraging patterns over these prey fields to explore the effects of changes in each aspect of prey availability and evaluate the relative importance of abundance, depth distribution and spatial configuration in determining foraging success and failure.

This study focuses on two seabird species: the Peruvian Booby Sula variegata (Tschudi) and Guanay Cormorant Phalacrocorax bougainvilliorum (Lesson). Both species are endemic to the northern Humboldt Current System (HCS), an upwelling system off the west coast of South America characterized by pronounced interannual variation in the abundance and distribution of forage fish (Chavez et al. 2008). Declines in seabird populations in the northern HCS since the mid-1950s have been attributed to a combination of severe oceanographic anomalies and industrial fisheries (e.g., Jahncke, Checkley & Hunt 2004). However, population trends for the two focal species have been strikingly different — populations of Peruvian Boobies have been comparatively stable at around two million birds, whereas Guanay Cormorants have declined from around 21 million to two million (Goya 2000) and are now listed as Near-Threatened by IUCN (2016). The factors underpinning these different population trajectories remain unclear. Several hypotheses are available to explain differences in seabird species’ resilience to variation in prey availability, including differences in diet specialization, flight proficiency, dive capacities and search strategies (Furness & Ainley 1984). Peruvian Boobies and Guanay Cormorants both feed primarily on Peruvian anchoveta Engraulis ringens (Jenyns), often foraging together in large flocks, apparently on the same prey aggregations (Duffy 1983). However, the pursuit-diving Guanay Cormorant is capable of reaching greater depths than the plunge-diving Peruvian Booby (Weimerskirch et al. 2012). There is also some evidence that
Guanay Cormorants may require denser prey schools for successful prey capture than Peruvian Boobies (Nelson 1978). Analysis of foraging site selection by Peruvian Boobies and Guanay Cormorants indicated that both species respond to a combination of the abundance and depth distribution of prey, but Guanay Cormorants may be more sensitive to variation in prey abundance than Peruvian Boobies (Boyd et al. 2015a). This led to our second hypothesis that the sensitivity of Peruvian Boobies and Guanay Cormorants to changes in prey availability differs because of differences in patch selection patterns (i.e., we expected Guanay Cormorants to be more sensitive to changes in abundance than Peruvian Boobies, and Peruvian Boobies to be more sensitive to changes in the depth distribution than Guanay Cormorants).

Materials and methods

OVERVIEW OF THE IBFM

The IBFM was designed to investigate the movement and foraging patterns of CPFs feeding on patchy prey. The IBFM has two main components: a prey field and individual CPFs (see Boyd et al. (2016) for a full description and Appendix S1, Supporting Information for implementation code in R; R Development Core Team 2016).

Prey field

The IBFM prey field comprises a set of hexagonal grid cells, each with information on the abundance and depth distribution of prey. Grid cell resolution was set to 2 km, corresponding to the resolution of processed acoustic survey data for anchoveta off Grupo Pescadores, Peru (c. 11.77°S, 77.27°W).

Scenarios. Acoustic survey data revealed contrasting foraging conditions in terms of the regional abundance, depth distribution and spatial configuration of anchoveta in early December 2008 and 2009 (Boyd et al. 2015a,b; Fig. 1). In 2008, anchoveta was relatively abundant, broadly distributed and shallow throughout the survey area. In contrast, in 2009, anchoveta was more spatially concentrated, with few areas where fish were relatively abundant and shallow, mostly near shore.

One hundred Bayesian posterior predictions of the abundance and depth distribution of anchoveta in each grid cell were generated based on acoustic survey data for 2008 and 2009 (Boyd et al. 2015a,b). Eight sets of 100 simulated prey fields were then...
constructed from the Bayesian posterior predictions, representing the eight possible combinations of high or low regional abundance with shallow or deep depth distributions and broad or concentrated spatial configurations (see Appendix S2 for further details).

Central place foragers

We ran the IBFM separately for Peruvian Boobies and Guanay Cormorants. Differences in the representation of the two species were restricted to decision rules relating to commuting vs. looping behaviours, patch selection and satiation time (see below).

In this study, each simulation represents a single day during the breeding season. Both Peruvian Boobies and Guanay Cormorants are diurnal foragers and most breeding adults return to the nest by dusk. The population density was set to 60 birds departing the colony per model hour, with each bird making a single foraging trip. Each IBFM simulation was allowed to run for three model hours; performance indicators were then recorded for the 60 birds that departed in the fourth model hour. Boyd et al. (2016) found that these simulation parameters were sufficient for the accumulation of social information on the distribution of prey.

Behaviour strategies and modes. On initialization, each individual decides whether to follow one of two behavioural strategies: a commuting or looping trajectory. Birds on commuting trips forage at a single patch, whereas birds on looping trips forage at two patches (see Weimerskirch et al. 2010; Boyd et al. 2016). The sequence of each foraging trip is summarized in Fig. 2.

Decomposition processes. Only broad-scale movement processes are modelled explicitly, based on analysis of GPS tracks for Peruvian Boobies (Boyd et al. 2014). GPS data for Guanay Cormorants indicated similar flight speeds, so we used the same movement parameters for both species to facilitate comparison.

Information and navigation. Modelled individuals have no prior information about the location of prey patches in this study as patches were assumed to be unpredictable and ephemeral. However, departing birds may use the direction of returning birds as an indicator of the likely direction of accessible prey and orient their outbound headings accordingly. Individuals in outbound or broad-scale search mode may also use the feeding behaviour of other birds to provide information on the location of accessible prey, leading to local enhancement (see Boyd et al. 2016 for further details).

Decision rules. Commuters vs. loopers. In the IBFM, both species determine whether to follow a commuting or looping trajectory based on a single Bernoulli trial prior to departure. The probability of a commuting trip was set at 0.40 for Peruvian Boobies and 0.60 for Guanay Cormorants (Weimerskirch et al. 2010).

Patch selection. On entering a new grid cell when in outbound travel, broad-scale search, or directed search mode, each bird decides whether to switch to feeding mode through a Bernoulli trial based on the abundance and depth distribution of prey within the cell. For both species, Boyd et al. (2015a) estimated the probability of patch selection, \( p_{\text{patch,}i} = \frac{\exp(q_{i})}{\exp(q_{i}) + 1} \), in each cell \( i \) from the observed probability than an individual made at least one dive in a cell as a function of the relative abundance of prey in the upper water column. Following this analysis, the probability of patch selection was parameterized for Peruvian Boobies in the IBFM as follows:

\[
\eta_{i} = -3.35 + 3.68 \cdot r_{i}^{0.03} \cdot P(d_{i} < 7.41)
\]

and for Guanay Cormorants as follows:

\[
\eta_{i} = -5.02 + 4.90 \cdot r_{i}^{0.02} \cdot P(d_{i} < 9.17)
\]

where \( r_{i} \) refers to anchoveta densities and \( d_{i} \) to the upper depth limit of anchoveta aggregations. The differences in parameter estimates for the two species indicate that Peruvian Boobies were more likely than Guanay Cormorants to dive at all levels of abundance when anchoveta was close to the surface. In contrast, Guanay Cormorants were more likely than Peruvian Boobies to dive when prey was deeper (see Fig. 3; Boyd et al. 2015a). Figure 4 shows sample distributions for the probability of patch selection for Peruvian Boobies and Guanay Cormorants given foraging conditions in 2008 and 2009.

Satiation time. Satiation time (i.e. the total amount of time spent in feeding mode prior to switching to homebound mode) was fixed at 23 min for Peruvian Boobies and 54 min for Guanay Cormorants, based on the average total time spent in grid cells where diving occurred at Grupo Pescadores in 2008 (Boyd et al. 2015a).

Depletion

The IBFM differs in one major respect from the model described by Boyd et al. (2016) – for this study, we incorporated a mechanism to account for depletion of prey by seabirds and, indirectly, by other natural predators and industrial fisheries, during the course of each simulation. Each time a forager switches to feeding in a grid cell, a fixed amount of prey biomass is removed from the upper surface waters, and the abundance and depth distribution of prey in the cell are recalculated. As true depletion rates are unknown, we ran the model without depletion and with depletion set at two rates differing by two orders of magnitude. The low depletion rate approximated the effects of the entire seabird colony and other natural predators, and the high rate approximated the entire seabird colony, other natural predators and the industrial anchoveta fishery at the time of the field study (see Appendix S3 for further details).
Performance indicators

The IBFM is based on the assumption that CPFs seek to minimize foraging trip duration subject to the constraint of satisfying energy needs (Ydenberg 2007; Boyd et al. 2014). This leads to two main performance indicators: foraging trip duration and foraging success (or, conversely, failure rates). Here, a simulated seabird was considered successful if it succeeded in locating prey at one or more patches and returning to the colony within 6 h of departure to allow its mate to undertake a trip of similar duration within daylight hours.

Relative importance of different aspects of prey availability

The relative importance of the three independent variables (i.e., regional abundance, depth distribution and spatial configuration) for predicting failure rates was assessed using random forests. Random forests are ensembles of classification or regression trees and are more robust than single trees. Each tree is grown independently using a random subsample of the available data and available predictors (Breiman 2001). For each species and each depletion rate, 2000 regression trees were grown, with the failure rate for each simulation as the response variable, using the randomForest package in R (Liaw & Wiener 2002). Given the limited number of predictors, the number of variables subsampled at each node was set to 1, so that the selection order of predictors in each tree was essentially random. The significance of the importance metric was tested against results for 100 replicates of each tree using the R package rfPermute (Archer 2016).

A similar approach was used to explore the relative sensitivities of each species to variation in prey availability; specifically, which aspects of prey availability are most important for predicting whether a failed individual is a Peruvian Booby or a Guanay Cormorant. Individual failures were extracted for both species and all three depletion rates and combined into a single data set; 2000 classification trees were grown with species as the binary response variable and the depletion rate as an ordered factor. The number of variables subsampled at each node was set to 2, given the increase in predictor variables. The significance of the importance metric was again tested using 100 replicates of each tree.

Results

IBFM simulation results compared to field data

Comparison of IBFM simulation results with observed data for 2008 indicated similar foraging trip durations and maximum distances under the high depletion rate, especially for Guanay Cormorants (Table 1). Insufficient field data were collected for comparison in 2009 because of low numbers of breeding adults at Grupo Pescadores and poor apparent breeding motivation.

Effects of changes in prey availability

Changes in overall foraging conditions

For both Peruvian Boobies and Guanay Cormorants at all three depletion rates, failure rates were higher for

Table 1. Foraging trip statistics for Peruvian Boobies (a) and Guanay Cormorants (b): observed data from GPS tracks collected at Grupo Pescadores in early December 2008 and IBFM simulation results based on foraging conditions in early December 2008 and 2009 (standard deviation shown in parentheses)

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<td>Observed</td>
<td>No depletion</td>
<td>Low depletion</td>
<td>High depletion</td>
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<td>(a) Mean failure rate (%)</td>
<td>NA 0.0-0.23</td>
<td>0.1-0.33</td>
<td>0.1-0.40</td>
<td>NA 0.3-0.64</td>
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<td>Mean foraging trip duration (min)</td>
<td>65 (28-75)</td>
<td>38 (13-47)</td>
<td>42 (14-76)</td>
<td>53 (21-56)</td>
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<td>Mean maximum distance from colony (km)</td>
<td>20.9 (9.02)</td>
<td>7.7 (4.28)</td>
<td>9.0 (4.71)</td>
<td>12.6 (6.67)</td>
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<td>(b) Mean failure rate (%)</td>
<td>NA 0.1-0.33</td>
<td>0.2 (0.90)</td>
<td>0.2 (0.48)</td>
<td>NA 0.8 (1.53)</td>
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<tr>
<td>Mean foraging trip duration (min)</td>
<td>83 (33-61)</td>
<td>69 (14-64)</td>
<td>73 (17-30)</td>
<td>85 (23-36)</td>
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<tr>
<td>Mean maximum distance from colony (km)</td>
<td>15.6 (5.71)</td>
<td>7.6 (4.85)</td>
<td>8.8 (5.31)</td>
<td>13.0 (7.30)</td>
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simulations based on 2009 foraging conditions compared to 2008 (Table 1). Foraging trip durations were also longer and the maximum distance from the colony was farther for simulations based on 2009 foraging conditions with high depletion rates. However, under lower depletion rates, successful birds achieved similar trip durations and maximum distances in 2009 as in 2008. This likely reflects the specific spatial configuration of anchoveta in 2009, with some prey available close to the colony despite low regional abundance and deeper prey (Fig. 1).

Failure rates were more sensitive than foraging trip durations to changes in foraging conditions, so we focused the remainder of our analysis on failure rates as the key performance indicator in the IBFM. Failure rates were more sensitive to the depletion rate when foraging conditions were poor, as in 2009 (Table 1). For both species, mean failure rates were similar between low and high depletion rates under 2008 foraging conditions, but there was a nearly 10-fold difference under 2009 foraging conditions.

**Changes in different aspects of prey availability**

The percentage of out-of-sample variation explained by random forests was greatest when failure rates were highest: 28.43% for Peruvian Boobies and 32.26% for Guanay Cormorants under the high depletion rate (Fig. 5).

The depth distribution of prey was identified as the most important predictor of failure rates and was significant \((P \leq 0.05)\) for both species and all three depletion rates (Fig. 5). Failure rates were consistently higher when prey was distributed more deeply, as in 2009 (i.e., D09, Fig. 6).

Regional prey abundance was identified as the second most important predictor and was significant \((P \leq 0.05)\) in all cases except for Peruvian Boobies in simulations with no depletion (Fig. 5). Failure rates were highest when low abundance was combined with deep prey distributions (i.e., A09.D09, Fig. 6). For both species, the relative importance of abundance increased with depletion rates and was similar to the importance of the depth distribution at the high depletion rate.

Spatial configuration was generally assessed as the least important of the three aspects of prey availability considered here, except for Peruvian Boobies in simulations with no depletion (Fig. 5). Nevertheless, it was significant \((P \leq 0.05)\) in all cases except for Guanay Cormorants in simulations with no depletion. The spatial configuration in simulations based on 2009 data, when prey was more spatially concentrated, generally favoured foraging success (i.e., C09, Fig. 6).

**Variation by species**

The most important variables for predicting whether a failed individual was a Peruvian Booby or a Guanay Cormorant were regional abundance followed by the depletion rate, with both variables significant at the 0.05 level (Fig. 7). The probability of a failed bird being a Guanay Cormorant was higher when regional abundance was low, especially under high depletion rates (Fig. 8). However, the out-of-sample classification error rate indicated only slight improvement on the expected error rate based on random assignment and class sizes (0.413 vs. 0.439).

**Discussion**

**EFFECTS OF CHANGES IN PREY AVAILABILITY**

Our research goal was to strengthen understanding of the effects of changes in abundance and distribution of prey

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**Fig. 5.** Relative importance of variables for predicting failure rates as measured by the mean decrease in accuracy using Random Forest, given (a) no depletion, (b) low depletion and (c) high depletion rates. Bars shaded grey are significant at the 0.05 level. VE refers to variation explained in each random forest.

on the foraging success of seabirds and other CPFs. IBFM simulation results based on foraging conditions in 2008 were reasonably consistent with observed seabird data under the high depletion rate, especially for Guanay Cormorants (Table 1). The difference between observed and modelled foraging trip statistics for Peruvian Boobies may reflect additional patch selection factors, not revealed in the acoustic survey data, such as the presence of sub-surface predators that drive prey closer to the surface. These results indicate that the IBFM provides a useful basis for investigating the effects of changes in prey availability and that the high depletion rate is a plausible approximation of combined depletion by seabirds, other natural predators and the industrial fishery. The industrial anchoveta fishery was active in the study area in early December 2008.

Changes in prey availability

Our first hypothesis was that seabird foraging success depends on the depth distribution and spatial configuration of prey, as well as prey abundance. The change in depth distribution of anchoveta off Grupo Pescadores between 2008 and 2009 was the primary factor influencing the foraging success of Peruvian Boobies and Guanay Cormorants in the IBFM, demonstrating that depth distribution of prey can have a greater effect on the biomass of prey accessible to surface foragers than regional abundance. Increasing regional abundance from 2009 to 2008 levels had a greater positive effect when prey was more deeply distributed, but was still insufficient to offset entirely the effects of reduced accessibility. Regional abundance was most important at the high depletion rate, suggesting that Peruvian Boobies and Guanay Cormorants may be able to cope with substantial interannual variation in regional prey abundance if low prey abundance is not combined with substantial fishing pressure. The spatial configuration of the prey field was generally less important than depth distribution and regional abundance. This may reflect the specific spatial configurations included in this analysis: broadly dispersed, as in 2008; or more spatially concentrated but with some accessible prey close to the colony, as in 2009. We can hypothesize that spatial configuration would have been more important had no prey been accessible close to the colony.

Our finding that prey accessibility is important is consistent with previous research on the population dynamics of seabirds in the northern HCS using ecosystem models. Ecosystem models based on forage fish abundance but not accessibility have performed well overall, but underpredict declines in seabird populations during severe oceanographic anomalies associated with low prey abundance and deeper prey distributions (e.g. Jahncke, Checkley & Hunt 2004; Taylor et al. 2008). In comparison, a model based on prey accessibility as a function of the horizontal and vertical spatial overlap between seabirds and anchoveta (Muck & Pauly 1987) was more effective at tracking the population response of seabirds to the severe 1957-8 El Niño event.

Variation by species

Our second hypothesis was that the sensitivity of Peruvian Boobies and Guanay Cormorants to changes in various aspects of prey availability differs because of differences in patch selection patterns. Both species exhibited increased IBFM failure rates when prey was deeper and less abundant, but Guanay Cormorants were more sensitive than Peruvian Boobies to reductions in abundance, especially at high depletion rates. There are limited differences in the way the two species were modelled – differences in sensitivity are most likely attributable to differences in patch selection patterns estimated from observed data (Fig. 3; Boyd et al. 2015a). This analysis indicated that Guanay Cormorants are less likely than Peruvian Boobies to select a patch where the accessible biomass is low. When prey is distributed through the water column, a higher proportion is accessible to the deeper-diving cormorants than the shallow-diving Peruvian Boobies. However, when regional abundance is low and further reduced by depletion such that prey biomass is low throughout the water column, Guanay Cormorants are expected to have lower rates of patch selection and consequently foraging success than Peruvian Boobies. These results may help to explain the differences in observed population trajectories between Peruvian Boobies and Guanay Cormorants since the mid-1950s.

An important caveat is that patch selection patterns were based on analysis of 2008 data when the distribution of anchoveta was relatively shallow. Several researchers have found that deep divers are less vulnerable to oceanographic variation because they can access deeper prey (e.g. Oedekoven, Ainley & Spear 2001). Guanay Cormorants may have adapted to deeper prey distributions in 2009 by increasing their probability of patch selection where prey was more deeply distributed. Adaptive foraging strategies may be critical to species’ future persistence in the context of fisheries and global change. With data for a range of foraging conditions, the IBFM could be used to assess the effectiveness of adaptive foraging strategies in maintaining foraging success in the context of natural variation in prey availability combined with fisheries and long-term climate change.

Performance indicators

Avoiding failure may be more important than minimizing foraging trip duration (see Caraco 1980). In the IBFM, mean failure rates were more sensitive to changes in prey depth and abundance than foraging trip duration and maximum distance from the colony. IBFM results, thus, highlight the importance of collecting data on foraging success in addition to more conventional indicators, such as foraging trip duration and maximum distance. However, foraging success is easier to define and measure in the IBFM than in the field. In practice, it may be best characterized as a spectrum from success in meeting all the energy requirements of adults and chicks to failure (see Grémillet et al. 2016). With additional information on prey capture and energy expenditure, the IBFM could be coupled with an individual-based energetics model (e.g., Langton, Davies & Scott 2014) to provide a tool for investigating the energetic implications of variation in prey availability (cf. Boyd et al. 2014; Grémillet et al. 2016). This would provide a more integrated approach to analysis of variation in seabird foraging strategies in response to variation in prey availability (Wilson & Vandenberghe 2012).
MANAGEMENT IMPLICATIONS

Most previous analyses of the effects of fisheries on prey availability and seabird populations have focused on stock abundance only (e.g. Cury et al. 2011; Smith et al. 2011). Our results demonstrate that changes in accessibility can be the major factor driving prey availability and, therefore, need to be incorporated as an explanatory variable in analysis of fisheries effects.

Aspects of prey availability vary in their susceptibility to management. In the northern HCS, for example, the depth distribution and spatial concentration of anchoveta are generally explained by oceanographic conditions beyond management control, such as the expansion or contraction of the cold coastal waters that provide suitable anchoveta habitat, whereas regional abundance is influenced by a combination of oceanographic conditions and broad-scale fisheries management (Chavez et al. 2008). In contrast, fisheries removals (i.e. depletion associated with fisheries) are more directly determined by fisheries management.

Our analysis indicates that a broad-scale fisheries management strategy that succeeds in maintaining sufficient levels of regional prey biomass to support dependent predators could have a substantial positive effect on seabird foraging success, especially when oceanographic conditions reduce the accessibility of prey to surface-foraging seabirds. This type of strategy, often implemented through a biomass threshold or constant escapement rule, is used by the Commission for the Conservation of Antarctic Marine Living Resources to manage Antarctic krill Euphausia superba (Dana) and by the Government of Peru to manage anchoveta since 2001 (Pikitch et al. 2012).

However, given that natural variation is a major driver of the abundance and distribution of forage fish (Chavez et al. 2003; Robinson, Butterworth & Plaganyi 2015), this type of management strategy may still need to be supplemented by targeted reductions in fishing effort in areas surrounding seabird colonies (e.g. Daunt et al. 2008; Sherley et al. 2015) during critical periods when regional abundance is low and/or oceanographic conditions reduce the accessibility of prey to surface-foraging seabirds. For both Peruvian Boobies and Guanay Cormorants, Table 1 indicates a 10-fold difference in failure rates between the low and high depletion rates when foraging conditions were poor as in 2009.

The IBFM as a tool for management strategy evaluation

The IBFM provides a spatially explicit framework for assessing the effects of fisheries on the foraging success of seabirds and other CPFs and evaluating the likely effects of a range of proposed fisheries management strategies, such as biomass thresholds, permanent spatial closures or flexible time-area closures. The IBFM is adaptable and could be reconfigured for other species and systems where effective management responses for safeguarding prey availability to seabirds are in question, such as the African Penguin Spheniscus demersus (Linnaeus) in the Benguela Current system (see Cherry 2014 and references therein). The effects of fisheries would be best addressed by modelling the fishing fleet explicitly over the course of the fishing season, for example, as additional CPFs operating from local ports. Vessel-monitoring system data could provide information on behaviour modes, movement patterns and decision rules, similar to the seabird data used here. Fishing vessels would then interact with seabirds or other CPFs through the prey field. The effectiveness of proposed management strategies will also depend on the movement patterns of forage fish – management strategy evaluation would be greatly strengthened by incorporating information (or plausible hypotheses) on the movement patterns of forage fish.

Climate warming and associated oceanographic changes may also impact the foraging success of CPFs. In developing the IBFM, initial foraging conditions were taken as given, based on acoustic survey data for forage fish. However, there is potential to couple the IBFM with models that predict the abundance and distribution of forage fish from oceanographic models to investigate the possible effects of climate change and evaluate proposed management responses (e.g. Brochier et al. 2013). The IBFM could then be run over simulated prey fields representing various climate scenarios to investigate the possible effects of climate change on the foraging success of seabirds and other CPFs. The ultimate goal is to provide a tool to support assessments of the effectiveness of proposed fisheries management strategies at safeguarding prey availability to CPFs that compete with fisheries in the context of environmental variability and climate change.

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Data accessibility

IBFM pseudocode and R code are provided in Appendix S1.

References

