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A structured seabird population model reveals how alternative forage fish control rules benefit seabirds and fisheries

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ABSTRACT

Fisheries for forage fish may affect the survival and reproduction of piscivorous predators, especially seabirds. However, seabirds have evolved life history strategies to cope with natural fluctuations in prey and it is difficult to separate effects of fishing on seabirds from impacts of natural variability. To date, potential impacts of forage fisheries on seabirds have mainly been explored using ecosystem models that simplify seabird-forage fish dynamics. We sought to explore how different forage fish harvest policies affect seabirds, accounting for structured population dynamics, life history specifics, and variation in forage fish dependencies across life stages; and how impacts vary across seabird and forage fish life histories. To explore these impacts, we developed an age-stage structured seabird model that incorporates seabird diet specialization, foraging behavior, and reproductive strategy, as well as different functional responses between prey availability and adult survival, juvenile survival, reproductive success, and breeder propensity. We parameterized this model for two contrasting seabird life histories – (1) a low fecundity, limited foraging range, diet specialist (“restricted”); and (2) a high fecundity, wide ranging, diet generalist (“flexible”). Each was paired with two different forage fish prey archetypes that were fished under various control rules. The restricted seabird population was expectedly less robust to constant fishing pressure than the flexible seabird, and this sensitivity was mainly due to functional response parameterization, rather than other life history parameters. Particularly, the restricted seabird was highly sensitive to the relationship between prey availability and adult survival but was not sensitive to the relationship between prey and reproductive success. An adaptive biomass-limit harvest rule for forage fish resulted in substantially higher seabird abundance compared to constant fishing across all scenarios, with minimal trade-offs to the fishery (depending on fishery management objectives). However, mechanisms governing the impact of the forage fish fishery on the seabird varied by forage fish type. Therefore, tailoring forage fish management strategies to forage fish life history can lead to mutually acceptable outcomes for fisheries and seabirds. If data or time are limited, an adaptive control rule is likely a safe bet for meeting seabird conservation objectives with limited impacts to fisheries.

Key words: Seabirds, Forage fish, Model simulations, Fisheries management

INTRODUCTION

With increasing demand for natural resources to support a growing and developing human population, we expect to see increasing conflict around balancing the benefits of natural resource uses and the value of conserving the environment and species within it. This is particularly relevant when the removal of a species or resource reverberates through the system via habitat loss or trophic interactions causing negative impacts to other economically, culturally, and ecologically valued species. Examples exist across ecosystems including; lumber use and forest management impacts on biodiversity (Chaudhary et al. 2016), ecosystem impacts of land conversion for agriculture (Power 2010), effects of the removal of large terrestrial predators due to predation on livestock (Baker et al. 2008), and impacts of fishery removals on other marine species (Travis et al. 2014, Bozec et al. 2016). A constant struggle in resource management is determining where there is significant conflict and finding ways to balance meeting multiple societal objectives of resource uses.

In marine ecosystems, one common concern is the potential conflict between the conservation of piscivorous predators - predatory fish, seabirds, and marine mammals - and the harvest of forage fish prey (Smith et al. 2011, Pikitch et al. 2012, Rice and Duplisea 2013). Particularly, seabirds are highly diet dependent on forage fish (Pikitch et al. 2014, Szoboszlai et al. 2015), and are greatly valued culturally, ecologically, and economically (Lewis et al. 2012, Kadin 2014, Konar et al. 2019). At the same time, their forage fish prey (small, mid-trophic level, pelagic species), have extensive provisional value as humans directly consume forage fish and forage fish are used as feed for agriculture and aquaculture resources that humans depend on (Alder et al. 2008, Tacon and Metian 2009). There is extensive evidence that changes in forage fish abundance affect seabirds (Tasker et al. 2000, Cury et al. 2011, Cook et al. 2014, Carroll et al. 2017), but drawing direct connections to impacts of fisheries harvest is difficult (Hilborn et al. 2017, Sydeman et al. 2017). Also, the effects of changes in forage fish abundance vary across seabird life history strategies and demographic processes (Piatt et al. 2007). Because of these complexities, many have called for precautionary management of forage fish for seabirds (Cury et al. 2011, Pikitch et al. 2012), and including more information about impacts to predators or predator status tactically in precautionary measures may reduce excessive fishery restrictions (Hill et al. 2020).

Seabirds have evolved alongside dynamic prey and have life history adaptations to cope with naturally occurring fluctuations in forage fish prey even in the absence of fishing (Crawford et al.

2006, Furness 2007), but specific life history traits can make seabirds sensitive to changes in forage fish prey availability (compared to other marine predators). Seabirds are central-place foragers; having restricted foraging ranges while breeding due to the need to trade-off time spent foraging, time away from offspring (reproductive success), and their own survival (Orlans and Pearson 1979, Burke and Montevecchi 2009). Additionally, small body size, specialized diet, energetic costs of flight, and other traits that limit foraging range, such as diving depth, also impact seabird vulnerability to changes in prey abundance and distribution (Furness and Tasker 2000, Piatt et al. 2007, Boyd 2012, Boyd et al. 2016). However, because forage fish dynamics are sensitive to environmental conditions and can undergo large-scale natural interannual fluctuations (Chavez et al. 2003, Checkley et al. 2009, Essington et al. 2015), seabirds have also adapted to variability in prey. Many seabirds have post-fledging care, flexible diets, and/or traits like early age at first breeding, larger clutch sizes, and long life spans that create multiple reproductive opportunities throughout their lifespans so seabirds can skip breeding in years with low availability of quality prey without great lifetime fitness costs (Crawford et al. 2006, Furness 2007, Weimerskirch 2007, Catry et al. 2013). These adaptations lead to fluctuations in demographic rates from year to year, particularly in reproductive success, that vary annually with or without fishing. However, fishing can modify forage fish availability and fluctuations as well (Beverton 1990, Dickey-Collas et al. 2010, Essington et al. 2015) and even well-managed stocks (not overfished) reduce abundance and may reduce availability for predators (Pikitch et al. 2004), so it is difficult to disentangle how additional changes in prey availability from fishing pressure may affect seabirds at a population level compared to natural prey changes.

The potential impacts of fisheries on seabirds at a population level have often been studied using ecosystem or food web biomass dynamic models (e.g.,(Smith et al. 2011, Pikitch et al. 2012, Kaplan et al. 2013, Koehn et al. 2016), that simplify seabird-prey dynamics, but models that account for unique life history traits would provide an opportunity to test the efficacy of alternative forage fish management strategies. Few models to date have included the structure needed to assess competition between fisheries and seabirds (Hilborn et al. 2017, Sydeman et al. 2017, Goedegebuure et al. 2017). Often, large aggregated models assume a single population-level functional response for all predator species (Plagányi 2007), without incorporating key interactions for specific species or age life stages (Sydeman et al. 2017, Goedegebuure et al. 2017). Certain models of intermediate complexity (MICE)

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have begun to incorporate more complexity in seabird functional responses for specific vital rates like seabird survival or reproductive success (Plagányi et al. 2014; for example, Punt et al. 2016; Robinson et al. 2015). However, these models are few and rarely consider the relationship between prey availability and other life stages (e.g. juvenile survival), impact of prey availability on breeder attendance, or how prey availability changes seasonally (especially in breeding vs. nonbreeding seasons) (see Piatt et al. 2007). More detailed structured simulation models that incorporate these factors are needed to explore the impacts of forage fish availability and management strategies on seabirds and potential conflicts between management objectives. Specifically, precautionary cut-off control rules that stop or curtail fishing if biomass drops below a threshold (like “hockey-stick” rules) have been proposed for forage fish to help mitigate potential impacts of fisheries on dependent predators. A model with seabird life history specifics could provide insight into the mechanisms by which alternate control rules might benefit seabirds while supporting continued fishing.

Here, we asked, what is the sensitivity of seabirds to fishing forage fish species given variation in the relationship between prey availability and different seabird biological components and how does this depend on seabird and forage fish life history and forage fish management? We investigate these questions by developing an age-stage structured model of a generic seabird population where multiple seabird vital rates are related to forage fish prey availability, and we account for specifics of seabird foraging strategies, prey accessibility, diet specialization, and reproductive strategy.

Furthermore, using this structured model framework we specifically investigate: (1) How do impacts of a forage fish fishery vary across seabird life history types and what are the main causes of this variation? (2) How do alternate forage fish harvest rules mitigate impacts of fishing on seabirds, and how does that depend on seabird and forage fish life histories? (3) How do the trade-offs between fisheries objectives and seabird conservation depend on characteristics of forage fish population dynamics? We explore these questions using two forage fish prey types in the seabird model, that exhibit different forage fish mortality rates and frequency of productivity variation – an anchovy-like and a sardine-like forage fish. The seabird and forage fish prey populations represented are generic and not specific to any one ecosystem so that results are applicable across systems but also so that in the future, the model can be tailored to specific seabird populations.

METHODS

Here, we present a detailed and structured seabird population model based on specific details of seabird life history to explore impacts of forage fish fisheries on seabird populations. Our goal was to keep the model flexible so that we could explore impacts across a range of seabird life histories, and so that future efforts can adjust the model to specific needs, while still incorporating the details of seabird ecology that likely impact seabird resilience to changes in prey availability. Therefore, we also needed the model to account for changes in seabird sensitivity to prey abundance across various seabird vital rates, variation in breeding strategies, and across seasons.

To accommodate these goals, we developed an age-stage structured seabird model, where seabird reproductive success (offspring survival), juvenile and adult survival, and breeding propensity (likelihood of breeding) depends on prey availability. Additionally, the impact of prey on survival varies by season (breeding vs. nonbreeding). Therefore, we used a flexible functional response function to model impacts of prey availability on seabird dynamics that can be parameterized for variance shapes and thresholds depending on seabird life history specifics and different seabird vital rates. Additionally, the seabird model can be parameterized across a range of reproductive strategies and foraging strategies. To model seabird prey, we used a recent model from Siple et al. (2019) to simulate forage fish biomass for two prey types: characterized by low natural mortality and low-frequency recruitment variation ('sardine-like', *Sardina*, *Sardinella*, and *Sardinops* spp.) and high natural mortality and medium-frequency recruitment variation ('anchovy-like', family *Engraulidae*). We then ran the seabird model under two contrasting seabird life history scenarios, the two forage fish prey scenarios, and five harvest control rules to model the impacts of fishing across seabird and forage fish life history.

Seabird model

The seabird model represents a single, closed colony of seabirds and is an age and stage-structured, two-season model with yearly time steps where reproduction and survival depend on prey availability (Figure 1). The full set of equations for all state functions in the beginning of the breeding season (subscript b) or nonbreeding season (subscript n) are:

$$N_{y,s=b,a} = \begin{cases} E_y & a = 0 \\ N_{y-1,n,a-1} S_{y-1,n,l} \delta_{y-1,n,l} & a = 1, \dots, a_x \end{cases} \quad \text{Eq. 1}$$

$$N_{y,s=n,a} = \begin{cases} f_y & a = 0 \\ N_{y,b,a} S_{y,b,l} \delta_{y,b,l} & a = 1, \dots, a_x \end{cases} \quad \text{Eq. 2}$$

where $N_{y,s,a}$ is the number of birds at year (y), season ($s = b$ or n), and age (a) (0 through maximum age, a_x), E_y is the number of eggs laid at the beginning of year (y) in the breeding season, and f_y is the number of chicks that fledge and become independent (in the second half of the year). $N_{y,s,a}$ is a function of stochastic bi-annual maximum survival rate ($S_{y,s,l}$) (Beta-distributed with mean \bar{S}_l and variance σ_l^2), and also a function of prey availability ($\delta_{y,s,l}$), which both vary across life stage l . Life stages are egg/chick (notated with a subscript e for egg specifically or a C; $a = 0, s = b$), juvenile (j; $a = 0, s = n$ and $a = 1, s = b$), immature (i; $a = 1, s = n$, or $1 < a < a_b$, the breeding age), breeding adults ($a_b \leq a < a_x$ and attempt to breed, $l = b$ subscript) and nonbreeding adults ($a_b \leq a < a_x$ breeding age but do not attempt to breed in a given year, subscript $l = n$) (Fig. 1). Maximum survival is the same for all breeding age adults ($S_{y,s,b} = S_{y,s,n}$) but $\delta_{y,s,l}$ depends on breeding status in a given year and breeding season. Seabirds are assumed to die after they reach the maximum age (a_x). See Table 1 for all seabird model parameters.

Survival rates $S_{y,s,l}$ are stochastic because survival varies in seabird populations due to weather/climate and predation (especially for eggs/chicks), and anthropogenic factors (e.g. oil spills, bycatch) (Schreiber and Burger 2001), where:

$$S_{y,s,l} \sim \beta(\bar{S}_l, \sigma_l^2) \quad \text{Eq. 3}$$

Mean survival (\bar{S}_l) values come from published values. We tested sensitivity of the model to variance (σ_l^2). Details of seabird model parametrizations are provided in “Seabird parameterization” section in Appendix S1 (parameters in Appendix S1: Table S1).

Offspring survival or reproductive success (surviving to the second half of the year [nonbreeding season] in the first year of life) in a given year is modeled as a function of the number of eggs laid at the beginning of the breeding season and egg and chick survival (fledging success).

Number of eggs laid (E_y) is an asymptotic function of breeder abundance to represent space limitation of seabird colonies such that at low population sizes, egg production is only limited by seabird physiology (Appendix S1: Figure S1). Number of eggs laid is also a function of prey availability such that:

$$E_y = E_{\max}(1 - e^{-r_y}) \quad \text{Eq. 4}$$

Where E_{\max} is the number of viable eggs that can be laid based on available nesting sites and r_y is the maximum per capita egg production, which is a function of total number of breeding seabirds and prey availability, defined as:

$$r_y = \frac{\tilde{c}}{2E_{\max}} \gamma_{y-1,n,l} \sum_{a=a_b}^{a_x} N_{y,b,a} \quad \text{Eq. 5}$$

Where the parameter \tilde{c} is the maximum clutch size possible (max number of eggs per pair) of the seabird and $\gamma_{y,s,l}$ is the impact of prey on the number of breeding age adults that breed (breeder propensity), similar to $\delta_{y,s,l}$, but impacting breeding numbers instead of survival. Therefore, Eq. 5 assumes when prey availability is low in the previous nonbreeding season ($s = n$), a proportion of breeding-age seabirds will skip the breeding season. We assumed no re-laying of eggs if eggs are lost, which can occur, especially if eggs are lost near the beginning of the breeding season, but is rare depending on species (Schreiber and Burger 2001, Boersma et al. 2013).

Fledging success, or chicks surviving to the non-breeding season in first year of life (f_y), is also a function of prey availability and is determined by the number of eggs that hatch to become chicks and the number of chicks that survive to reach independence (fledge):

$$f_y \sim \text{Binomial}(S_{y,b,e} S_{y,b,c} \delta_{y,b,c,c} N_{y,b,0}) \quad \text{Eq. 6}$$

Number of offspring that fledge is a random variable drawn from a binomial distribution where the fledging probability is the product of the maximum survival rate of eggs ($S_{y,b,e}$), the maximum survival rate of chicks ($S_{y,b,c}$) (which are both stochastic, see above), and the impact of prey availability on pre-fledge survival (i.e., the product of egg and chick survival) in a clutch of size c ($\delta_{y,b,c,c}$), which can equal one, two, or three. This is to account for differences in the amount of prey needed to provision one versus multiple chicks; i.e. the impact of prey on fledging varies depending on the total number of chicks per breeding pair.

Functional responses

The variable $\delta_{y,s,l}$ reduces survival (including offspring survival or reproductive success, Figure 2) and variable $\gamma_{y,s,l}$ reduces number of adults breeding, both based on prey availability. We defined the function for $\delta_{y,s,l}$ and $\gamma_{y,s,l}$ so that the shape of the relationship between prey availability and vital rate can be easily adjusted depending on the vital rate and depending on the level of diet

dependence (at which point seabirds would switch to alternative prey). Our solution was the following asymptotic, logistic function:

$$\delta_{y,s,l} = \gamma_{y,s,l} = \min \left(1, \alpha + \frac{1 - \alpha}{1 + e^{-m \left(\frac{P_{y,s,l}}{\bar{P}_l} - \beta \right)}} \right) \quad \text{Eq. 7}$$

where $P_{y,s,l}$ is the forage fish prey biomass available to the seabird in year y , season s , and for a seabird life stage/breeding status l . \bar{P}_l is the long-term average biomass of forage fish for seabird life-stage l when there is no fishing. For $\gamma_{y,s,l}$, s is always equal to the nonbreeding season n , and l is all adult breeding age birds (subscript $l = b$ or n). The parameter α denotes the lowest possible value of $\delta_{y,s,l}$ or $\gamma_{y,s,l}$ (i.e., the y-intercept) and can be roughly thought of as the fraction of the maximum vital rate that occurs when a seabird has switched to an alternative, less energetically rewarding prey. The other parameters control: the inflection point of prey availability (β) and the rate at which the seabird parameters vital rates decline (m or slope).

Values of parameters α , β , and m were chosen to produce functional forms similar to those hypothesized by Cairns (1987) and shown by Piatt et al. (2007) for seabird demographic rates of adult survival, juvenile survival, and breeding attendance at low vs. high prey availability. For fledging success, we chose functional response parameters to match the empirical relationships revealed in the meta-analysis in Cury et al. (2011) for the relationship between reproductive success and prey availability. Additionally, the functional response for chick fledging success (% fledged) is modified to account for the number of chicks per reproductive pair (Figure 2, bottom), as more prey is needed to feed and fledge a chick if multiple chicks need to be fed. See Appendix S1 for specifics on functional response parameterization (Appendix S1: Table S2 and “Functional response parameterization”).

Forage fish model

To test the performance of the seabird model in relation to prey availability, we needed to simulate realistic forage fish dynamics both with and without fishing. We did so using the model in Siple et al. (2019), which is an age-structured forage fish population model where population dynamics are driven by recruitment deviations, with life history parameters and recruitment variation based on real populations to generate realistic forage fish dynamics (see Appendix S1: Figure S2,

Appendix S1 “Forage fish model”, and Siple et al. [2019] for further details). Within the seabird model, we did not include a top-down impact of seabird abundance on forage fish biomass as most seabirds contribute little to forage fish mortality (see Koehn et al. 2016), and others have noted top-down impacts by seabirds is likely limited (discussed in Cury et al. 2000).

We converted forage fish biomass generated by the Siple et al. (2019) model to prey availability for use in the seabird model. Fishing can reduce the availability of prey within a year. Therefore, we calculated the average biomass in year y of the forage fish at each age group (a) given the biomass at the start of the year, using the following equations:

$$\varphi = \log (B_{a+1,y+1}/B_{a,y}) \quad \text{Eq. 8}$$

$$\bar{B}_{a,y} = B_{a,y}(e^{(\varphi)} - 1)/\varphi \quad \forall a = 1, \dots, a_x - 1 \quad \text{Eq. 9}$$

$$\bar{B}_y = \left(\sum_{a=1}^{a=x-1} \bar{B}_{a,y} \right) + B_{a=x,y} \quad \text{Eq. 10}$$

Where $B_{a,y}$ is the biomass of forage fish at age a and start of year y , \bar{B}_y is the total average possible forage fish biomass available to a seabird at year y (summed over forage fish age 1 to $a = x-1$, where x is max age), and $\bar{B}_{a,y}$ is the average biomass at year y , for age a . Finding the average biomass in a year was applied to all forage fish age classes except for the forage fish “plus group” (at $a = x$). The plus group comprises a small portion of the total fish biomass and therefore their age structure is not explicitly represented, so we simply used the initial biomass in each year for this group. We assumed that seabirds target forage fish age 1+ (not age 0), which has been shown for certain species (Sunada et al. 1981) and assumed in other models (Robinson et al. 2015, Punt et al. 2016). The yearly average biomass was assumed to be the available biomass to the seabird in both seasons (breeding and nonbreeding) within a year. Therefore, we don’t make any assumptions about when fishing is occurring.

Because seabirds are central place foragers while breeding, the actual amount of prey available likely varies intra-annually (between breeding and non-breeding seasons), depends on the foraging strategy of the seabird (diving depth, foraging distance, etc.), and can vary inter-annually due to changes in spatial distribution of forage fish from year to year due to oceanographic conditions. To represent local processes generated by interactions between fish and seabird movement and foraging

variation across seabird life history, we added lognormal random variation to total prey biomass (\bar{B}_y) to create seabird prey availability for the seabird model ($P_{y,s,l}$, in Eq. 7).

$$P_{y,s,l} = \bar{B}_y v_{s,l} \quad \text{Eq. 11}$$

$$v_{s,l} \sim \text{lognormal}\left(-\frac{\sigma_{v_{s,l}}^2}{2}, \sigma_{v_{s,l}}\right) \quad \text{Eq. 12}$$

Where $v_{s,l}$ is the variation in prey available. The level of variation $v_{s,l}$ depends on seabird life history (diving depth, foraging distance from colony), life stage/breeding status (l) and season (s), as seabirds without offspring (either lost offspring, skipped breeding that year, are not of breeding age, or during the nonbreeding season) will have less constrained foraging range than those with offspring. The constraint to diving depth will be the same (physiologically) for seabirds with and without offspring. Seabirds with more limited foraging range and/or shallower diving will have greater variability in prey (higher $v_{s,l}$) as there is more variability in what they are able to reach in a year given localized movement of prey.

Scenarios

We parameterized the seabird model for two seabird types that represent contrasting life histories and ran each seabird type with each of two forage fish types (sardine and anchovy) that represent two realistic forage fish fluctuation frequencies (long slow cycles vs. rapid fluctuations). We tested five forage fish harvest control rules: two constant fishing rates and three alternative harvest control rules with biomass limits (also called ‘hockey-stick’ rules), for a total of 20 scenarios (Figure 3).

Seabird scenarios bound a range of life history variation in terms of demographic parameters impacted by prey/with functional responses (diet) and those not directly impacted by prey, e.g., foraging range and reproductive strategy: clutch size, age at breeding, max age) (Fig. 3). This gives two contrasting life history types: (1) a spatially restricted, low fecundity, specialist diet seabird, which we label the “restricted” scenario, and (2) a wider spanning, high fecundity, generalist diet seabird that we label “flexible”. While no two chosen seabird life history types can capture the full diversity of life history strategies and combination of traits found in the real world, we used these two to represent collections of traits that are plausible, and to provide contrast in terms of expected

sensitivity to forage fish fisheries. Other combinations of traits would likely result in intermediate sensitivity and there are likely other combinations not considered here that would be important for application of the model to any specific species.

Seabird life history types varied in diet specialization, where the seabird was specified as a specialist or generalist for all functional responses – survival, fledging success, and breeding attendance. Functional forms are the same general shape between the generalist and specialist for all parameters impacted by prey availability (Figure 2). But the generalists have higher survival, breeding attendance, or fledging success at low prey availability, compared to the specialist, to reflect that at these low levels, the generalist would switch to alternative prey and vital rates would not be as drastically impacted (see functional response parameters in Appendix S1: Table S2).

For variation in foraging ranges between the two seabird life histories (flexible and restricted), we used low ($\sigma_{v_{s,l}} = 0.1$) and high ($\sigma_{v_{s,l}} = 0.2$) variance in prey availability in Eq. 11 during the breeding season to create seabird scenarios of wide versus limited foraging ranges, respectively (only for birds with offspring). A wide foraging range represents seabirds that can either travel moderate to large distances from a colony to forage while breeding and/or dive deeper than other seabirds (depending on feeding method, for example pursuit diving vs. surface plunging, see Barbraud et al (2017)). Limited foraging range is shorter distances and/or shallower divers. The restricted seabird is given a higher variance of prey availability (Figure 3) because there is greater fluctuation in what that seabird can reach (with movement of the prey). In the non-breeding season and for seabirds without offspring during the breeding season (juveniles, immatures, breeding age adults with no offspring), we used low ($\sigma_{v_{s,l}} = 0.01$) and high ($\sigma_{v_{s,l}} = 0.05$) variance in prey availability for seabirds with wide versus limited ranges. These variances are lower because seabirds are less constrained in range without offspring/when not breeding but there is still variation in access between the restricted and flexible seabird types due to variation in diving depth.

Forage fish harvest scenarios

For fishing control rule scenarios, we first fished the modeled forage fish prey population (sardine or anchovy) under two conservative realistic levels (see example rates in RAM Legacy Stock Assessment Database (2020)) of constant fishing mortality – a rate of $0.5 F_{msy}$ (half the fishing

mortality at which maximum sustainable yield [MSY] is achieved), and a lower fishing mortality of equal to $0.25 F_{msy}$ (see Appendix S1: Figure S2 for example biomass). These rates allow us to capture the effects of an increase in constant fishing on the seabird for conservative fishing rates. These mortality rates were constant over time.

To test the impacts of alternative, precautionary harvest control rules on seabirds, we also fished the forage fish according to three precautionary ‘hockey-stick’ control rules with biomass limits below which the fishery is closed (Figure 3, Appendix S1: Figure S3). For these rules, forage fish is fished at a maximum rate when biomass is above a certain threshold. When forage fish biomass is below another threshold, the cut-off, the fishing rate is set to 0. Between these two thresholds, the fishing rate increases linearly with forage fish biomass. We varied thresholds and fishing levels to create three variations on the hockey stick rule, that match those ran in Siple et al. (2019); one with moderate biomass cut-off level and moderate fishing level (labeled the “moderate” hockey stick rule), one with a higher maximum fishing rate, and one with a lower biomass cut-off level.

Model Implementation

We first tested seabird model sensitivity to various seabird life history parameters by changing one parameter at a time from the “base” restricted seabird parameterization (initial parameters in Figure 3) to flexible parameterization. Specifically, we ran the initial “base” parameterization of the model for both the flexible and restricted seabird both with (1) an unfished prey and (2) a prey fished at a constant rate, with either anchovy or sardine prey. We then changed one parameter at a time in the restricted seabird model to the flexible seabird model parameterization in both the unfished and fished models. After the sensitivity analysis, we ran the “base” seabird scenarios (flexible and restricted) with prey fished under each of the five harvest control rule scenarios (Figure 3) for each prey type, sardine or anchovy. We started each seabird model run at an equilibrium age distribution. For all results we compare each seabird scenario population with a fished prey to the same scenario population with an unfished prey (seabird “unfished population”), and report metrics for both seabird and forage fish populations. When summarizing results, the first 200/1000 years of each of 100 simulations were removed to account for model stabilization for both the seabird and its prey.

For all seabird scenarios, we calculated the mean seabird population size relative to the population size with unfished prey in each simulation (across years) and then calculated and report the median proportion across 100 simulations as well as inner 75th and 95th quantiles of proportions. We also report the variance in mean seabird proportion across simulations and the probability the population drops to below 10% of the median average unfished population abundance across simulations and call this “probability of extinction” (a 90% population decline follows the IUCN (2012) metric for “critically endangered” when causes are known).

For forage fish, we calculated mean and standard deviation of both biomass and catch for each simulation and the probability of collapse for the forage fish (the proportion of years with biomass less than 20% unfished initial biomass). This is the same collapse threshold as used by Siple et al. (2019), which we used here to compare results across related studies. We also calculated the number of years with zero catch for hockey-stick rules to investigate trade-offs between seabird conservation and consistent fisheries catch. Unless otherwise described, the values we report are the median and quantiles across all simulations.

Finally, we calculated trade-offs between seabird conservation objectives and fisheries objectives for each fishery harvest control rule. When determining trade-offs, we looked at the reduction in a metric (for the seabird or fishery) that resulted from the forage fish harvest control rule, compared to the maximum possible outcome for that metric across all harvest control rules.

Models and simulations were developed and run in R (R Core Team 2020) using RStudio version 1.2.5042 (Rstudio Team 2020).

RESULTS

Fishing impacts across seabird life history

In general the seabirds responded as expected to fishing pressure: the flexible seabird was moderately robust to constant fishing, while the restricted seabird population was substantially reduced or went extinct when prey were fished at a constant fishing mortality (Figure 4). These responses were similar for both primary prey types. For seabirds preying on anchovy, the flexible seabird maintained 68-93% (median proportions across simulation yearly averages) of the seabird population without fishing but the restricted seabird declined to 0-50% of the unfished population

with constant fishing at 0.5 and 0.25 Fmsy respectively (Figure 4). Similarly with sardine prey, the restricted seabird declined to 4-51% of the population without fishing, compared to 78-93% for the flexible seabird. If we increase fishing to Fmsy, the flexible seabird is reduced to similar levels as the restricted seabird with lower constant fishing; 26% and 0% for sardine and anchovy prey, respectively (see Appendix S1: Figure S4). The difference between seabird scenarios allows us to explore what parameters are contributing to the large impact on the restricted seabird population.

The impacts of sardine fishing on the seabird population varied substantially between simulations, while impacts of anchovy fishing were less variable. At low constant fishing, variance in the mean restricted seabird population was 0.05 across simulations with sardine prey versus 0.02 with anchovy prey (Figure 4). With sardine prey, this variance led to a range in average restricted seabird population proportion of 0-87% across simulations versus a smaller range of 19-75% for seabirds preying on anchovy. Similarly, at higher constant fishing, with anchovy prey, restricted seabirds maintained only 0-1% of unfished population across all simulations and went extinct in 100% of simulations. But restricted seabirds preying on sardine maintained up to 44% of unfished population size in some simulations and did not go extinct in 8% of simulations.

Sensitivity analysis revealed that the large impacts of fishing on the restricted seabird are mainly due to functional response parameterization compared to other life history parameters. Changing all functional responses from specialist to generalist in the restricted seabird parameterization resulted in an increase in population from 50-51% to 79-80% of the unfished population, across prey types (at low constant fishing, Figure 5). Increasing reproductive opportunity by lowering the age at first breeding or increasing clutch size also led to greater population size (62-74%), but less so than changing functional response parameterization. Different levels of variance in prey availability (representing differences in foraging range) had little impact on model behavior as changing variance from high to low only slightly increased seabird abundance (50% to 55% with anchovy prey and 51% to 53% with sardine).

Of the seabird parameters impacted by prey availability, restricted seabird model behavior is most sensitive to the relationships between prey availability and adult survival or breeding attendance. With anchovy prey, changing the adult survival functional response from specialist to generalist increased the restricted seabird population from 50% to 69% of the unfished population (Figure 5).

With sardine prey, results were similar, 51% to 67%. Switching the breeder attendance relationship from specialist to generalist also increased seabird abundance; from 50-51% to 57-58% across prey. Switching the juvenile survival functional response also somewhat improved the outcome for seabirds, but less so (only increased to 53% with either prey type).

In contrast, the functional response linking prey availability and reproductive success had little impact on model seabird sensitivity to fishing and did not contribute to model sensitivity to functional response parameterization. Changing only the egg/chick survival (reproductive success) functional response from specialist to generalist led to approximately the same restricted seabird population size as the base scenario with all specialist responses, no matter the prey type (Figure 5). The restricted seabird population remained at 50% and 51% of the unfished population for seabirds preying on anchovy and sardine, respectively.

Impacts of alternative harvest control rules

The impact of fishing on seabirds was substantially reduced when prey was fished with a moderate hockey-stick control rule. The restricted seabird population maintained a median population size of 80% (of the unfished population, across simulations) when anchovy were fished with a moderate hockey-stick control rule, compared to 0 – 50% when fished at a constant rate (Figure 6). The flexible seabird also maintained highest population sizes with a moderate hockey-stick control rule for anchovy (97% of the unfished population versus 68-93% with constant fishing).

Overall patterns of seabird responses to harvest control rules were similar across prey types, except for fishing with a high fishing mortality hockey-stick. Similar to fishing anchovy, when sardine were fished with a moderate hockey-stick control rule, the restricted seabird declined to only 85% of the unfished population size, compared to 4-51% when fished at a constant rate (Figure 6). Fishing sardine with a hockey-stick with a higher maximum fishing mortality also resulted in higher abundance proportion (81%) for the restricted seabird than constant fishing. But the opposite was true for seabirds with anchovy prey; the hockey-stick with higher maximum fishing reduced both the restricted and flexible seabirds to even lower populations than with constant fishing (1% and 87%, respectively).

Though seabird responses to various control rules were similar across prey types, the mechanisms governing the sensitivity of seabirds to fishing varied by prey type, especially for the restricted seabird. For seabirds preying on sardine, harvest control rules that result in lower probability of forage fish collapse led to higher seabird population sizes, while harvest control rules that have higher sardine biomass did not necessarily lead to higher seabird abundance. For instance, low constant fishing resulted in the highest sardine biomass but not the highest seabird abundance (Figure 7 and Appendix S1: Figure S5 for flexible seabird), while the moderate hockey stick had lower sardine biomass but also the lowest probability of collapse and corresponding highest seabird abundance. The opposite was true for seabirds preying on anchovy. Control rules with higher anchovy biomass led to higher restricted seabird populations but rules that decrease probability of collapse did not necessarily result in higher seabird abundance (similar but weaker for the flexible seabird, Appendix S1: Figure S5). This variation in mechanisms across prey life history may be related to variation in fluctuation frequency between sardine versus anchovy simulated populations, as modeled sardine collapses (less than 20% unfished initial biomass) last longer than anchovy collapses (on average 4-12 years for sardine vs. 0-2.6 years for anchovy across simulations depending on harvest control rule, Appendix S1: Table S3).

Tradeoffs

Though the moderate hockey-stick rule resulted in the best outcome with fishing for all seabird scenarios, it also resulted in trade-offs in catch stability. For both prey types, the moderate hockey-stick resulted in more years with zero catch than most other control rules (Figure 8). In addition, there was higher variation in catch from year to year with the moderate hockey-stick rule (did not minimize standard deviation of catch), more so than all other control rules except the high max fishing hockey-stick. There were also losses of catch with a moderate hockey-stick rule, but these were only slight; 13-17% less catch compared to maximum catch (with a high fishing rate hockey-stick rule) across prey types but similar catch to moderate constant fishing.

For other control rules, it is possible to maximize fishery catch with moderate outcomes for seabirds (not maximized but not extinct), but this varies by prey type. For maximizing catch of sardine, the high fishing hockey stick resulted in the highest catch and second highest seabird

abundance (81% of seabird population without fishing) (Figure 8). However, when anchovy prey was fished with a high fishing hockey stick, the restricted seabird went extinct. Also, this control rule resulted in the most years with zero catch and highest variance in catch of all harvest control rules. Alternatively, with anchovy prey, low constant fishing and the low cut-off hockey-stick rule resulted in a slight loss of catch (68-84% of max catch) but maximized stability - no years with zero catch and high stability of catch (low variance) - and the restricted seabird did not go extinct but was reduced to approximately 50% of the unfished population.

DISCUSSION

Here, we presented a seabird model designed to test the impact of fishing forage fish prey on seabirds by incorporating specifics of seabird life history and seabird-forage fish dynamics that previous models have not explored in depth. We identified functional response relationships between specific seabird demographics and forage fish availability that may cause greater seabird sensitivity to fishing, forage fish life history characteristics that may exacerbate impacts of fishing forage fish prey on seabirds, but also harvest control rules that reduce impacts to seabirds with minimal trade-offs to fisheries. Seabird sensitivity to fishing was mainly dependent on the relationship between specifically adult survival and prey availability, and not dependent on the relationship between reproductive success and prey availability. Additionally, mechanisms behind seabird sensitivity to fishing varied by prey type in that seabirds with slow fluctuating prey (sardine) were more sensitive to increases in prey collapses and seabirds with fast fluctuating prey (anchovy) were sensitive to reductions in overall prey biomass. Finally, through this modeling exercise, we found that a moderate precautionary hockey-stick harvest control rule can lead to better outcomes for seabirds, and these benefits accrue without substantial reductions in fishery average catches.

Model results presented here suggest that the benefits of tailoring harvest control rules to forage life history, as claimed by Siple et al (2019), extend from forage species to seabird predators. Control rules that minimized the probability of sardine collapse led to better outcomes for the seabird, likely due to the long, cyclic fluctuations of sardine like species. When sardines collapse, either due to fishing, natural causes, or the interaction between the two, seabirds have to endure low prey abundance for long periods. Impacts of fishing on seabirds with sardine prey varied substantially

across simulations and average collapse length ranged from 0 to 40 years depending on the simulation (see Appendix S1: Table S3, when the collapse threshold is 0.2 unfished initial biomass). Seabirds have evolved to cope with fluctuating prey through life history traits that help populations sustain during low prey periods (Furness 2007, Weimerskirch 2007, Catry et al. 2013). However, if these lows are magnified by fishing, increased in frequency (Essington et al. 2015), and/or prolonged, our model points to high risk of significant population reduction and possible extinction of specialist, restricted seabirds. Alternatively, seabirds can possibly weather collapses of prey with more rapidly fluctuating prey like anchovy. In these cases, total forage fish biomass becomes more important to seabirds than collapse frequency. This was further exemplified by the substantial decline in the flexible seabird when fishing on anchovy was increased to F_{msy} (decreasing biomass further).

Alternative, responsive harvest control rules like hockey-stick strategies can likely provide great benefits in terms of seabird conservation with minimal impacts to fisheries, leading to potentially win-win or mutually acceptable outcomes (where performance was not maximized for both measures but only slight losses). Across all seabird (flexible and restricted) and forage fish prey scenarios, the moderate hockey-stick rule resulted in relative seabird populations (compared to no fishing) at ~80% or greater – the highest of any harvest control rule. This control rule also resulted in similar mean catch to fishing at a moderate constant rate (even greater catch for sardine), but did result, understandably, in more years with zero catch. Notably, the low biomass cut-off hockey-stick control rule led to OK restricted seabird abundance (~50% of population without fishing), moderate average catch, and no years with zero catch with anchovy prey. Depending on the objective of fisheries stakeholders – maximize catch or minimize years of zero catch – there are options that create win-win or OK-OK outcomes for the fishery and seabirds; and win-lose scenarios can be avoided.

Our analysis assumed that we could detect forage fish abundance with complete accuracy, but in reality this is not the case, further supporting the argument for harvest control rules that can be highly responsive and/or provide buffers for uncertainty. In forage fish management, application of harvest control rules are based on population estimates that can have considerable error (Ludwig 1994, Privitera-Johnson and Punt 2020). Therefore, differences in modeled seabird responses to fishing across various harvest control rules may be greater than shown here. Siple et al. (2019) showed for forage fish that delayed detection of changes in abundance by the assessment can result in

lower catches, higher probability of collapse, and longer collapses. Because of this, it is likely that delays in the detection of productivity shifts would magnify the negative effects shown here for seabirds. However, Siple et al. (2019) also showed that many of the negative effects of delayed detection were mitigated by precautionary harvest control rules and in some cases minimized trade-offs (depending on forage fish life history), and this has also been shown by others (Wiedenmann and Jensen 2019). Therefore, precautionary rules would likely be beneficial to seabirds and potentially fisheries as well.

Our analysis highlights a need for more empirical information on the impacts of prey abundance on seabird parameters, especially in relation to adult survival and also breeding seabird colony attendance. Life history theory suggest that even small changes in adult mortality can have large impacts on seabird population dynamics, much more so than changes in reproductive successes (Croxall and Rothery 1991, Nur and Sydeman 1999, Weimerskirch 2001, Furness 2003) and our model results led to similar conclusions. Despite this, most research effort has focused on the relationship between reproductive success and prey availability across species (Furness 2007, Field et al. 2010, Cury et al. 2011), and less so for other parameters like adult mortality (but see: (Piatt et al. 2007, Robinson et al. 2015)) and juvenile mortality, especially over time spans long enough to capture enough data to establish relationships. Also, the flexible seabird population (with a generalist diet) crashed when their anchovy prey was fished at Fmsy, suggesting that data are needed on particular thresholds of prey availability where seabirds switch prey for all functional response relationships. As others have stated before (Cury et al. 2011, Hunsicker et al. 2011, Sydeman et al. 2017), information is needed on the relationships between predator demographic parameters and prey abundance as well as thresholds in which seabird demographic rates begin to decline to accurately predict seabird-fisheries dynamics. Adult survival and breeding propensity (probability of attempting to breed) are not as easy to estimate compared to reproductive success (Weimerskirch 2001, Sydeman et al. 2017). Our model was particularly sensitive to the adult survival functional response and breeder attendance functional response. Therefore, these relationships should be captured in future models and more focus is needed on determining particular prey availability levels where colony attendance by breeders and adult survival begin to decline and seabirds switch to alternative prey.

Some of the best known and documented sensitivities of seabirds to prey availability relate to reproductive success (i.e. Cury et al. 2011), yet our model shows that these are likely the least important in governing the impact of forage fish fisheries on overall seabird population dynamics. Wildlife monitoring tends to focus on more easily measured indicators like nest success even though dynamics of seabird populations are less influenced by reproductive success compared to other population demographics (Croxall and Rothery 1991, Nur and Sydeman 1999, Sæther and Bakke 2000, Gownaris and Boersma 2019), and protecting life stages with highest reproductive value has greater conservation benefit (Crouse et al. 1987, Crooks et al. 2008). Also, seabird reproductive success fluctuates substantially from year to year due to variation in environmental conditions unrelated to prey (Wooller et al. 1992, Weimerskirch 2001). Therefore, looking at relationships between prey availability and reproductive success alone may not give a clear picture of how prey availability is impacting seabird populations. However, if periods of low prey availability are prolonged or more chronic, leading to multiple years of reproductive failure, this could result in population-level effects. Even so, our results overwhelmingly suggest that more effort should be focused on measuring more difficult to quantify demographic parameters such as adult survival, compared to reproductive success.

We represented variation in foraging ranges between the two seabird life histories with low versus high variance in prey availability, which contributed little to model seabird sensitivity to fishing, but this does not capture potential consequences of persistent directional shifts in prey availability. Both depth distribution and spatial distribution (distance from colony) of prey can be important drivers of seabird foraging success (Boyd et al. 2016) and reproductive success (Frederiksen et al. 2008, Boersma and Rebstock 2009). Short-term spatial shifts due to annual variability in prey distributions may not have substantial impacts on seabird dynamics (as suggested by our results). However, long-term shifts in prey concentrations away from seabird breeding colonies have been connected to substantial declines in seabird populations (Crawford et al. 2008, 2011, 2016). Additionally, persistent shifts in depth distributions of prey due to climate events have also been suggested as a mechanism for declines in seabirds (Barbraud et al. 2017). We modeled dynamic spatial foraging processes with a non-spatial model using changes in variability of prey, therefore, our model simplifications may not fully capture all governing processes of spatial dynamics, including

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persistent shifts that could lead to further negative impacts on seabirds. Additionally, though we modeled a closed population, immigration and emmigration may be important for some real-world seabird populations in response to localized depletion (see Oro et al. (2004)) and could be added to the model if known to be a key component of population dynamics for a particular population.

General patterns of the impacts of fishing on seabirds may hold across levels of model complexity, especially when comparing alternative precautionary control rules to constant fishing. Results shown here of the benefits of alternative hockey-stick control rules to seabirds match those shown by modeling exercises with more simplified predator-prey dynamics. Large ecosystem models (particularly Ecopath with Ecosim) that use a single population-level functional response showed significantly smaller declines in predators (especially seabirds) using hockey-stick rules for forage fish compared to constant fishing (Pikitch et al. 2012, Surma et al. 2018). However, these models could not capture the potential mechanisms underlying why hockey-stick control rules result in greater seabird abundance and how this varies by life history. Future work could investigate these mechanisms further by tailoring the model presented here to a particular seabird species or populations, and specific forage fish prey, to look at impacts of current fishing practices on potentially vulnerable species and across population life histories.

This work highlights both empirical information needs and guidance for managing the effects of forage fish fisheries on seabirds. There remains the need for greater understanding of prey abundance effects on seabird demographic rates like adult survival, adult breeding attendance, and juvenile survival. Particularly important is the detection of prey thresholds where rates begin to decline or thresholds where seabirds switch prey. At the same time, forage fish harvest control rules that meet both seabird conservation and fisheries management objectives can be found but their performance may vary depending on life history of the seabird and forage fish. In situations where resource or data constraints prevent simulation analyses like these for specific seabird-forage fish populations, a precautionary control rule (such as a hockey-stick rule) is likely a safe bet for both seabirds and fisheries. This is especially the case if fishery management prioritizes long-term average catch over stability in catches.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: [link to be added in production]

OPEN RESEARCH

R codes reported in this paper available on Zenodo: <https://doi.org/10.5281/zenodo.4603988>

REFERENCES

- Alder, J., B. Campbell, V. Karpouzi, K. Kaschner, and D. Pauly. 2008. Forage Fish: From Ecosystems to Markets. Pages 153–166. Annual Reviews, Palo Alto.
- Baker, P. J., L. Boitani, S. Harris, G. Saunders, and P. C. L. White. 2008. Terrestrial carnivores and human food production: impact and management. *Mammal Review* 38:123–166.
- Barbraud, C., A. Bertrand, M. Bouchón, A. Chaigneau, K. Delord, H. Demarcq, O. Gimenez, M. G. Torero, D. Gutiérrez, R. Oliveros-Ramos, G. Passuni, Y. Tremblay, and S. Bertrand. 2017. Density dependence, prey accessibility and prey depletion by fisheries drive Peruvian seabird population dynamics. *Ecography* 41:1092–1102.
- Beverton, R. J. H. 1990. Small marine pelagic fish and the threat of fishing; are they endangered?

Journal of Fish Biology 37:5–16.

- Boersma, P. D., E. Frere, O. Kane, L. M. Pozzi, K. Pütz, A. Raya Rey, G. A. Rebstock, A. Simeone, J. Smith, and A. Van Buren. 2013. Magellanic penguin (*Spheniscus magellanicus*). Penguins: natural history and conservation. University of Washington Press, Seattle:233–263.
- Boersma, P. D., and G. A. Rebstock. 2009. Foraging distance affects reproductive success in Magellanic penguins. *Marine Ecology Progress Series* 375:263–275.
- Boyd, C. 2012. The Predator's Dilemma: Investigating the responses of seabirds to changes in the abundance and distribution of small pelagic prey (Doctoral dissertation). University of Washington, Seattle, WA.
- Boyd, C., D. Grünbaum, G. L. Hunt, A. E. Punt, H. Weimerskirch, and S. Bertrand. 2016. Effects of variation in the abundance and distribution of prey on the foraging success of central place foragers. *Journal of Applied Ecology* 54:1362–1372.
- Bozec, Y. M., S. O'Farrell, J. H. Bruggemann, B. E. Luckhurst, and P. J. Mumby. 2016. Tradeoffs between fisheries harvest and the resilience of coral reefs. *Proceedings of the National Academy of Sciences of the United States of America* 113:4536–4541.
- Burke, C. M., and W. A. Montevecchi. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *Journal of Zoology* 278:354–361.
- Cairns, D. K. 1987. Seabirds as indicators of marine food supplies. *Biological oceanography* 5:261–271.
- Carroll, M. J., M. Bolton, E. Owen, G. Q. A. Anderson, E. K. Mackley, E. K. Dunn, and R. W. Furness. 2017. Kittiwake breeding success in the southern North Sea correlates with prior sandeel fishing mortality. *Aquatic Conservation: Marine and Freshwater Ecosystems* 27:1164–1175.
- Catry, T., J. A. Ramos, I. Catry, D. Monticelli, and J. P. Granadeiro. 2013. Inter-annual variability in the breeding performance of six tropical seabird species: influence of life-history traits and relationship with oceanographic parameters. *Marine Biology* 160:1189–1201.
- Chaudhary, A., Z. Burivalova, L. P. Koh, and S. Hellweg. 2016. Impact of Forest Management on Species Richness: Global Meta-Analysis and Economic Trade-Offs. *Scientific Reports* 6:1–10.
- Chavez, F. P., J. Ryan, S. E. Lluch-Cota, and M. Niquen. 2003. From anchovies to sardines and back:

multidecadal change in the Pacific Ocean. *Science* 299:217–221.

Checkley, D., J. Alheit, Y. Oozeki, and C. Roy, editors. 2009. *Climate Change and Small Pelagic Fish*. Cambridge University Press.

Cook, A. S. C. P., D. Dadam, I. Mitchell, V. H. Ross-Smith, and R. A. Robinson. 2014. Indicators of seabird reproductive performance demonstrate the impact of commercial fisheries on seabird populations in the North Sea. *Ecological Indicators* 38:1–11.

Crawford, R., E. Goya, J.-P. Roux, and C. Zavalaga. 2006. Comparison of assemblages and some life-history traits of seabirds in the Humboldt and Benguela systems. *African Journal of Marine Science* 28:553–560.

Crawford, R. J. M., R. Altwegg, B. J. Barham, P. J. Barham, J. M. Durant, B. M. Dyer, D. Geldenhuys, A. B. Makhado, L. Pichegru, P. G. Ryan, L. G. Underhill, L. Upfold, J. Visagie, L. J. Waller, and P. A. Whittington. 2011. Collapse of South Africa's penguins in the early 21st century. *African Journal of Marine Science* 33:139–156.

Crawford, R. J. M., R. M. Randall, T. R. Cook, P. G. Ryan, B. M. Dyer, R. Fox, D. Geldenhuys, J. Huisamen, C. McGeorge, M. K. Smith, L. Upfold, J. Visagie, L. J. Waller, P. A. Whittington, C. G. Wilke, and A. B. Makhado. 2016. Cape cormorants decrease, move east and adapt foraging strategies following eastward displacement of their main prey. *African Journal of Marine Science* 38:373–383.

Crawford, R. J. M., P. S. Sabarros, T. Fairweather, L. G. Underhill, and A. C. Wolfaardt. 2008. Implications for seabirds off South Africa of a long-term change in the distribution of sardine. *African Journal of Marine Science* 30:177–184.

Crooks, K. R., M. A. Sanjayan, and D. F. Doak. 2008. New Insights on Cheetah Conservation through Demographic Modeling. *Conservation Biology* 12:889–895.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation. *Ecology* 68:1412–1423.

Croxall, J. P., and P. Rothery. 1991. Population regulation of seabirds: implication of their demography for conservation. Pages 272–296 in C. M. Perrins, J.-D. Lebreton, and G. M. Hirons, editors. *Bird Population Studies: Relevance to Conservation and Management*. Oxford University Press.

- Cury, P., A. Bakun, R. J. Crawford, A. Jarre, R. A. Quiñones, L. J. Shannon, and H. M. Verheye. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science: Journal du Conseil* 57:603–618.
- Cury, P. M., I. L. Boyd, S. Bonhommeau, T. Anker-Nilssen, R. J. M. Crawford, R. W. Furness, J. A. Mills, E. J. Murphy, H. Osterblom, M. Paleczny, J. F. Piatt, J. P. Roux, L. Shannon, and W. J. Sydeman. 2011. Global Seabird Response to Forage Fish Depletion-One-Third for the Birds. *Science* 334:1703–1706.
- Dickey-Collas, M., R. D. M. Nash, T. Brunel, C. J. G. van Damme, C. T. Marshall, M. R. Payne, A. Corten, A. J. Geffen, M. A. Peck, E. M. C. Hatfield, N. T. Hintzen, K. Enberg, L. T. Kell, and E. J. Simmonds. 2010. Lessons learned from stock collapse and recovery of North Sea herring: a review. *ICES Journal of Marine Science* 67:1875–1886.
- Essington, T. E., P. E. Moriarty, H. E. Froehlich, E. E. Hodgson, L. E. Koehn, K. L. Oken, M. C. Siple, and C. C. Stawitz. 2015. Fishing amplifies forage fish population collapses. *Proceedings of the National Academy of Sciences of the United States of America* 112:6648–6652.
- Field, J. C., A. D. MacCall, R. W. Bradley, and W. J. Sydeman. 2010. Estimating the impacts of fishing on dependent predators: A case study in the California Current. *Ecological Applications* 20:2223–2236.
- Frederiksen, M., H. Jensen, F. Daunt, R. A. Mavor, and S. Wanless. 2008. Differential effects of a local industrial sand lance fishery on seabird breeding performance. *Ecological Applications* 18:701–710.
- Furness, R., and M. Tasker. 2000. Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series* 202:253–264.
- Furness, R. W. 2003. Impacts of fisheries on seabird communities. *Scientia Marina* 67:33–45.
- Furness, R. W. 2007. Responses of seabirds to depletion of food fish stocks. *Journal of Ornithology* 148:247–252.
- Goedegebuure, M., J. Melbourne-Thomas, S. P. Corney, M. A. Hindell, and A. J. Constable. 2017. Beyond big fish: The case for more detailed representations of top predators in marine ecosystem models. *Ecological Modelling* 359:182–192.

- Gownaris, N. J., and P. D. Boersma. 2019. Sex-biased survival contributes to population decline in a long-lived seabird, the Magellanic Penguin. *Ecological Applications* 29:e01826.
- Hilborn, R., R. O. Amoroso, E. Bogazzi, O. P. Jensen, A. M. Parma, C. Szuwalski, and C. J. Walters. 2017. When does fishing forage species affect their predators? *Fisheries Research* 191:211–221.
- Hill, S. L., J. Hinke, S. Bertrand, L. Fritz, R. W. Furness, J. N. Ianelli, M. Murphy, R. Oliveros-Ramos, L. Pichegru, R. Sharp, R. A. Stillman, P. J. Wright, and N. Ratcliffe. 2020. Reference points for predators will progress ecosystem-based management of fisheries. *Fish and Fisheries* 21:368–378.
- Hunsicker, M. E., L. Ciannelli, K. M. Bailey, J. A. Buckel, J. W. White, J. S. Link, T. E. Essington, S. Gaichas, T. W. Anderson, R. D. Brodeur, K. S. Chan, K. Chen, G. Englund, K. T. Frank, V. Freitas, M. A. Hixon, T. Hurst, D. W. Johnson, J. F. Kitchell, D. Reese, G. A. Rose, H. Sjodin, W. J. Sydeman, H. W. van der Veer, K. Vollset, and S. Zador. 2011. Functional responses and scaling in predator-prey interactions of marine fishes: contemporary issues and emerging concepts. *Ecology Letters* 14:1288–1299.
- IUCN. 2012. IUCN Red List Categories and Criteria: Version 3.1. Second edition. Gland, Switzerland and Cambridge, UK: IUCN.
- Kadin, M. 2014. Seabirds as food for thought : an integrative study on seabird ecology and ecosystem services in changing marine systems. Stockholm University.
- Kaplan, I. C., C. J. Brown, E. A. Fulton, I. A. Gray, J. C. Field, and A. D. m. Smith. 2013. Impacts of depleting forage species in the California Current. *Environmental Conservation* 40:380–393.
- Koehn, L. E., T. E. Essington, K. N. Marshall, I. C. Kaplan, W. J. Sydeman, A. I. Szoboszlai, and J. A. Thayer. 2016. Developing a high taxonomic resolution food web model to assess the functional role of forage fish in the California Current ecosystem. *Ecological Modelling* 335:87–100.
- Konar, M., S. Qiu, B. Tougher, J. Vause, M. Tlusty, K. Fitzsimmons, R. Barrows, and L. Cao. 2019. Illustrating the hidden economic, social and ecological values of global forage fish resources. *Resources, Conservation and Recycling* 151:104456.
- Lewis, S. E. F., J. K. Turpie, and P. G. Ryan. 2012. Are African penguins worth saving? The ecotourism value of the Boulders Beach colony. *African Journal of Marine Science* 34:497–504.

- Ludwig, D. 1994. Uncertainty and Fisheries Management. Pages 516–528. Springer, Berlin, Heidelberg.
- Nur, N., and W. J. Sydeman. 1999. Demographic processes and population dynamic models of seabirds. Pages 149–188 *Current Ornithology*. Springer.
- Orians, G. H., and N. E. Pearson. 1979. On the theory of central place foraging. Pages 155–177 in J. Horn, G. R. Stairs, and R. D. Mitchell, editors. *Analysis of ecological systems*. Ohio State Press, Columbus, OH.
- Oro, D., E. Cam, R. Pradel, and A. Martínez-Abraín. 2004. Influence of food availability on demography and local population dynamics in a long-lived seabird. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271:387–396.
- Piatt, J. F., A. M. A. Harding, M. Shultz, S. G. Speckman, T. I. van Pelt, G. S. Drew, and A. B. Kettle. 2007. Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series* 352:221–234.
- Pikitch, E., P. D. Boersma, I. L. Boyd, D. O. Conover, P. Cury, T. Essington, S. S. Heppell, E. D. Houde, M. Mangel, and D. Pauly. 2012. Little fish, big impact: managing a crucial link in ocean food webs. *Lenfest Ocean Program*, Washington, DC 108.
- Pikitch, E. K., K. J. Rountos, T. E. Essington, C. Santora, D. Pauly, R. Watson, U. R. Sumaila, P. D. Boersma, I. L. Boyd, D. O. Conover, P. Cury, S. S. Heppell, E. D. Houde, M. Mangel, E. Plagányi, K. Sainsbury, R. S. Steneck, T. M. Geers, N. Gownaris, and S. B. Munch. 2014. The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries* 15:43–64.
- Pikitch, E. K., C. Santora, E. A. Babcock, A. Bakun, R. Bonfil, D. O. Conover, P. Dayton, P. Doukakis, D. Fluharty, B. Heneman, E. D. Houde, J. Link, P. A. Livingston, M. Mangel, M. K. McAllister, J. Pope, and K. J. Sainsbury. 2004. Ecosystem-based fishery management. *Science* 305:346–347.
- Plagányi, É. E. 2007. Models for an ecosystem approach to fisheries. *FAO Fisheries Technical Paper*, 477. FAO, Rome, pp. 108.
- Plagányi, É. E., A. E. Punt, R. Hillary, E. B. Morello, O. Thébaud, T. Hutton, R. D. Pillans, J. T. Thorson, E. A. Fulton, and A. D. Smith. 2014. Multispecies fisheries management and

conservation: tactical applications using models of intermediate complexity. *Fish and Fisheries* 15:1–22.

Power, A. G. 2010. Ecosystem services and agriculture: tradeoffs and synergies. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2959–2971.

Privitera-Johnson, K. M., and A. E. Punt. 2020. A review of approaches to quantifying uncertainty in fisheries stock assessments. *Fisheries Research* 226:105503.

Punt, A. E., A. D. MacCall, T. E. Essington, T. B. Francis, F. Hurtado-Ferro, K. F. Johnson, I. C. Kaplan, L. E. Koehn, P. S. Levin, and W. J. Sydeman. 2016. Exploring the implications of the harvest control rule for Pacific sardine, accounting for predator dynamics: A MICE model. *Ecological Modelling* 337:79–95.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

RAM Legacy Stock Assessment Database. 2020. RAM Legacy Stock Assessment Database v4.491 (Version v4.491) [Data set]. Zenodo. <http://doi.org/10.5281/zenodo.3676088>.

Rice, J., and D. Duplisea. 2013. Management of fisheries on forage species: the test-bed for ecosystem approaches to fisheries. *ICES Journal of Marine Science* 71:143–152.

Robinson, W. M., D. S. Butterworth, and É. E. Plagányi. 2015. Quantifying the projected impact of the South African sardine fishery on the Robben Island penguin colony. *ICES Journal of Marine Science: Journal du Conseil*:1822–1833.

Rstudio Team. 2020. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL <http://www.rstudio.com/>.

Sæther, B.-E., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642–653.

Schreiber, E. A., and J. Burger. 2001. *Biology of Marine Birds*. CRC Press, Boca Raton, Florida.

Siple, M. C., T. E. Essington, and É. E. Plagányi. 2019. Forage fish fisheries management requires a tailored approach to balance trade-offs. *Fish and Fisheries* 20:110–124.

Smith, A. D. M., C. J. Brown, C. M. Bulman, E. A. Fulton, P. Johnson, I. C. Kaplan, H. Lozano-Montes, S. Mackinson, M. Marzloff, L. J. Shannon, Y.-J. Shin, and J. Tam. 2011. Impacts of Fishing Low-Trophic Level Species on Marine Ecosystems. *Science* 333:1147–1150.

- Sunada, J. S., P. R. Kelly, I. S. Yamashita, and F. Gress. 1981. The brown pelican as a sampling instrument of age group structure in the northern anchovy population. *CalCOFI Rep.* 22:65–68.
- Surma, S., T. J. Pitcher, R. Kumar, D. Varkey, E. A. Pakhomov, and M. E. Lam. 2018. Herring supports Northeast Pacific predators and fisheries: Insights from ecosystem modelling and management strategy evaluation. *PLOS ONE* 13:e0196307.
- Sydeman, W. J., S. A. Thompson, T. Anker-Nilssen, M. Arimitsu, A. Bennison, S. Bertrand, P. Boersch-Supan, C. Boyd, N. C. Bransome, R. J. M. Crawford, F. Daunt, R. W. Furness, D. Gianuca, A. Gladics, L. Koehn, J. W. Lang, E. Logerwell, T. L. Morris, E. M. Phillips, J. Provencher, A. E. Punt, C. Saraux, L. Shannon, R. B. Sherley, A. Simeone, R. M. Wanless, S. Wanless, and S. Zador. 2017. Best practices for assessing forage fish fisheries-seabird resource competition. *Fisheries Research* 194:209–221.
- Szoboszlai, A. I., J. A. Thayer, S. A. Wood, W. J. Sydeman, and L. E. Koehn. 2015. Forage species in predator diets: Synthesis of data from the California Current. *Ecological Informatics* 29:45–56.
- Tacon, A. G. J., and M. Metian. 2009. Fishing for feed or fishing for food: increasing global competition for small pelagic forage fish. *AMBIO: A Journal of the Human Environment* 38:294–302.
- Tasker, M. L., C. J. Camphuysen, J. Cooper, S. Garthe, W. A. Montevecchi, and S. J. Blaber. 2000. The impacts of fishing on marine birds. *ICES Journal of Marine Science: Journal du Conseil* 57:531–547.
- Travis, J., F. C. Coleman, P. J. Auster, P. M. Cury, J. A. Estes, J. Orensanz, C. H. Peterson, M. E. Power, R. S. Steneck, and J. T. Wootton. 2014. Integrating the invisible fabric of nature into fisheries management. *Proceedings of the National Academy of Sciences* 111:581–584.
- Weimerskirch, H. 2001. Seabird demography and its relationship with the marine environment. Pages 128–149 *in* E. A. Schreiber and J. Burger, editors. *Biology of marine birds*. CRC press, Boca Raton, Florida.
- Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography* 54:211–223.
- Wiedenmann, J., and O. P. Jensen. 2019. Could recent overfishing of New England groundfish have been prevented? A retrospective evaluation of alternative management strategies. *Canadian*

Journal of Fisheries and Aquatic Sciences 76:1006–1018.

Wooller, R. D., J. S. Bradley, and J. P. Croxall. 1992. Long-term population studies of seabirds.

Trends in Ecology & Evolution 7:111–114.

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TABLES

Table 1. Parameters and functions related to the recursive equations for the age-stage structured seabird model.

Parameter/function	Definition
Seabird model	
$N_{y,s,a}$	Number of seabirds in year y , season, s , and age a
a_b	Age at first breeding
a_x	Maximum age (life-span); assumed to die after max age
E_{\max}	Max amount of viable eggs that can be laid based on assumptions of carrying capacity and dependent on clutch size (maximum possible eggs per pair)
E_y	The number of eggs laid at the beginning of year y
f_y	The total number of eggs/chick that fledge and reach independence in year y
\tilde{c}	Clutch size– total possible number of eggs laid by each breeding seabird pair
$S_{y,s,l}$	Maximum bi-annual survival rate for each year and season and life stage, where life stage is either egg (e), chick (c), juvenile (j), immature (i, not juvenile but not yet breeding age), and all adults (same value for breeding or nonbreeding, b and n). Pulled from a beta distribution with mean \bar{S}_l and variance σ_l^2
\bar{S}_l	Mean maximum survival rate per life stage – egg, chick, juvenile, immature, or adult
σ_l^2	Variance of maximum survival rates for each life stage – egg, chick, juvenile, immature, or adult
Related to prey and impacted by prey	
$r_y(N_{y,s,a}, \gamma_{y,s,l})$	Annual per capita egg production rate – function of number of breeders and prey availability reduction on number of breeders (breeding

	propensity)
$\gamma_{y,s,l}$	Impact of prey availability on the number of breeding adults that attempt to breed (breeding propensity) where $s = n$ for the nonbreeding season and life stage l is adults (both nonbreeding and breeding)
$\delta_{y,s=b,l=C_c}$	Impact of prey availability on the survival to fledging for eggs/chicks (survival to independence), that is dependent on the total number of offspring, one, two, or three ($C_c = 1, 2, \text{ or } 3$)
$\delta_{y,s,l}$	Impact of prey availability on the survival rate for life stage l – juvenile (j), immature (i), breeding adult (b), or non-breeding breeding-age adult (n)
$P_{y,s,l}$	Amount of forage fish prey biomass available to the seabird in year y , season s , and seabird life stage l where life stage is egg/chick (C), juvenile (j), immature (i), breeding adult (b), or non-breeding breeding-age adult (n)
\bar{P}_l	Average $P_{y,s,l}$ in the absence of fishing for each life stage l
Functional response parameters	
α	Lowest possible value of $\delta_{y,s,l}$
β	Point in prey availability of the initial decline in $\delta_{y,s,l}$
m	Slope of the function $\delta_{y,s,l}$

FIGURE LEGENDS

Figure 1. Schematic of seabird age-stage structured population model. Processes (arrows) with a fish symbol denote processes that are influenced by prey availability. Therefore, survival rates are related to non-prey related mortality and prey related mortality, which vary by life stage. At the left of the schematic, the number of eggs and chicks that survive leads to the number of adults with surviving offspring which is directly related to the number of chicks that fledge (reach independence). Fish, eggs, and seabird images modified from the symbol libraries courtesy of the Integration and Application Network (IAN), University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

Figure 2. Functional responses for each demographic parameter across two scenarios of diet specialization on forage fish prey (specialist = solid line, generalist = dotted line). The proportion of prey available ($P_{y,s,l}/\tilde{P}_l$) is the relationship between prey in a given year (y), season (s), for a specific seabird life stage (l) ($P_{y,s,l}$), over average prey availability when the prey is not fished (\tilde{P}_l). The variable $\delta_{y,s,l}$ modifies seabird survival and $\gamma_{y,s,l}$ modifies the number of seabirds breeding (breeding propensity) to adjust for prey availability impacts. (A) Shows variation in functional response between adult survival (red), breeder colony attendance/propensity (black), and juvenile survival (blue). General functional response shapes are similar to those in Piatt et al. 2007 and Robinson et al. 2015 (for adult survival). (B) Shows variation in functional response depending on the number of total chicks where more prey is needed to successfully fledge a chick if there are multiple chicks. General shape and thresholds match those seen in Cury et al. 2011.

Figure 3. Factors and different levels of each scenario modeled in the analysis including seabird, forage fish, and harvest control rule scenarios. At the top, parameters/specifications for the seabird life history types are given for both flexible and restricted seabird life history scenarios. Types of forage fish (sardine-like and anchovy-like) scenarios and specific life history related to each are listed along with example biomass time series. Harvest control rule scenarios tested are also given with specific parameter values and graphical representation of the harvest control rule.

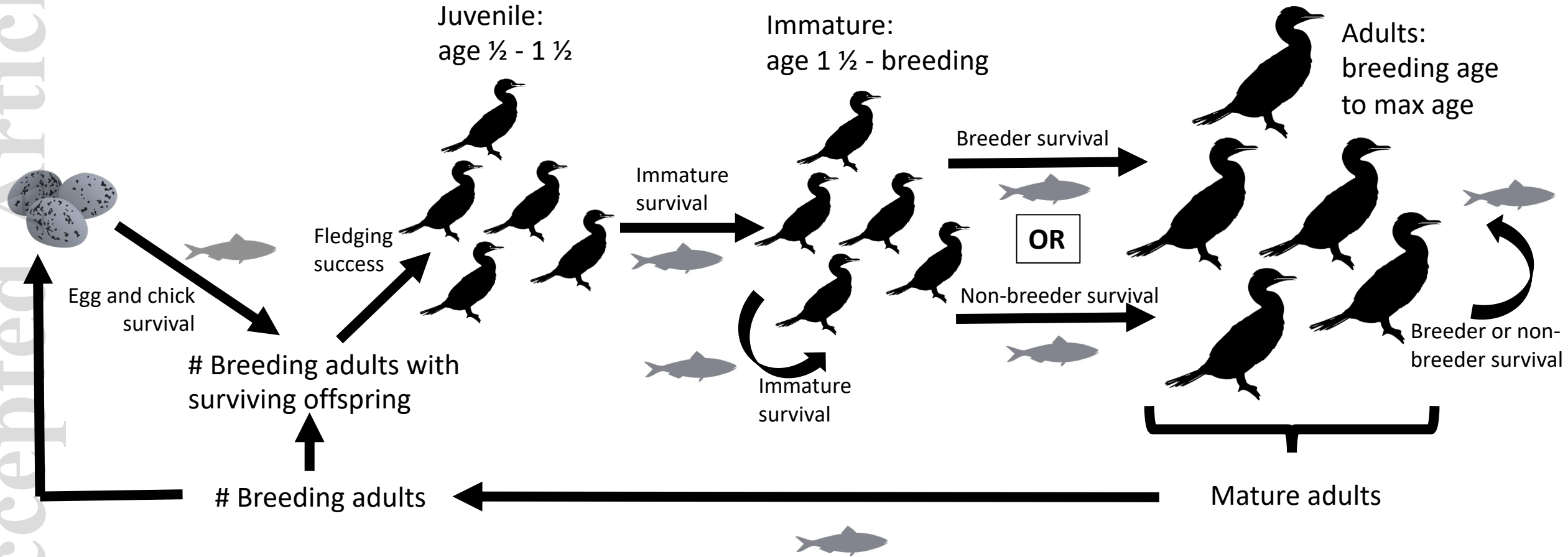
Figure 4. Seabird population metrics across 100 simulations for a restricted seabird (solid dots) and flexible seabird (open dots) for fishing different seabird prey (sardine or anchovy) at two constant harvest rates (low - 0.25 F_{msy} and moderate - 0.5 F_{msy}). Shown at the top is median seabird abundance (median of average values across simulations) relative to unfished abundance; middle is the probability the population declines to <10% of the unfished population across simulations; bottom is the variance in mean seabird populations across simulations.

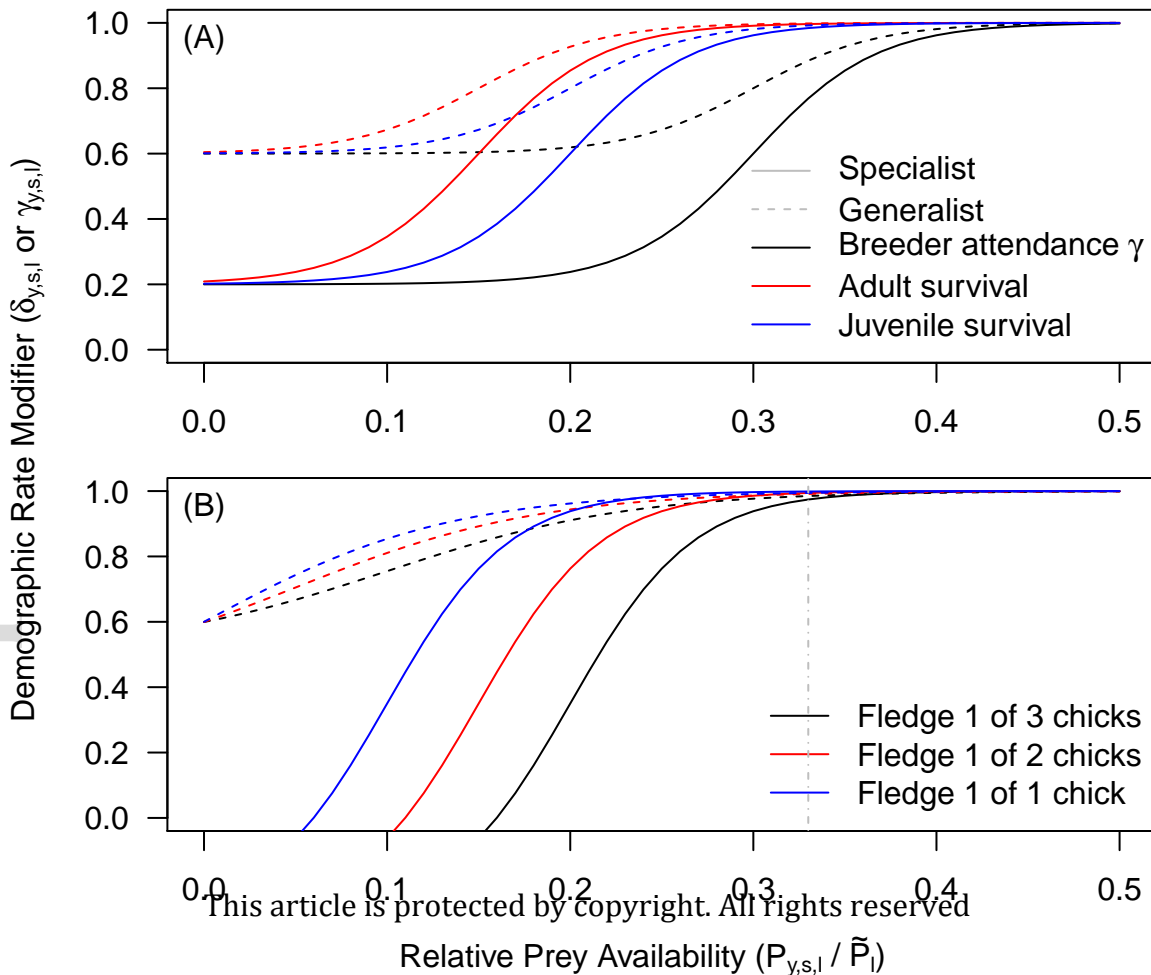
Figure 5. Median (dots), 50% quantiles (thick lines), and 95% quantiles (thin lines) of average relative seabird abundance (relative to population with unfished prey) across 100 simulations for sensitivity analysis in seabird model parameterization for fishing either prey (anchovy - grey or sardine - black) at constant fishing at 0.25 F_{msy} . For the sensitivity analysis, we changed a parameter/function in the base model for the restricted seabird (prey variability variance, clutch size, age at first breeding, and functional response type) individually to the flexible seabird value or type, or changed a single functional response (adult survival, juvenile survival, reproductive success, breeder attendance) from specialist to generalist (below dotted line). Prey variability variance, clutch size, age at first breeding are not impacted by prey availability in a given year while functional responses are impacted prey. The model is most sensitive to functional response parameterization especially for adult survival and breeder attendance.

Figure 6. Median (dot) and 95% quantile (line) of seabird average relative abundance (compared to no fishing scenario) across simulations for different scenarios of forage fish harvest control rules and forage fish prey (anchovy or sardine). Control rules include two levels of constant fishing and three hockey-stick cut-off rules: (A) moderate cut-off and fishing, (B) low biomass cut-off, and (C) high max fishing rate. Results for the flexible seabird scenario are presented in red and for the restricted seabird are presented in black. The moderate hockey stick control rule leads to the highest relative seabird abundance across seabird and prey scenarios.

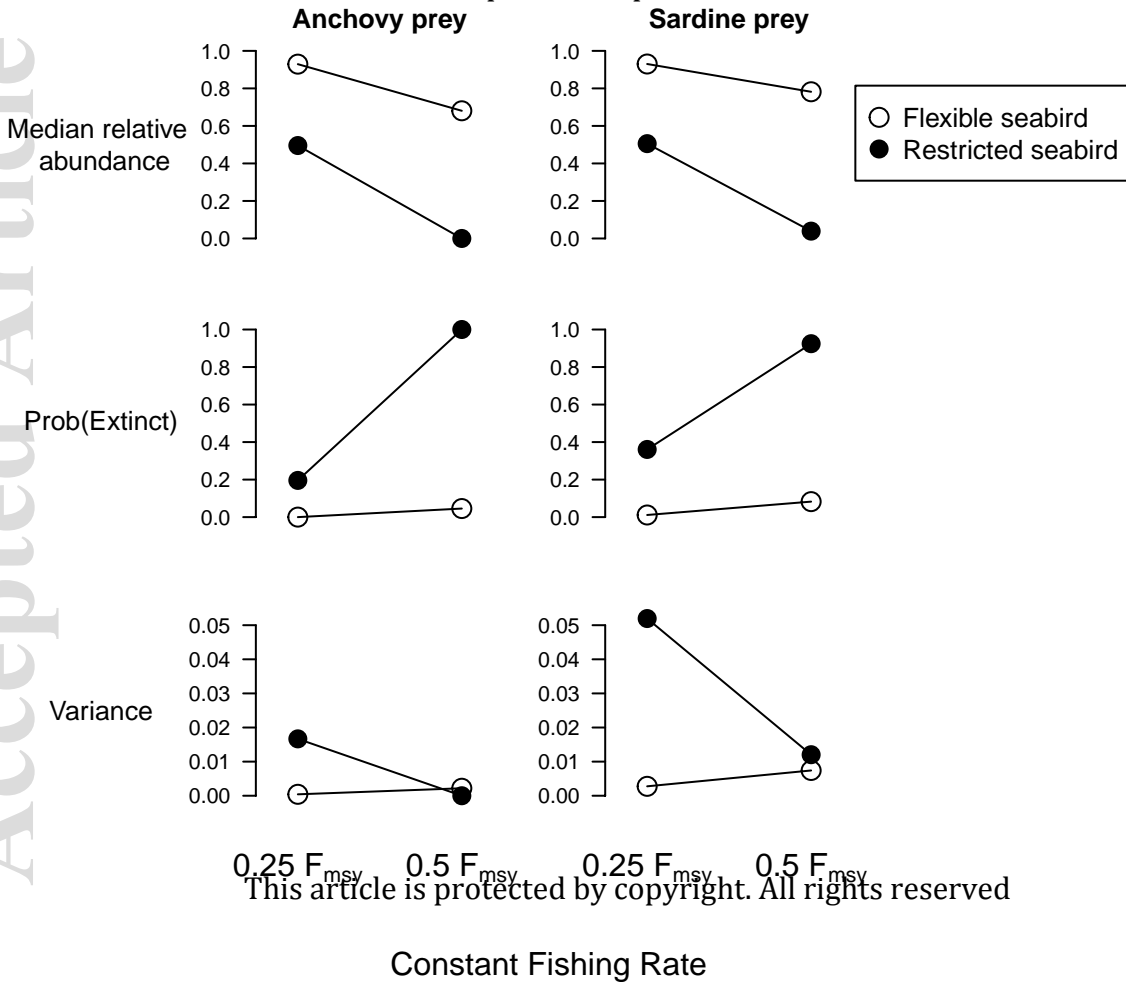
Figure 7. Relationships between restricted seabird abundance and (1) forage fish probability of collapse (left) and (2) forage fish biomass (right), for seabirds that prey on sardine (top) or anchovy (bottom) across five forage fish harvest control rules. All values are scaled for a minimum of 0 and a maximum of 3, where 3 is the best, either largest abundance or biomass, or minimal probability of collapse. Control rules that minimize probability of collapse for sardine lead to higher seabird abundance while control rules that maximize anchovy biomass lead to higher seabird abundance.

Figure 8. Trade-offs between fishery objective metrics: median average forage fish catch, catch standard deviation, and years with zero catch, for fishing sardine (top) and anchovy (bottom) across five harvest control rules across 100 simulations. Metrics are scaled between 0 (worst performance of all control rules) and 3 (“best” performance of all control rules) – where best refers to maximizing catch, or minimizing variance of catch or years with zero catch.



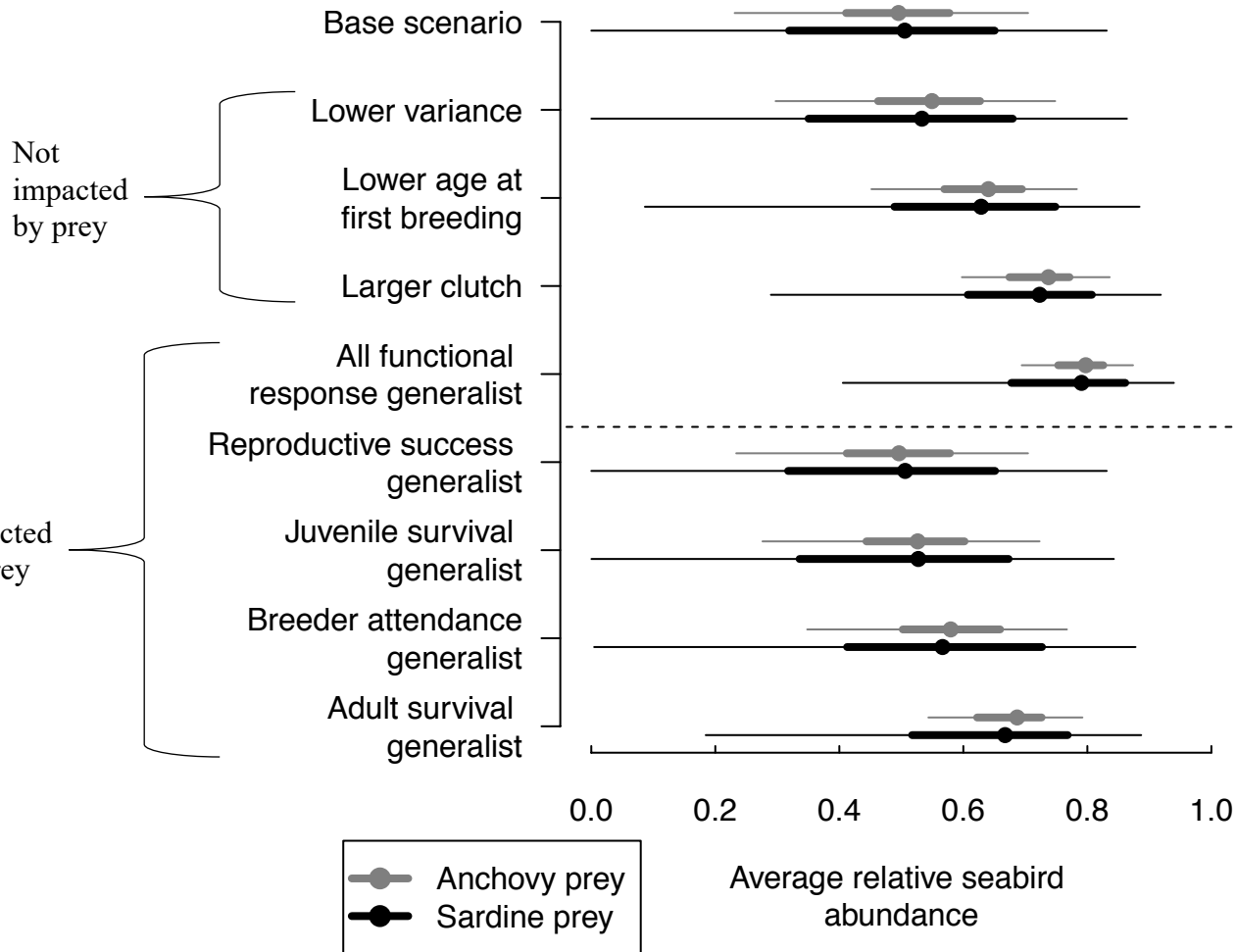


Factor	Levels	Base Parameterization				
Seabird life history types		<u>Impact of prey</u>		<u>Not impacted by prey</u>		
	<u>Name</u>	<u>Diet specialization</u>	<u>Foraging – prey deviation</u>	<u>Max age</u>	<u>Age at 1st breeding</u>	<u>Clutch size</u>
	Restricted	Specialist	High variance (shallow and/or nearshore foraging)	High (30 yrs)	Older (5 yrs)	1
	Flexible	Generalist	Low variance (deep and/or offshore foraging)	Low (15 yrs)	Young (3 yrs)	3
Forage species	<u>Species</u>	<u>Life history</u>				
	Sardine	Low M; low-frequency fluctuations				
	Anchovy	High M; rapid fluctuations				
Harvest control rules	<u>Type</u>	<u>Fishing rate</u>				
	Constant fishing	Low (0.25 Fmsy)				
		Moderate (0.5 Fmsy)				
	Hockey stick cut-off	Moderate				
		Low cut-off[
High fishing						



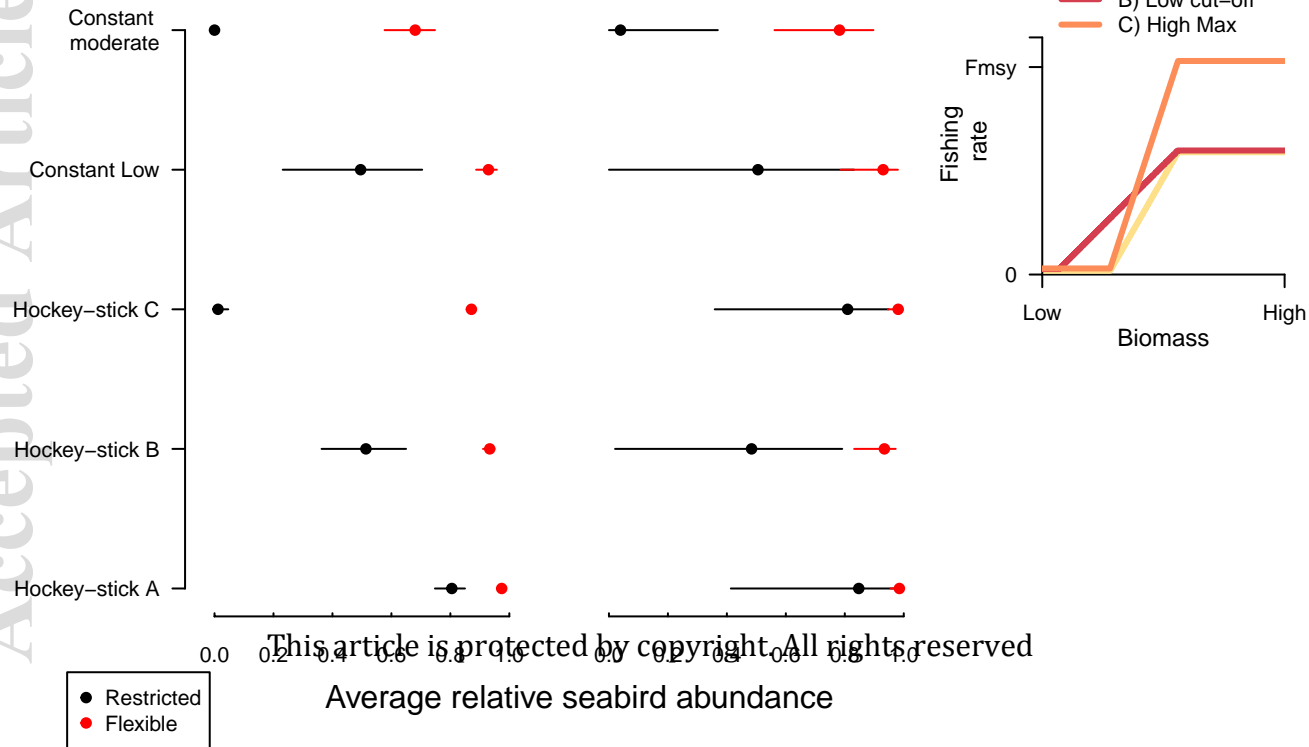
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Constant Fishing Rate



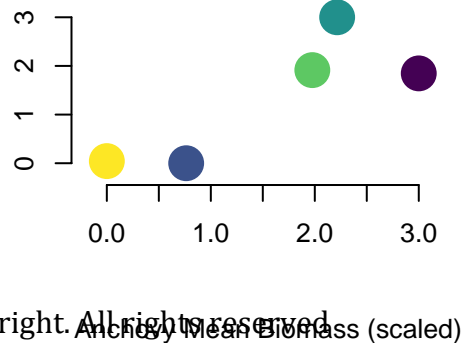
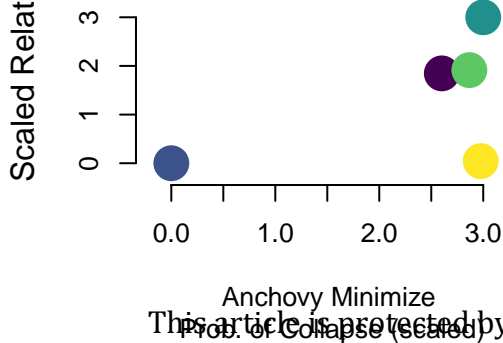
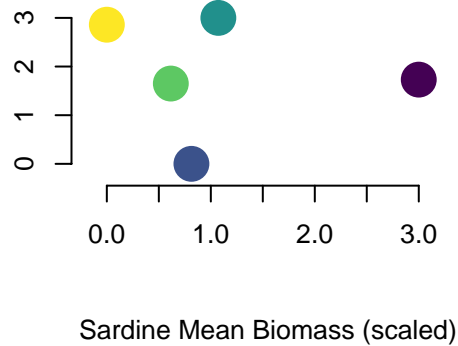
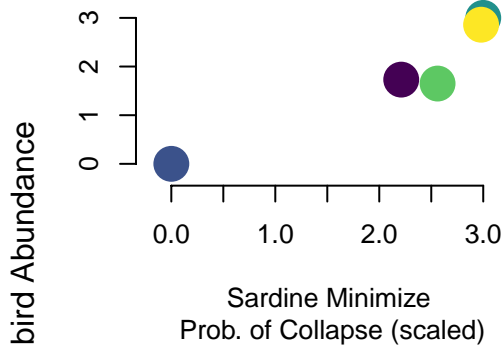
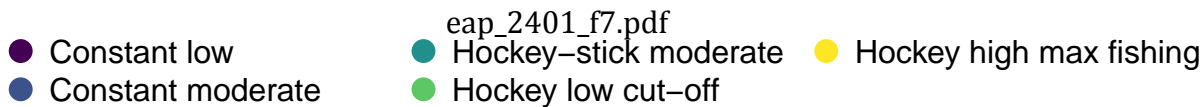
Anchovy Fishery

Sardine Fishery



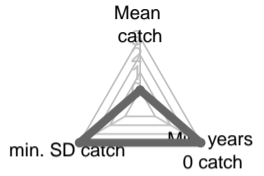
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Average relative seabird abundance

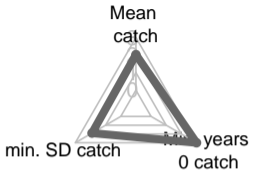


Sardine

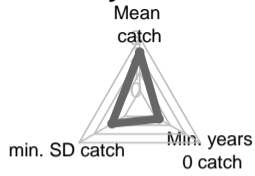
Constant low



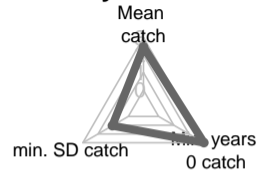
Constant moderate



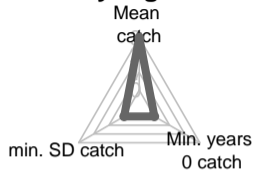
Hockey moderate



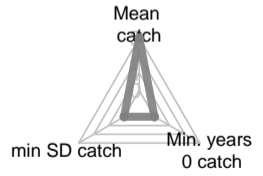
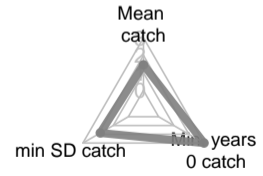
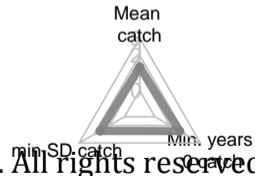
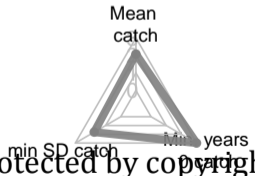
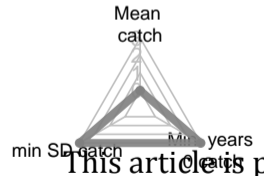
Hockey low cut-off



Hockey high F max



Anchovy



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