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Best practices for assessing forage fish fisheries-seabird resource competition

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ABSTRACT

Worldwide, in recent years capture fisheries targeting lower-trophic level forage fish and euphausiid crustaceans have been substantial (~20 million metric tons [MT] annually). Landings of forage species are projected to increase in the future, and this harvest may affect marine ecosystems and predator-prey interactions by removal or redistribution of biomass central to pelagic food webs. In particular, fisheries targeting forage fish and euphausiids may be in competition with seabirds, likely the most sensitive of marine vertebrates given limitations in their foraging abilities (ambit and gape size) and high metabolic rate, for food resources. Lately, apparent competition between fisheries and seabirds has led to numerous high-profile conflicts over interpretations, as well as the approaches that could and should be used to assess the magnitude and consequences of fisheries-seabird resource competition. In this paper, we review the methods used to date to study fisheries competition with seabirds, and present "best practices" for future resource competition assessments. Documenting current fisheries competition with seabirds generally involves addressing two major issues: 1) are fisheries causing localized prey depletion that is sufficient to affect the birds? (i.e., are fisheries limiting food resources?), and 2) how are fisheries-induced changes to forage stocks affecting seabird populations given the associated functional or numerical response relationships? Previous studies have been hampered by mismatches in the scale of fish-eries, fish, and seabird data, and a lack of causal understanding due to confounding by climatic and other

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ecosystem factors (e.g., removal of predatory fish). Best practices for fisheries-seabird competition research should include i) clear articulation of hypotheses, ii) data collection (or summation) of fisheries, fish, and seabirds on matched spatio-temporal scales, and iii) integration of observational and experimental (including numerical simulation) approaches to establish connections and causality between fisheries and seabirds. As no single technique can provide all the answers to this vexing issue, an integrated approach is most promising to obtain robust scientific results and in turn the sustainability of forage fish fisheries from an ecosystem perspective.

1. Introduction

Industrial fisheries for forage fish, and to a lesser extent euphausiid crustaceans, have recently increased to meet growing demands for fish meal and nutritional sources for humans (Alder et al., 2008; Tacon and Metian, 2009; Nicol et al., 2012). Landings of forage fish and euphausiids, combined, have averaged ~20 million metric tons (MT) annually since the mid-1990s (Smith et al., 2011); forage fish stocks in this estimate include herring (*Clupea* spp.), sardines (*Sardinops* spp.), anchovies (Engraulidae), capelin (*Mallotus villosus*), sandeels (Ammodytidae), and sauries (Scomberesocidae) (Table 1). Seabirds, marine mammals, and large predatory fish also rely on these forage stocks for sustenance (Cury et al., 2000), and therefore may be in direct competition with fisheries for food resources (Smith et al., 2011; Pikitch et al., 2014; Rountos et al., 2015). Indeed, apparent competition between fisheries and top marine predators has led to numerous recent high-profile conflicts over interpretations (e.g., Cherry, 2014) and what approaches could and should be used in assessing competition between fisheries and seabirds (Crawford, 2007; Cury et al., 2011), marine mammals (Mangel, 2010; Conn et al., 2014), and marine predators in general (Hilborn et al., 2017).

Concerns about if and how fisheries compete with seabirds, as well as attempts to document and manage this issue, date back to the 1930s. In one of the first comments made about seabird-fisheries competition and how to resolve it, Murphy (1936) proposed that areas closed to fisheries around Peruvian seabird colonies could reduce competition between the humans and seabirds that target anchoveta (*Engraulis ringens*). Schaefer (1970) subsequently estimated that, in the early 1960s, Peru's ~16 million seabirds consumed upwards of 2.5 million MT of anchoveta yearly, and suggested that both the fishery and birds were responsible for annual stock fluctuations. Notably, climatic variations and effects on the fish were not considered by Schaefer at the time, although by the early 1970s, anchoveta stock fluctuations relative to major El Niño events became well known (e.g., Parrish et al., 1983). Subsequently, it was shown that the moderately strong El Niño event of 1972–1973 led to a decline in anchoveta productivity, and that the fishery and seabird population collapses at that time were associated with this climatic event (Pauly and Tsukayama, 1987; Jahncke et al., 2004).

In the United States (U.S.), concern about potential detrimental impacts of fisheries on seabirds also rose in the early 1970s when the California brown pelican (*Pelicanus occidentalis occidentalis*) was listed as endangered. Although the pelican's demise was principally related to egg-shell thinning due to use of organochlorine pesticides (DDT, Anderson et al., 1975), the primary prey of pelicans in California at the time, northern anchovy (*Engraulis mordax*; Szoboszlai et al., 2015), was targeted by fisheries operating in proximity to southern California pelican colonies. This take of prey important for the pelican was thought to decrease nesting success and hamper the recovery of the species (Anderson et al., 1982). Indeed, concerns for the recovery of the pelican resulted in the first inclusion of the food resource needs of a seabird population in a U.S. Fishery Management Plan (FMP and amendment; PFMC/NMFS, 1978, 1983). In brief, the Northern Anchovy FMP control rule included a cutoff parameter, below which directed harvest was not allowed; this cutoff was set at 300,000 MT, and was informed, in part, by the relationship between brown pelican breeding success and regional anchovy abundance (PFMC/NMFS, 1983). This control rule was supported by recreational fishers concerned with game fish in the region that also relied on anchovy for sustenance. More generally, seabird-fisheries competition became a global concern in the 1970s and 1980s. Widespread declines in seabird populations were apparently related to the expansion (and in some cases collapse) of large-scale industrial fisheries for anchovies and sardines, as well as shifts in fisheries from groundfish to small pelagics, such as sandeels, which were important seabird food (Furness, 1978, 1982; Duffy, 1983; MacCall, 1984). The literature on seabird responses to fluctuations in food resources grew substantially at that time and is now diverse and substantial, covering aspects of seabird biology from foraging ecology to population biology (e.g., Cairns, 1987; Piatt et al., 2007). In addition to previous references, early evidence of seabird populations tracking changes in forage fish abundance came from southern Africa (e.g., Furness and Cooper, 1982; Crawford et al., 1983), Peru (e.g., Duffy, 1983), and Norway (e.g., Vader et al., 1990). More often, however, changes in vital rates, as a proxy for population fluctuations, were attributed to changes in prey resource availability (e.g., Anderson et al., 1982 on brown pelicans off southern California; Monaghan et al., 1989 for Arctic terns (*Sterna paradisaea*) in the North Sea). Changes in food resources are hypothesized as the mechanism for large-scale breeding failures of central Pacific seabirds relative to the major climatic events, such as the El Niño event of 1982–1983 (Schreiber and Schreiber, 1984) and even long-term ocean warming (Veit et al., 1996). This voluminous and ever-growing ecological literature stands in stark contrast to a recent paper (Hilborn et al., 2017) in providing robust evidence that seabird populations respond to prey depletion, whether it is due to a fishery or via some other mechanism such as environmental change.

Fisheries targeting forage fish may be detrimental to seabirds by

Table 1

Global landings (metric tons) of forage fish fisheries, 2010–2015, to illustrate the potential for fisheries-seabird resource competition. Data were obtained from the Global Capture Production Database (FAO, 2016).

Species	2010	2011	2012	2013	2014	5-year average
Krill, planktonic crustaceans	215,175	181,010	188,147	239,950	316,408	228,138
Herrings, sardines, anchovies	17,269,000	21,164,496	17,569,534	17,600,048	15,215,458	17,763,707
Atlantic sandeels	423,209	443,604	107,577	284,138	270,401	305,786
Pacific sand lance	237,938	187,559	175,892	161,949	153,433	183,354
Atlantic saury	7,436	5,628	15,329	8,547	1,560	7,700
Pacific saury	432,372	458,954	460,961	428,390	628,569	481,849
Capelin	506,897	853,449	992,491	763,948	282,833	679,924
Total	19,092,027	23,294,700	19,509,931	19,486,970	16,868,819	19,650,489

reducing the abundance or density of prey availability below *thresholds* necessary for successful foraging, offspring provisioning, and survival; indeed, empirically-derived thresholds in numerical response curves have been demonstrated in a global meta-analysis of seabird breeding success (Cury et al., 2011), as well as adult survival (Robinson et al., 2015). To date, however, few studies on seabird-fisheries resource competition have provided unequivocal results that fisheries are responsible for the resource limitations that affect seabird population parameters. A fundamental (and growing, owing to climate change) challenge to establishing strong connections between fisheries impacts on seabirds via prey limitation (i.e., localized prey depletion) is the fact that most forage populations also vary naturally on orders of magnitude in relation to climatic factors that affect stock size, recruitment, distribution, and spatial organization (Baumgartner et al., 1992; Chavez et al., 2003; Trivelpiece et al., 2011; Checkley et al., 2017; Hilborn et al., 2017). Another confounding factor concerns the effects of fisheries for mammals or large predatory fish in the same regions of interest. Fisheries targeting large predatory fish or mammals may be beneficial to seabirds by reducing the abundance of potential competitors, and 'releasing' forage populations from predation pressure (Furness, 2002). Taken together, climatic and other ecosystem factors may operate to dampen or amplify competitive interactions between fisheries and seabirds, but understanding these details is difficult. The complexity of the issue has been well documented in the North Sea, where both changes in ocean climate (Frederiksen et al., 2004) and the lack of consumption of forage fish by large predatory fish (Furness, 2002) appear to have influenced fisheries competition with seabirds. These complexities make documenting causal relationships between forage fish fisheries and seabirds very difficult.

As the science and understanding of potential fisheries competition with seabirds has evolved, it is now possible and timely to review and evaluate the methods used to investigate fisheries resource competition with seabirds, and present good practices for future studies. Our objectives are to 1) review the ecological theory underpinning competition and approaches available to investigate competitive interactions between fisheries and seabirds, 2) review and evaluate previous approaches and methods to study and document seabird-fisheries competition across the globe, and 3) present a unified approach on best practices to obtain unambiguous results in the future. While fisheries bycatch and fisheries discards are important fisheries-seabird interactions requiring management action, we consider these issues outside the scope of this paper. We conclude that an integration of approaches is needed to investigate how fisheries competition may be affecting seabird populations.

2. Resource competition and seabird ecology

Interspecific competition may come in the form of *exploitative* or *interference* (often conceived of as behavioral) competition (Fig. 1). Most studies on seabird-fisheries competition have implicitly considered the mechanism of competition to be exploitative, whereby one group (the fisheries) outcompetes another group (one or more seabird species) for a limited resource; usually the mechanism is thought to be localized prey depletion causing food limitation (Daunt et al., 2008; Bertrand et al., 2012; Santora et al., 2017). An important assumption behind this mechanism is that food resources are limited (Schoener, 1982), something that is rarely stated or tested.

Alternatively, interference competition, whereby one group prevents another from using a resource, has been a less well-studied mechanism of fisheries-seabird competition. Interference competition may play an important role in altering the availability of prey to seabirds if fishing activities affect the horizontal and vertical distribution or the aggregative behavior of the forage species (Garrison and Link, 2000; Haugland and Misund, 2011). As an example, fisheries impacts on sardines in South Africa may have played a role in the redistribution of sardine from the Western Cape to Agulhas Bank region (Coetzee et al., 2008), with associated impacts on seabirds, notably African penguins (*Spheniscus demersus*) (Table 2, Crawford et al., 2015). There is also evidence from the North Sea of interference competition. In this system, only surface-feeding black-legged kittiwakes (*Rissa tridactyla*) were affected by the sandeel fishery; diving species, such as common murre (*Uria aalge*) and European shags (*Phalacrocorax aristotelis*) showed no impacts, indicating that the fishery may have caused a redistribution of sandeels to deeper in the water column where they were unavailable to kittiwakes, but still available to the deeper diving shags and murres (Frederiksen et al., 2008).

In addition to diving depth, the strength of competitive interactions between fisheries and seabirds depends on many factors related to seabird ecology, including foraging ambit, degree of prey specialization, body size, and energetic requirements during breeding, to name a few. Seabirds are diverse taxa, and some species are more susceptible to localized prey depletion than others (Furness and Tasker, 2000; Piatt et al., 2007). Stronger competitive interactions are hypothesized for species with specialized diets, small body mass (i.e., higher energetic constraints), and limited foraging range. Seabird foraging ranges are most restricted during the breeding season when birds operate as central place foragers from colonies (Orians and Pearson, 1979; Boyd et al., 2015, 2016). Additionally, seabird energetic needs are highest when they are provisioning food for developing offspring, or before or after molt, so in these critical periods seabirds are most likely to experience detrimental effects from fisheries if they deplete prey resources.

Last, it is also well known that seabird population dynamics are more sensitive to changes in adult survival or juvenile recruitment than breeding productivity (Croxall and Rothery, 1991; Nur and Sydeman, 1999; Russell, 1999). Thus, generally speaking, competition with fisheries that impacts prey availability during the period in which adult survival or juvenile recruitment to adult age classes is of the greatest relevance to population dynamics (Sherley et al., 2015, 2017). However, breeding success may have similar population impacts to reductions in survival or recruitment if prey depletion is chronic, as could be

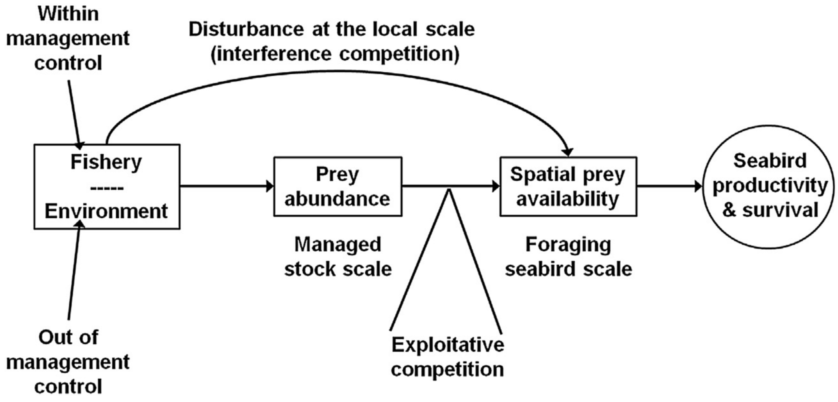

Fig. 1. Flow chart of fisheries − seabird competition interactions.

Table 2
Summary of ecosystems, forage fish stocks, seabird species studied and approaches taken to investigate fisheries-seabird competition. See Supplemental Materials for case histories describing these systems in more detail.

Ecosystem	Fish stocks assessed	Seabird species studied	Observations	Numerical models	Experiments
North Sea	Sandeel	Arctic skua Black-legged kittiwake Great skua Arctic tern Northern gannet Common guillemot European shag Atlantic puffin	X		X
Benguela	Sardine Anchovy	African penguin Cape cormorant Cape gannet	X	X	X
California	Sardine Anchovy Rockfish	Puffins Cormorants Marbled murrelets Brown pelican Other misc. species	X	X	
Humboldt	Anchoveta	Guanay cormorant Peruvian booby Peruvian pelican Humboldt penguin	X	X	X

possible with long-term fisheries impacts on forage stocks (Cury et al., 2011; see also Gaillard and Yoccoz, 2003).

3. Approaches used to date

To date, various approaches have been used to test the hypothesis that fisheries and seabirds compete for limited food resources (Table 2). Observational approaches include time series studies employing correlations and statistical models to link observed changes in fisheries landings, forage stocks, and seabird population parameters (e.g., Anderson et al., 1982; Furness and Tasker, 2000; Frederiksen et al., 2004; Field et al., 2010; Cury et al., 2011; Sherley et al., 2013). Experimental approaches include numerical simulations and field-based fisheries manipulations. Numerical experiments include static and dynamic bio-energetic, mass-balance, and ecosystem experiments of fisheries-forage-seabird relationships relative to variation in landings (Furness, 1978; Jahncke et al., 2004; Smith et al., 2011; Kaplan et al., 2013; Pikitch et al., 2014). Field-based fisheries manipulations typically involve time-area closures (and rarely openings) to measure effects on central-place foraging seabirds (and mammals) operating from colonies (e.g., Daunt et al., 2008; Frederiksen et al., 2008; Mangel, 2010; Pichegru et al., 2009, 2010; Bertrand et al., 2012; Conn et al., 2014; Sherley et al., 2015). Interpretations from each of these approaches have been placed in context by retrospective analyses of climate, ecosystem, and fisheries responses (e.g., Francis and Hare, 1994; Furness, 2003).

To quantify approaches, we conducted a literature search to identify publications on seabird-fisheries competition from 1970 through 2015. We used two approaches to identify relevant studies. First, we conducted a systematic literature search on the Web of Science and Google Scholar databases using combinations of the search terms ‘seabird’, ‘mammal’, ‘fish’, and ‘competition’, but excluded the terms ‘bycatch’ and ‘discards’ to omit references related to fisheries bycatch or discards. Here, we report on the seabird references only. Second, we compiled a list of foundational research papers and searched within the citations of those papers for other papers of interest. Foundational papers were identified by participants of two workshops (see http://www.faralloninstitute.org/seabirdfisheries-competition). Forward and backward searches of the citations within the reference lists of these foundational papers revealed additional relevant publications. Third, we used Web of Science and Google Scholar to search for more recent publications that cited foundational research papers. The idea behind conducting a concurrent, but separate, search of Web of Science using the key words was specifically to avoid potential biases just based on a search of foundational paper citations. In short, our methodology included two parallel searching methods that should minimize any biases in using one approach or the other. The results of these two approaches and searches were then combined, repeated entries eliminated, and summarized. Subsequently, we screened the titles and abstracts and compiled a list that included only papers in which changes in prey abundance due to fisheries activities or natural causes (e.g., regime shifts) were explicitly linked to seabird responses, with discussion of the implications for fisheries. Each publication was then categorized as an observational study, a field experiment, a numerical simulation model, or a literature review. Reviews were defined as publications that did not include any original data or data analyses. The geographic regions reported in each publication were recorded.

We found 163 papers that reported on seabird-fisheries competition (see Supplementary Materials). Observational studies comprised the greatest percentage of papers (54%; Fig. 2). Reviews comprised the next largest proportion (26%, Fig. 2). Models (16%, Fig. 2) were a relatively small proportion of all studies in early years, but appeared with increasing frequency in the early 2000s. Field experiments were rare, representing only 4% of the papers. Notably, the seven papers that reported findings from field experiments were limited to the North Sea (UK) and the Benguela Upwelling System (South Africa). Overall, most studies focused on the Atlantic Ocean (Fig. 3). Research on seabird-fisheries competition has tended to focus on regions of the world that support both large commercial fisheries for small pelagic fish and large seabird populations. This may explain why the literature is dominated by studies conducted in highly productive marine regions, such as the North Sea and the major upwelling systems of the world (Table 2). A gap in understanding may therefore exist in regions of the world with relatively small-scale fisheries and seabird populations, such as the tropics. Failure of numerical simulations or field experiments to provide clear results may have caused a small bias in this summary of the literature, but as most experimental approaches have been recently developed, we do not think publication bias is a significant factor in this assessment of the approaches used to date.

4. Strengths and weaknesses in approaches

Fundamentally, evaluating fisheries competition with seabirds involves two inter-related steps: 1) an assessment of fisheries effects on

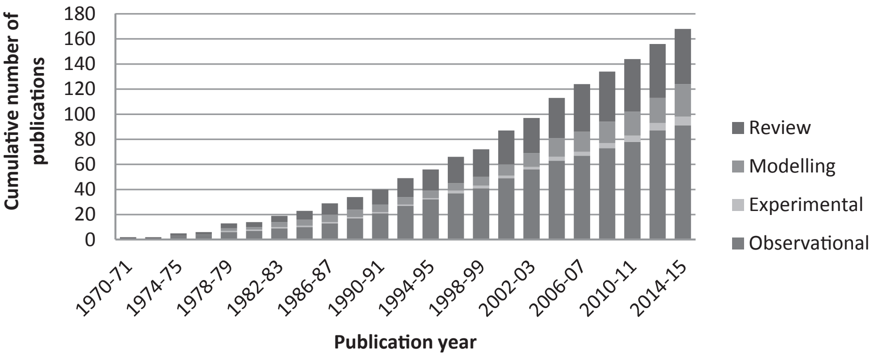

Fig. 2. Cumulative number of peer-reviewed publications reporting on seabird-fisheries competition by approach over a 45-year period (1970–2015). Observational studies included those presenting new data that also examined relationships between fisheries effort and seabird populations. Experimental studies were those that presented data from regions where fishery or seabird prey was altered and seabird metrics were measured. Modeling reports include those using numerical simulations. Review papers included all synthesis and discussion reports that did not present new data on the topic.

forage stocks within the foraging ambits of the birds to address the question: *are the fisheries causing localized prey depletion sufficient to affect seabirds?*; and 2) an assessment of how changes in forage availability within areas of interest are affecting seabird foraging and vital rates such as productivity, survival, and recruitment, to address the question: *how are the fisheries-related changes to forage stocks affecting seabird functional or numerical response relationships?* In this section, we review and discuss strengths and weaknesses in observational and experimental approaches in considering these fundamental questions (Table 3; see also case studies in the Supplementary Materials).

4.1. Observations

There are many strengths to the observational approach, and critically, some aspects of seabird-fisheries competition can only be documented using observations. For example, the form of the numerical relationships between prey abundance and seabird demography can only be established using long-term observations (Anderson et al., 1982; Cairns, 1987; Furness, 2007; Piatt et al., 2007; Field et al., 2010; Cury et al., 2011; Punt et al., 2016). Conceivably, experimental approaches could be used to establish functional relationships, but to date no experiments have been conducted for a long enough period to accomplish this (e.g., Sherley et al., 2013, 2015). Other key numerical response relationships based on observations have been developed. For example, Robinson et al. (2015) provide one of the few models of adult survival relative to prey availability. Observations have thus been used primarily to parameterize population dynamics models, and in conjunction with viability assessments (Sherley et al., 2015).

Knowledge of the form of numerical response relationships is relevant to design considerations and hypothesis testing for field experiments. For example, assuming a log-linear relationship, when prey availability is high, fisheries closure experiments would have a low probability of detecting effects on seabird breeding success. Moreover, hypothetical thresholds of prey abundance useful for establishing benchmarks for small pelagic fisheries (e.g., cutoff in harvest control rules), below which seabird production or survival may decline, can best be determined using observations. To date, within the time period of contemporary observations, studies demonstrate that seabird population parameters decline when prey abundance falls below 1/3 to 1/4 of maximum (often unfished) biomass (Cury et al., 2011; Robinson et al., 2015). These reference points are seemingly consistent with fisheries biomass targets of 25–40% of the unfished level (e.g., Hilborn, 2010). Observations also provide an opportunity to use long time series in an historical context to understand long-term impacts of fisheries on food webs and indirect (e.g., top-down) effects on seabird food resources (Ainley and Lewis, 1974; Furness, 2002, 2003). Finally, observations of environmental and ecosystem conditions are needed for numerical experiments and field manipulations. In comparison with field experiments, observations can be relatively simple to obtain, but they may be more expensive than numerical simulations.

The main drawback to the observational approach is that long time series are needed, generally ~15 years (see Cury et al., 2011 Supplemental Material) before most fisheries-fish-seabird interactions can be modeled statistically, and due to lack of controls and appropriate data in many cases, causal relationships cannot be established with confidence. This is particularly relevant to efforts to document seabird-fisheries competition since the entire range of environmental conditions and forage fish stock and seabird abundances are almost impossible to observe. Furthermore, effects of fisheries may be most noticeable at the low end of local forage stock abundance, and/or when seabird populations have not been reduced. Observational studies are also limited by data quality and there may be significant mismatches between seabird and fisheries data, which are often not collected by the same investigators and for the same reasons. Efforts to enhance the scale of observations, especially for fisheries and fish data, can be scientifically difficult and prohibitively expensive. The use and importance of multiple forage species is another complexity that is infrequently studied (Abraham and Sydeman, 2006; Thayer and Sydeman, 2007; Smout et al., 2013). Most observational studies focus on a single species of prey, whereas the entire forage community may be important for seabird breeding success and other demographic traits.

As noted above, some seabird measurements (e.g., the number of chicks successfully fledged per breeding pair, chick growth rates, fledging weights) are easy to obtain, but key population parameters such as juvenile survival, breeding propensity, or adult survival may be missing, thereby limiting the capacity to model populations. Seabird population fluctuations often are also buffered by or lag changes in forage fish abundance (Duffy, 1983; Barrett and Krasnov, 1996; Anker-Nilssen et al., 1997; Jahncke et al., 2004; Crawford et al., 2011), such that it is impossible to establish relationships using simple correlations. Seabird populations integrate ocean and ecosystem conditions over

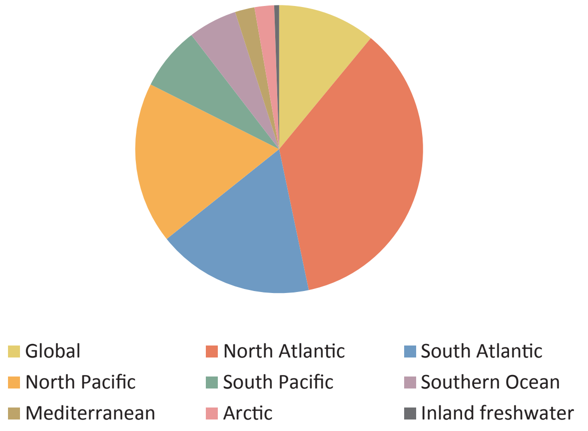

Fig. 3. The geographic range of the papers reporting on seabird-fisheries competition between 1970 and 2015. Each major ocean area listed includes multiple regions, such as the California Current and Bering Sea in the North Pacific. The global category includes papers that reported on multiple major ocean areas or did not specify a region.

Table 3
Select lessons learned from previous studies of fisheries-seabird competition (see Supplementary Materials case studies).

Effects of fisheries on forage availability

Lessons Learned	North Sea	Benguela	California	Humboldt	Representative reference
Forage fish fisheries may develop following collapse of fisheries targeting large predatory fish	X				Furness, 2002
Bottom up climatic and top-down predator-based factors may complicate interpretations of fisheries impacts on forage fish stocks	X	X	X	X	Furness, 2002 Ainley and Lewis, 1974
Forage fish fisheries may be international, complicating studies of fisheries impacts on forage fish stocks	X	X			Furness, 2002 Roux et al., 2013
Forage fish fisheries have explicit spatial dynamics that make impacts assessments difficult when forage fish stocks are measured at regional scales	X	X			Furness, 2002 Crawford, 2007
Sustained over-exploitation of forage resources may have unexpected long-term ecosystem effects		X	X		Roux et al., 2013
Production of juvenile (age-0) forage fish may be affected by fisheries targeting adult fish			X		Field et al., 2010
Closure experiments should be designed to account for variation in seabird ecology, including diet specialization and foraging ambit	X	X	X	X	Furness and Tasker, 2000
Local fisheries closures may enhance prey availability, even for highly mobile forage fish resources	X	X			Frederiksen et al., 2008 Pichegru et al., 2012
Fisheries impacts assessments indicate threshold responses in forage fish stocks during anomalous environmental conditions				X	

Effects of forage availability on seabird populations

Lessons Learned	North Sea	Benguela	California	Humboldt	Representative reference
Spatial and temporal variability of food resource availability need to be considered relative to understanding fisheries impacts on seabirds	X		X		MacCall, 1984 Furness, 2002
Linking seabird demography to changes in forage fish abundance is possible with long time-series, i.e. contemporaneous observational datasets of ≥ 10 years	X	X	X		Cury et al., 2011
Relationships between seabirds and forage nekton stocks are often non-linear, vary by species, and may be noisy and difficult to establish, especially for generalist species	X	X	X		Furness and Tasker, 2000 Cury et al., 2011
Seabirds that have evolved in highly dynamic ecosystems have developed life history and foraging strategies to cope with variability in food availability	X	X	X	X	Crawford et al., 2006
Depletion of forage resources below key ecological thresholds may cause seabird population declines		X	X		Crawford, 2007
Seabirds can recover from the effects of El Nino events within a few years, but recovery can be reduced when fisheries operate in the region of interest				X	Jahncke et al., 2004
In addition to prey abundance, modeling studies highlight the importance of prey accessibility (particularly prey depth distribution) to seabird numerical responses				X	Boyd et al., 2015
Fisheries closures may help to establish seabird-forage nekton numerical responses, but are complicated by climate and other factors	X				Frederiksen et al., 2004
Depending on life history characteristics, population-level responses to changes in forage availability may be density-dependent and lagged at various durations		X	X		MacCall, 1984
Forage fish data need to be matched to an area reflective of the ambit of central place foraging seabirds to study/establish forage fish - seabird numerical responses	X				Furness, 2002
Effects of other fisheries (e.g., discards) may complicate interpretations of seabird-forage numerical responses for species capable of using discard resources		X			Crawford et al., 2007
Simultaneous investigations of seabird species that do not compete with fisheries for prey may provide useful insights	X	X			Frederiksen et al., 2008
Seabird foraging success depends on a combination of fisheries effects and environmental conditions– these factors are difficult to disentangle				X	

long time scales, and are thus likely influenced by carryover and/or cumulative effects. Autoregressive models may be used to model seabird populations over long time scales (MacCall, 1984), but this approach has been rare.

Long-term funding for long-term observations is difficult to obtain from managers and policy-makers who focus on near real-time management applications of the data (Birkhead, 2014). Without long-term investments, data quality and reliability may be compromised, and methods may change, affecting the integrity of time series (Hughes et al., 2017). Existing observations may be difficult to access, especially spatial information on fisheries landings which are often viewed as proprietary, but these data are essential to understanding localized prey depletion and food resource limitation. Last, while communications to managers or policy-makers about observations may be more tractable than describing complex model outputs or the details of the field experiments, because observational studies often have no design, describing confounding variables is a challenge. All of these factors make using a purely observational approach to assessing fisheries-seabird competition difficult. Observations should be coupled with experiments to derive robust results and establish potentially causal relationships.

4.2. *Experiments*

The main strength of experiments (both numerical simulations and field manipulations) is that they can be used to alter variables in a controlled manner to measure interaction strengths and account for confounding factors. Numerical simulations can provide general insight on potential effects of uncontrolled environmental and ecosystem interactions, are relatively inexpensive, and may inform key design characteristics (e.g., time-area fisheries closures) for field-based fisheries and prey base manipulations. Arguably, though, only by the use of field experiments can current fisheries impacts on seabirds be causally demonstrated.

4.2.1. *Numerical simulations*

Various classes of numerical simulations have been used to infer *potential competition* between fisheries and seabirds; these models cannot demonstrate current competition, but they can provide great insight into potential dynamics of interest. These include: a) mass-balance models such as Ecopath (and the time-dynamic Ecopath with Ecosim, EwE) (Polovina, 1984; Christensen and Walters, 2004), b) bioenergetics models of prey consumption (e.g., Furness, 1978), c) individual-based models of foraging ecology and population dynamics (e.g., Langton et al., 2014; Schaub and Abadi, 2011; Boyd et al., 2016), and/or bioenergetics (e.g., Fort et al., 2011; Teixeira et al., 2014), and d) system-dynamics models (e.g., Weller et al., 2014, 2016) and end-to-end system models such as Atlantis (e.g., Fulton et al., 2011; Heath, 2012). Ecopath and Atlantis, the most well known of these frameworks, were designed primarily for studies of fisheries on fish communities, may not include seabirds as predators of interest, or may represent seabirds as a single functional group, which can be a problem as different seabird species in the same location are known to respond differently to fisheries-related prey depletions. Essington and Plagányi (2014) indicated that the majority of Ecopath models do not include sufficient taxonomic detail to capture seabird (and more generally predator) sensitivities to forage depletion. Ecopath and Atlantis models also use biomass (the basic currency of most fisheries studies) as the fundamental unit of measurement. As seabird population-level responses to prey depletion are often buffered and are always lagged to changes in prey populations (e.g., Crawford et al., 2014), biomass-based models may miss relationships that might have been evident when using seabird demographic or foraging traits that respond at higher frequencies. Despite these issues, Ecopath-type models have illuminated many important food web factors relevant to seabird-fisheries competition. For example, Ecopath-type models have shown that forage fish fisheries with higher trophic connectivity to predators (including seabirds) have greater impact on populations, and that forage groups of higher relative abundance (e.g., anchoveta) generally have larger influences on predator biomasses, though the latter was not always the case (Smith et al., 2011; Pikitch et al., 2014).

Kaplan et al. (2013) compared EwE and Atlantis simulations for effects of fishing on seabirds and other predators in the California Current. Although there were differences between the results from each model, the magnitude of modeled fisheries impacts on seabirds was small in this ecosystem. Kaplan et al. (2013) attribute this lack of effect to a mismatch in the spatial scale of the fisheries data and the scale at which competition between seabirds and the fisheries may occur (fishing was simulated coast-wide, while local prey depletion presumably would have had stronger impacts on the seabirds). In this study, seabirds were also aggregated into large functional groups, so species' sensitivities to fisheries impacts could have been masked. In a similar study comparing modeling frameworks, but over a global scale, Smith et al. (2011) also found that forage fisheries impacts on seabirds were generally small. However, Ecopath, Atlantis, and other food web models could be developed with higher taxonomic resolution (Koehn et al., 2016). Models of higher taxonomic resolution could be used in combination with analytical trade-off models (e.g., Essington and Munch, 2014), or used in dynamic modeling, to assess the impacts of specific forage fish fisheries on different seabird populations, but to date this has yet to be attempted. Ecospace, a spatially-resolved version of Ecopath with Ecosim (Walters et al., 1999), allows for more realistic modeling of the spatial overlap between prey, seabird predators, and fisheries. Thus, with increasing complexity, some of the more subtle effects of fisheries on seabirds could be revealed in Ecopath-type food web models, but with greater time and computational expense.

Ecosystem models of intermediate complexity (also known as 'MICE'; Plagányi et al., 2014) appear to have greater potential for linking fisheries, fish, and seabirds as they can be focused on species, populations, scale, and parameters of interest. While not referred to at the time as MICE, MacCall (1984) developed simulations of anchovy fisheries impacts on brown pelican population dynamics in California that included many of the same approaches codified by Punt and Butterworth (1995) and others more recently as MICE. Importantly, the study by MacCall (1984) remains one of the only studies to date to assess seabird population dynamics relative to the temporal autocorrelation of prey fields.

In testing for effects of sardine and anchovy fisheries on African penguin population parameters using MICE, Plagányi et al. (2014) found that penguin adult survival responded strongly to sardine depletion, but not to the biomass of sardine and anchovy combined. Hence this study demonstrated that forage fish fisheries targeting different forage species may influence seabird population parameters differently. In this case, penguin survival was related to one species of forage, sardine, rather than the forage community more generally. Sardines are thought to be disproportionately important to penguin survival due to their energy content (Sherley et al., 2013, 2014, 2017). Similarly, in the California Current, variability of sardine biomass is higher than that of anchovy, so increasing the proportion of sardine in pelican diet can lead to a pelican decline (Punt et al., 2016). MICE-type approaches also show that when seabird populations are already reduced, the effect of changing prey abundance can be highly unpredictable (Watters et al., 2013).

MICE and other less complex approaches (in comparison with mass-balance food web models) can also be used to test and demonstrate spatial components of seabird-fishery competition. For instance, Robinson et al. (2015) showed that the spatial distribution of South African sardine biomass had a larger impact on African penguin survival than prey depletion by the fishery. Thus, these models can also help provide information that may apply to spatial fisheries management strategies. Plagányi and Butterworth (2012) used a spatial multispecies model to test the impacts of various spatial harvest control rules of krill on predators, such as penguins in the Scotia Sea. Due to the central-place foraging nature of seabirds, the inclusion of spatial dynamics in models to test potential seabird-fishery competition is of the utmost importance. Finally, comparing fishing scenarios in the model to a no-fishing simulation may allow for the identification of the potential impacts of fishing without other confounding effects (Watters et al., 2013). Seabirds can be affected by reductions in prey resources even in the absence of fishing, but including fishing in the models accelerated seabird declines (Watters et al., 2013; Punt et al., 2016). For example, modeled pelican declines occur at very low abundances of sardine and anchovy ($< 10\%$ of unfished biomass), abundances unfortunately not that uncommon (Punt et al., 2016). In some seabird species, higher productivity can lead not only to increased abundance, but also to resilience to prey depletion due to fishing pressure in reality. In other species, responses may be limited following the cessation of fishing; in the model run by Watters et al. (2013), krill abundances rebounded but penguin abundance did not return to no-fishing levels within 20 years, which could be attributed to competition with predatory fish and marine mammals, or other factors.

4.2.2. *Field experiments*

Due to their capacity to provide causal understanding, the "holy grail" of seabird-fisheries competition studies are localized prey depletion experiments (i.e., fisheries closures or openings). These studies are rare. Frederiksen et al. (2008) used a Before-After-Control-Impact (BACI) design to analyze breeding success of black-legged kittiwakes at North Sea colonies in a region where the sandeel fishery had been operating in the 1990s and was closed in 2000, in comparison with a control region in which a sandeel fishery operated throughout the period. This analysis provided compelling results showing that breeding success was depressed during the fishery period relative to the control zone, and that breeding success was negatively correlated with fishery effort in the zone where fisheries were closed, but not in the control zone.

However, while there are compelling examples of success, field experiments are difficult to implement (fishers may not cooperate with anticipated fisheries closures or openings), and without a solid program of habitat and environmental observations, these types of experiments may not fully succeed. In part, this is because each seabird colony has its own characteristics, including differences in abundance, distribution, and organization of localized prey fields (Daunt et al., 2008; Pichegru et al., 2009; Sherley et al., 2015), making appropriate "control" sites difficult to select. Field experiments may be effectively implemented if they are designed at a meaningful spatial scale and take into account the natural prey depletion 'halo' that may surround seabird colonies (Ashmole, 1963; Birt et al., 1987), but this has not always been the case. Some of the previous studies, however, have shown that the efficacy of small-scale closures around breeding colonies was poor because birds regularly foraged beyond the limits of closed areas. Seabird foraging may also be impacted by heavy fishing pressure at the boundaries of fisheries closures (i.e., 'fishing the line'; Pichegru et al., 2012). Inter-annual differences in foraging zones, as shown by many species throughout the breeding cycle, can complicate whether closures are indeed affecting localized prey depletion. Closed areas will be more or less effective depending on movements of the forage species under consideration. In short, the movement scale of the fish and seabirds needs to be considered in experimental designs, and in setting expectations for possible demographic responses (Croll et al., 1998; Sherley et al., 2015, 2017). Taken together, all of these issues suggest that experimental fishery closures may need to incorporate appropriately-sized buffer zones around presumed foraging ranges, which may be difficult to explain to industry and cause enforcement issues.

5. Best practices

5.1. Hypothesis development and articulation

Table 4 summarizes best practices for investigations of fisheries-seabird resource competition. In considering the overarching hypothesis that fisheries impact seabirds through competitive interactions, one must first articulate whether the competitive effects are expected to be exploitative, the result of interference, or both. The potential mechanism(s) of competitive response should also be stated. For example, assuming the hypothesis of exploitative competition, mechanisms of prey depletion could be a reduction in prey biomass or prey density, changes in the horizontal or vertical (depth) distribution, or change in age or size distributions of available prey (Bertrand et al., 2012; Boyd et al., 2015; Crawford et al., 2016). Expected changes in these parameters should be presented when formulating the hypothesis.

For studies involving multiple species of seabirds or forage prey, expectations should be stated concerning which species and parameters are expected to respond to prey depletion, and which mechanisms are likely to affect each parameter. This comparative approach may provide insights into key questions concerning mechanisms of response, which may vary by seabird and forage species (e.g., Crawford et al., 2014). Careful consideration should be given to the burden of evidence required to accept or reject the hypothesis of competition. Bayesian frameworks that quantify the probabilities of competitive effects may be particularly valuable as an alternative to null hypothesis testing (Hobbs and Hilborn, 2006).

5.2. Baseline analyses

Summarizing observations is an obvious starting point for any research, as this leads to pertinent questions and hence more directed research efforts. Initial analyses should include an assessment of changes in the environment and ecosystem under consideration that may affect interpretations. This assessment should include a quantification of coinciding environmental and ecosystem factors (e.g., regime shifts and removal of competitors) that are likely to confound fisheries effects on forage, hence interpretations of localized prey depletion and seabird demographic or foraging responses to changes in forage availability. Documenting long-term changes in fishing practices in the region is an important first step toward understanding how changes in the ecosystem and food web controls (e.g., lessening of top-down control by reduction in piscivorous fish) may dampen or amplify apparent fisheries-seabird competition. Low- and high-frequency (i.e., interdecadal to interannual) climate variability should be summarized to provide perspective on the potential for environmental confounding of fisheries to forage stock relationships. Implementing a basic ecosystem model

Table 4
Summary of best practices for investigations of fisheries-seabird competition.

1.	Hypothesis development and articulation
a.	state whether competitive effects are expected to be exploitative or based on interference
b.	state mechanisms of competitive response (changes in abundance, density, or distribution)
c.	present expected changes in key seabird parameters to localized prey depletion
d.	state expectations about which species will most likely show effects and why
e.	consider the burden of evidence required to accept or reject hypothesis of competition
2.	Baseline analyses
a.	assess and present changes in the environment and ecosystem that may confound interpretations of fisheries-related prey depletion
b.	document and describe long-term changes in fishing landings, including shifts in target species
c.	document how climate variability may affect forage stocks of interest
d.	implement models to place potential relationships between fisheries, forage stocks, ecosystem dynamics, and the environment in context
e.	use a model to determine appropriate scales for linking fisheries, forage stocks, and seabirds
f.	summarize tracking/movement studies to determine the scale of potential seabird responses to variation in forage stock availability
g.	synthesize information on non-breeding range and prey availability if fisheries impacts on seabird survival or juvenile recruitment are of concern
h.	address temporal scales of potential fisheries impacts by quantifying the timing of fishing activities
i.	quantify the age and size classes of forage species being taken by both the seabirds and fisheries
3.	Selection of response variables
a.	select fish stock response variables appropriate to the temporal and spatial scale of fisheries activities
b.	select seabird demographic response variables appropriate to the temporal and spatial scale of hypothesized fisheries competition
c.	determine how to integrate information on energy intake into studies of seabird foraging behavior and/or movements in relation to current fisheries activities
4.	Testing mechanisms and causation
a.	design long-term, spatially-explicit experiment to establish causality between fisheries and seabirds through localized prey depletion:
b.	identify appropriate controls to provide replication, and incorporate realized fisheries activities
c.	obtain "buy-in" from fisheries to fish in accordance with experiment protocols
d.	conduct numerical simulations with maximum likelihood or Bayesian methods to consider how uncertainty in parameters, environmental driver, and functional forms of relationships could affect experiments
e.	use spatial modeling to address how fisheries time/area closures could affect long-term prey depletion experiments
f.	conduct experiments using a Before-After-Control-Impact (BACI) design
g.	measure prey movements, distribution, and population variability during BACI experiments
h.	quantify seabirds on at sea surveys of forage stock to provide information on seabird distribution and abundance at sea in relation to forage fish biomass
i.	conduct experiments on time scales relevant to seabirds, often at least a decade
j.	focus experiments on threatened or endangered seabirds species or populations

would help place long-term fisheries, ecosystem, and environmental relationships into context (Fulton, 2010; Hill et al., 2007).

As scaling matching or mismatching has been one of the major issues hampering previous seabird-fisheries competition research, a conceptual model should be used to develop an understanding of appropriate scales for linking fisheries, fish, and seabirds. In the event that a field program may be part of the research, the scale of seabird responses to variation in prey availability could be determined by movement studies of breeding seabirds from colonies (see for example Weimerskirch et al., 2007; Davies et al., 2013; Wakefield et al., 2013). If there are concerns about fisheries impacts on seabird survival or recruitment of juveniles, tracking studies of central-place foraging breeding birds will be insufficient, and information on non-breeding range and prey availability in that range would need to be specified (Fort et al., 2013; Reiertsen et al., 2014; Sherley et al., 2017). In addition to spatial scale, temporal scales of impact should be specified in relation to the timing of fishing activities (Pichegru et al., 2009). Finally, to document the potential for fisheries competition with seabirds, baseline analyses should include an examination of the size classes of forage species taken by the birds and the fisheries. While the potential for competition would be greatest for situations where the birds and fisheries take the same age/size classes (Hilborn et al., 2017), fisheries impacts may be possible when different classes of forage are used (Field et al., 2010).

5.3. *Selection of response variables*

Research on fisheries competition with seabirds needs to focus on appropriate response variables to demonstrate mechanistic linkages between a) fisheries and forage availability and b) forage and seabird population indicators. Many field studies have focused on correlating various aspects of foraging behavior and demographic variability with forage availability. Measures of foraging behavior typically include time away from the colony, trip length, maximum distance, number of dives, dive duration, and dive depths. These data can be readily collected by observers at the colony or by using satellite trackers, GPS data loggers, wet/dry loggers, or time-depth recorders (e.g., Davoren and Montevecchi, 2003; Wilson and Vandenabeele, 2012; Grémillet et al., 2016). While these measurements can be extremely valuable, they are inter-related to one another, highly variable between individuals (leading to high variance), and plastic, which makes them difficult to interpret and they may or may not link to population-level variation. For example, birds may compensate for variation in net energy gain per trip simply by adjusting trip frequency, and this can be done on short or long time scales (Pinaud et al., 2005). In short, measurements of foraging behavior may be misleading without parallel information on energy intake (Jodice et al., 2006; Fort et al., 2009; Boyd et al., 2014; Daunt et al., 2014). Individual-level variation in seabird foraging behavior is well known (Lescroël et al., 2010), and some species show individual diet specialization (Woo et al., 2008; Camprasse et al., 2017). Such divergent individual responses to varying prey availability (or prey depletion) could mask or accentuate population-level responses. Understanding this variability will be important to quantify functional and numerical responses at the population level. Large sample sizes are required to distinguish between individual and population-level variation in foraging behavior, or more specifically to ensure that the effects represent effects on the population rather than just individual responses. Methods appropriate for disaggregating individual responses versus population-level effects include models with individual random effects; these and similar methods should be used wherever possible.

As the energy balance of seabirds ultimately determines their demographic success, we do not recommend measuring foraging behaviors as primary response variables unless simultaneous information on energy intake is also obtained. Estimates of prey intake by free-living seabirds can be achieved using stomach-temperature recorders (Ropert-Coudert et al., 2006; Grémillet et al., 2016), wing beat frequency (Sato et al., 2008), or water off-loading (Daunt et al., 2007). Bill-loading seabirds provide opportunities to estimate the amount of energy provided to chicks (Burke and Montevecchi, 2009; Gaglio et al., 2017), as do automated nest balances, which may also provide non-invasive information on resultant chick growth (Prince and Walton, 1984; Sugishita et al., 2017). These techniques, however, are expensive and difficult to implement on many individuals. Other variables (e.g., change in body mass or body condition of chicks) may provide proxies of energy intake (Campbell, 2016) and should be explored. Nonetheless, we emphasize focusing on energy intake as a mechanistic link between forage availability and seabird demography (Grémillet et al., 2016). Integration of demographic measurements (breeding success, survival, recruitment) with measurements of energy intake should be used to estimate population consequences of potential seabird-fisheries competition.

5.4. *Testing mechanisms and causation*

No study of seabird-fisheries competition can be complete without experiments, broadly speaking. Experiments are needed to deal with the thorniest issue in fisheries-seabird competition research − establishing causality. Good practices in this regard involve conducting some numerical simulations, in which the model of the fisheries, seabird populations (or population parameters), and forage fish stocks are fit to available data using maximum likelihood or Bayesian methods (Punt et al., 2016). Uncertainty in model parameters, environmental drivers of population dynamics, and functional forms for relationships should be considered (e.g., in a management strategy evaluation (MSE) framework). While basing fisheries scenarios on levels of constant fishing mortality is simple, actual fisheries are often based on time/area closures, necessitating some form of spatial modeling. While these issues could be included in Ecopath/Atlantis-type models, the complexity of these models means that only limited exploration of uncertainty is possible. In contrast, MICE-type approaches are generally less computationally intensive, allowing a more thorough evaluation of uncertainty, albeit at the loss of the ability to fully represent ecosystem dynamics. Model structure and precision will be enhanced when informed by relevant field data, so integration of models with key observations, such as consistent thresholds in numerical responses, is important and should be emphasized (Cury et al., 2011; Robinson et al., 2015). Indeed, if one does not understand the functional forms of relationships between seabirds and prey availability, the results of most modeling exercises will not provide insight. Examining seabird responses to prey abundance and quantifying functional and numerical relationships under naturally pulsed resource circumstances is one way of estimating functional relationships, but takes a great deal of time. Localized prey depletion experiments are another means of studying these key relationships, but they also present challenges (see below).

Other key seabird data to integrate (and verify using observations) for models include: the dominant prey species used by the seabird species of interest year-round as well as by season, the size and age classes of prey taken, foraging ambit, and primary foraging location of the species of interest. The foraging ambit of seabirds is important to take under consideration in all situations, especially those where the forage species is resident in the area where seabirds breed, overwinter, or reside year-round. However, some forage species are highly migratory and, thus, may become depleted during a period when they do not overlap with seabirds, which could still result in prey depletion for the seabirds during the period of the year when they do normally overlap in time and space.

The key and most difficult question to address is: does the fishery cause local prey depletion to the extent that it affects seabird populations? While time series observations and analyses may be useful for generating correlations, and models are appropriate for testing scenarios, only by conducting *localized prey depletion experiments* (LPDE), such as those ongoing in South Africa (e.g., Sherley et al., 2015), can the null hypothesis of no fishery effects (or the probability of fishery effects in Bayesian terms) be evaluated in an unbiased manner. Notably, the scale for this work often will be considerably smaller than the scale at which commercial fisheries are studied for the purpose of stock assessment and management, although it is on scales provided by Vessel Monitoring Systems (VMS), which are increasingly common in many fisheries. In our view, LPDE are best accomplished using a BACI design (Stewart-Oaten et al., 1992; Underwood, 1994; Frederiksen et al., 2008), in which the measured quantity (forage) is the percentage difference in abundance, distribution, or density over time, and replicated over space. BACI design allows for the expected seasonal and small-scale spatial variability in fish abundance, and provides the replication needed for hypothesis testing. Integrated acoustic-trawl methods (Misund, 1997; Simmonds and MacLennan, 2005) to survey forage fish before, during, and after fishing would provide the requisite data, but these surveys should be replicated often enough to provide precision in forage abundance or density estimates. Power analyses should be used to determine sample size for acoustic-trawl surveys of forage (*sensu* Ross-Gillespie and Butterworth, 2016). Prey movements, distribution, and population variability are mediated by environmental factors related to time of day, habitat quality (including zooplankton (i.e., prey) abundance, e.g., Mullowney et al., 2016), water column structure, and fronts (e.g., Haury et al., 1978; Gutierrez et al., 2007; Hollowed et al., 2007; Logerwell et al., 2007), so to the extent possible, these variables should be measured concurrently with forage surveys. Also, quantifying seabirds and marine mammals on surveys can provide valuable information on the utilization of the forage fish by top predators, as well as relationships between their distribution and abundance in relation to forage fish biomass (e.g., Fauchald and Erikstad, 2002; Santora et al., 2011).

Identifying appropriate controls and incorporating realized fishing impacts (fishing is not always sufficiently conducted in the open periods or at the right locations) are challenges to implementing LPDE. For example, during a prey depletion experiment focusing on the pollock fishery in Alaska, differences in many of the parameters examined (e.g., fish biomass, vertical and horizontal distribution) were greater between the experimental and control areas than between pre-fishery and fishery periods (Walline et al., 2012). Valid conclusions may be drawn in the absence of replication through logic and biological reasoning if the perturbation applied is strong and the differences are large (Oksanen, 2004), though covariance between fishing and environmental effects may preclude robust interpretation. In short, the so-called “control” sites in many LPDE experiments must be considered as only reference sites where the changes in forage populations may be related to factors other than fishing.

Given this, short-term field experiments are likely to be severely limited in their scope to discern causal mechanisms, and we recommend that experimental studies are conducted on time scales relevant to the generation times of seabirds, which may well be on the order of at least a decade. This longer-term approach matches what we know is needed to estimate seabird numerical response relationships (Cury et al., 2011). A power analysis for a fisheries manipulation experiment off South Africa also indicated that between 10 and 25 years is needed to detect significant changes in penguin populations (Ross-Gillespie and Butterworth, 2016). Unfortunately, short-term alterations of experimental protocols, especially in regions of substantial temporal environmental variability (such as upwelling systems), are likely to suffer from site-to-site effects that may swamp the fisheries effects. Shorter-term field experiments may be possible if the environmental factors affecting forage nekton populations are relatively constant over time, but as the prediction of low-frequency environmental variability and regime shifts is not yet possible, this would be difficult to forecast. Finally, we note that LPDE should focus on seabird species that have limited foraging ranges and specialist diets and fisheries that target single forage species because these study groups would be the most likely to show robust results.

6. Conclusions

i Seabird-fisheries competition is a difficult problem in applied marine ecology. Often in the past, specific questions and hypotheses, appropriate spatial and temporal scales, and expected pathways of response from fisheries to fish and from fish to seabirds have been poorly articulated. The conceptual framework of future studies could and should be improved.

ii Forage nekton for seabirds includes small pelagics, invertebrates such as euphausiid crustaceans and squid, and age-0 juvenile predatory fishes. It is possible for fisheries on adult fish to affect the availability of juvenile fish, leading to detrimental (or positive when adults are cannibalistic) effects on seabirds. Potential fisheries competition for any of these species or age classes should be examined.

iii Investigations of fisheries effects on forage and seabird food availability must be localized and spatially-explicit, especially during the breeding season when seabirds are constrained to forage near colonies.

iv Confounding environmental factors should be modeled or integrated into LPDE to avoid a serious impediment to making reliable assessments of fisheries impacts on forage fish stocks, hence food availability to seabirds.

v As seabird population dynamics are often driven by adult survival or juvenile recruitment, fisheries competition with seabirds should be examined in both breeding and non-breeding seasons.

vi While devices are easily deployed on seabirds, foraging behaviors as primary response variables without inclusion of estimates of energy intake should be interpreted with great care. Measuring seabird demographic variables is essential and these can be synthesized in population dynamics models to estimate population consequences of fisheries competition.

vii A gap in knowledge concerns tropical/subtropical and polar regions with large industrial fisheries. A list of regions should be developed to show where fisheries for forage are incipient or could be established. This proactive approach may provide opportunities to establish baselines in terms of forage stock biomass and seabird indicators, prior to inception of large-scale industrial fisheries.

Acknowledgments

To review past approaches and develop guidelines and best practices to document ongoing seabird-fisheries competition for inclusion in modern-day ecosystem approach to fisheries, we held two multidisciplinary workshops (31 October 2015 in Cape Town, South Africa, and 19 January 2016 in Seattle, Washington, see http://www.faralloninstitute.org/seabirdfisheries-competition), convened specifically to address this issue. Each workshop was designed to bring together experts as well as early-career scientists in the fields of seabird ecology, fisheries science, and oceanography. This demographic breadth meant that institutional memory on the subject contributed to capacity building in this subject area. Funding for workshops and development of this manuscript was provided by The Pew Charitable Trusts. We are grateful to South Africa's Department of Environmental Affairs for hosting the Cape Town workshop. RJMC is grateful to South Africa's National Research Foundation for funding support. We sincerely thank the reviewers and editors of Fisheries Research for providing constructive comments on the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2017.05.018.

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