






# Evaluating impacts of forage fish abundance on marine predators

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**Abstract:** Forage fish—small, low trophic level, pelagic fish such as herrings, sardines, and anchovies—are important prey species in marine ecosystems and also support large commercial fisheries. In many parts of the world, forage fish fisheries are managed using precautionary principles that target catch limits below the maximum sustainable yield. However, there are increasing calls to further limit forage fish catch to safeguard their fish, seabird, and marine mammal predators. The effectiveness of these extra-precautionary regulations, which assume that increasing prey abundance increases predator productivity, are under debate. In this study, we used prey-linked population models to measure the influence of forage fish abundance on the population growth rates of 45 marine predator populations representing 32 fish, seabird, and mammal species from 5 regions around the world. We used simulated data to confirm the ability of the statistical model to accurately detect prey influences under varying levels of influence strength and process variability. Our results indicate that predator productivity was rarely influenced by the abundance of their forage fish prey. Only 6 predator populations (13% of the total) were positively influenced by increasing prey abundance and the model exhibited high power to detect prey influences when they existed. These results suggest that additional limitation of forage fish harvest to levels well below sustainable yields would rarely result in detectable increases in marine predator populations.

**Keywords:** ecosystem-based fisheries management, ecosystem models, forage fish, marine mammals, precautionary management, predator-prey dynamics, seabirds, small pelagics

Evaluación de los Efectos de la Abundancia de Peces Forrajeros sobre los Depredadores Marinos

**Resumen:** Los peces forrajeros—peces pequeños, pelágicos y de bajo nivel trófico como el arenque, las sardinillas y las anchoas—son especies presa importantes en los ecosistemas marinos y además mantienen a grandes pesquerías comerciales. En muchas partes del mundo, las pesquerías de los peces forrajeros son manejadas mediante el uso de principios precautorios que se enfocan en los límites de captura por debajo de la producción máxima sostenible. Sin embargo, cada vez hay más peticiones para incrementar la limitación de la captura de peces forrajeros para salvaguardar a las especies depredadoras de peces, aves y mamíferos marinos asociadas a estos peces. La efectividad de estas regulaciones, que están basadas en el supuesto de que al incrementar la abundancia de presas incrementa la productividad de los depredadores, está en debate. Usamos modelos poblacionales vinculados a la presa para medir la influencia de la abundancia de los peces forrajeros sobre las tasas de crecimiento poblacional de 45 poblaciones de depredadores marinos (28 peces, 10 aves marinas y 7 mamíferos) en cinco regiones alrededor del mundo. Usamos datos simulados para confirmar la habilidad del modelo estadístico para detectar certeramente las influencias de la presa bajo niveles variantes de fuerza de influencia y de proceso de variabilidad. La productividad del depredador rara vez afectó a la abundancia de su presa forrajera. Sólo seis poblaciones de depredadores (13% del total) estuvieron afectadas positivamente por la creciente abundancia de la presa y el modelo exhibió un poder alto para detectar las influencias de la presa cuando estuvieron presentes.

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Estos resultados sugieren que las limitaciones sobre la pesca de peces forrajeros a niveles muy por debajo de la productividad sostenible pocas veces resultarían en incrementos detectables en las poblaciones de depredadores marinos.

**Palabras Clave:** aves marinas, dinámicas depredador-presa, mamíferos marinos, manejo de pesquerías basado en el ecosistema, manejo precautorio, modelos de ecosistemas, peces pelágicos pequeños

## Introduction

Forage fish are small pelagic fish (e.g., herrings, sardines, and anchovies) that provide benefits to both people and marine ecosystems. They represent the largest species group landed in marine capture fisheries (21 million tons or 25.5% of reported landings in 2015) (FAO, 2018) and are under increasing demand as a source of fish meal for livestock and aquaculture and as food for humans (Tacon & Metian, 2015). Seabirds, marine mammals, and large piscivorous fish also rely on forage fish for food (Cury et al., 2000) and may therefore be in direct competition with fisheries (Pikitch et al., 2014; Rountos et al., 2015; Smith et al., 2011). Although many forage fish populations are already managed with precautionary principles that target catch limits below the maximum sustainable yield (Hilborn et al., 2020), there are increasing calls to further limit forage fish catch to safeguard populations of valuable fish predators (e.g., tuna and salmon) and protected seabird and marine mammal species (Pikitch et al., 2012). For example, the Forage Fish Conservation Act (H.R. 2236), introduced to the U.S. Congress in April 2019 and currently undergoing hearings, would require reducing catch limits significantly below sustainable yields in consideration of predator needs.

However, the need for such “extra-precautionary” regulations is under debate (Hilborn et al., 2017a, 2017b; Pikitch et al., 2012, 2018). On the one hand, forage fish represent a large portion of marine predator diets and reductions in prey availability below the thresholds necessary for successful foraging, offspring provisioning, or survival could affect predator population growth. Indeed, field studies show that fishing forage fish can reduce seabird breeding success (Frederiksen et al., 2008) and a number of ecosystem models predict that marine predator populations should be sensitive to prey depletion (Pikitch et al., 2014; Smith et al., 2011). On the other hand, marine predators often exhibit high mobility and diet flexibility, and species with location-based breeding tend to locate breeding sites where prey abundance is high and stable. Together, these behaviors could make them resilient to changes in prey abundance at a wider scale. Thus, for many predator populations, there is limited if any correlation between a predator population’s growth rate and the abundance of its primary prey (Hilborn et al., 2017a).

The lack of consensus regarding management of forage fish is likely due to the complexity of predator-prey

systems and common pitfalls in the way these systems are studied (Sydeman et al., 2017). Although field studies offer the opportunity to establish a causal understanding of the impact of fishing and subsequent prey depletion on marine predators, they are difficult to design given natural variability in forage fish and the movements of both predators and prey (Sherley et al., 2018). Ecosystem models can reveal direct and indirect effects stemming from predator-prey relationships, but these models can be sensitive to (often implicit) assumptions about prey switching, top-down versus bottom-up control, and other poorly understood processes. Furthermore, ecosystem models seldom include sufficient taxonomic resolution to capture predator-specific sensitivities to prey depletion (Essington & Plagányi, 2014) (but see Koehn et al. [2017]) and their results can be sensitive to model choice (Kaplan et al., 2013). Finally, correlational studies present the opportunity to use historical data to evaluate observed predator-prey relationships but cannot demonstrate causal relationships. Furthermore, they often fail to account for spatial and temporal mismatches between predator and prey data as well as the lagged effects of prey depletion on predator dynamics (Sydeman et al., 2017).

Ecosystem models of intermediate complexity (MICE) (Plagányi et al., 2014a) are used to balance the advantages of single-species and whole-of-ecosystem models and may better show the impact of fishing for forage fish on their predators. By representing the minimum number of ecosystem components required to address the question under consideration, MICE are generally more focused and resolved than typical whole-of-ecosystem models. Such models have been used to show that fisheries targeting different forage species can influence predator populations differently (Plagányi et al., 2014b), that the effect of changing prey spatial distributions can be larger than the effect of changing abundance (Robinson et al., 2015), and that the impact of changing prey abundance can be unpredictable when predator populations are already low (Watters et al., 2013). Although each of these models was tailored to a specific predator-prey system, simpler MICE could be used to assess predator-prey systems across many regions in a single analysis.

We used a MICE approach to measure the influence of forage fish abundance on the productivity (i.e., population growth rate) of 45 marine predator populations of 32 species. The populations were from 5 regions—U.S.

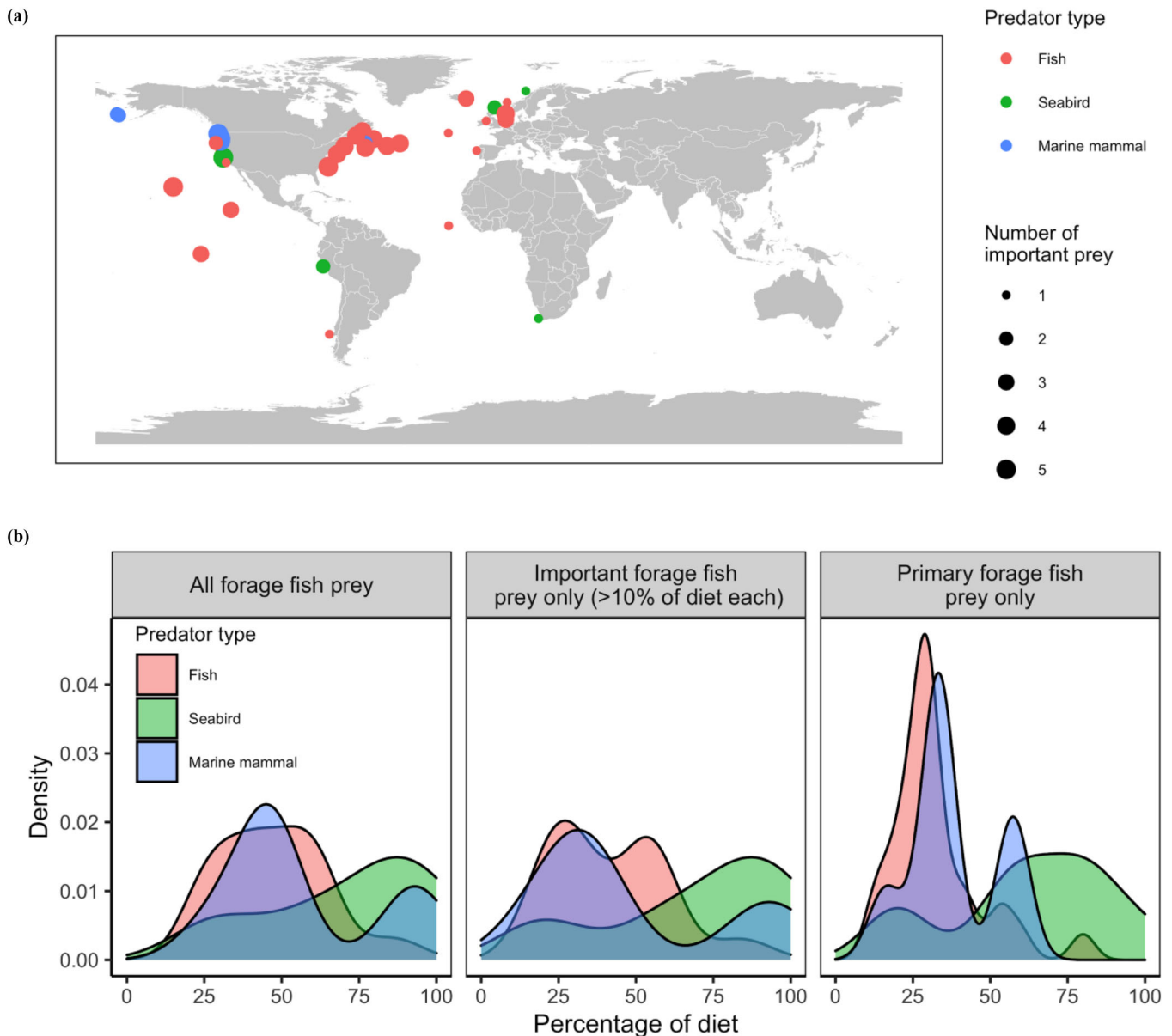


Figure 1. The (a) location of evaluated marine predator populations and the number of important prey species and (b) their dependence on forage fish as a source of prey. In (b), density distributions show the percentage of predator diets composed of all forage fish prey, important forage fish prey (i.e., all species individually representing >10% of the diet), and the primary forage fish prey (i.e., the species representing the largest percentage of the diet).

West Coast, U.S. East Coast, Europe, Humboldt Current, and South Africa—where forage fish support large fisheries and are important to marine ecosystems. We used a simulation analysis to confirm the ability of our statistical model to accurately detect prey influences if they exist. We quantified the frequency with which forage fish abundance influences predator productivity and used these findings to reflect on the extent to which extra-precautionary regulations on forage fish are likely to have the intended benefits for their predators.

## Methods

### Data Collection

We identified 28 fish, 10 seabird, and 7 mammal predator populations (Figure 1) that rely on forage fish for  $\geq 20\%$  of their diet; spatially overlap with an assessed population (i.e., population has an estimate or index of abundance) of an important prey species (i.e.,  $\geq 10\%$  of their diet); and share  $\geq 20$  years of overlapping abundance data with an important prey species if they are fish predators or  $\geq 15$  years of such data if they are seabird or marine

mammal predators (see Appendix S1 for details). The data requirements for seabirds and marine mammals were relaxed because their time series were generally shorter and less complete than those for fish. The majority of fish abundance time series were sourced from the RAM Legacy Stock Assessment Database (version 4.4) (Ricard et al., 2012). Fourteen came from government or academic stock assessments not included in the database. All fish predator time series were reported as total biomass in metric tons. Most prey time series were reported as absolute biomass, but some were reported as indices of relative abundance. Marine mammal abundance time series came primarily from National Oceanic and Atmospheric Administration (NOAA) Marine Mammal Stock Assessments (Hayes et al., 2017; Carretta et al., 2017) and were reported largely as total abundance or pup abundance. Seabird abundance time series were sourced from a mixture of peer-reviewed journal publications, technical reports, books, theses, and government websites. They were reported in a mixture of units including total abundance, adult abundance, and number of nests or breeding pairs.

### Population Models

We modeled marine predator productivity in 3 stages. First, we modeled productivity without environmental covariates and used this base model as a benchmark for evaluating models with additional environmental covariates. Second, we extended the base model to evaluate whether abundance of either the primary prey species or sum of all important prey species with available data influenced predator productivity. Finally, we used the extended model to measure the influence of sea surface temperature (SST) on predator productivity and evaluate the importance of temperature relative to the importance of prey abundance. All analyses were performed using the R computing software (R Core Team, 2020).

#### Base model

We modeled predator productivity with a Pella-Tomlinson surplus production model (Pella & Tomlinson, 1969) because it contains a shape parameter ( $p$ ) that allows it to replicate either the Fox ( $p \rightarrow 0$ ) or Schaefer ( $p = 1$ ) production models (Schaefer, 1954; Fox, 1970):

$$SP_{i,t} = \frac{r_i}{p} B_{i,t} \left( 1 - \left( \frac{B_{i,t}}{K_i} \right)^p \right) + \varepsilon_{i,t}, \quad (1)$$

where  $SP_{i,t}$  is the surplus production for population  $i$  in year  $t$ ,  $N_{i,t}$  is the abundance,  $r_i$  divided by  $p$  is the intrinsic rate of growth,  $K_i$  is the carrying capacity, and  $\varepsilon_{i,t}$  is assumed to be independent identically distributed log-normal residual process variability. Surplus production is the (annual) net change in abundance in the absence of

harvest. It was calculated here as follows:

$$SP_{i,t} = B_{i,t+1} - B_{i,t} + C_{i,t}, \quad (2)$$

where  $SP_{i,t}$  is the surplus production for population  $i$  over year  $t$ ,  $N_{i,t}$  and  $N_{i,t+1}$  are the abundances of population  $i$  at the start of years  $t$  and  $t+1$ , respectively, and  $C_{i,t}$  is the catch for population  $i$  removed in year  $t$  ( $C_{i,t} = 0$  for seabirds and marine mammals, which are not subject to harvest). We evaluated models with shape parameters ( $p$ ) that maximize productivity at 50% ( $p = 1.00$ ), 45% ( $p = 0.55$ ), 40% ( $p = 0.20$ ), and 37% ( $p = 0.01$ ) of carrying capacity and selected the model with highest likelihood (lowest negative log-likelihood) as the base model. We evaluated these shape parameter values because 50% produces the symmetric Schaefer model, 40% is the meta-analytic mean for fish (Thorson et al., 2012), and 37% corresponds to the Fox model.

In this model and its extensions below, we scaled predator abundance and production to each population's maximum abundance to ease model fitting; placed a likelihood penalty on carrying capacities  $> 5$  times the maximum abundance to constrain unrealistically large carrying capacities (likelihood penalty was invoked for 3–5 populations, depending on the model [Appendices S15 & S16]); and fitted the models with maximum likelihood estimation in the TMB package (Kristensen et al., 2016) in R (R Core Team, 2020).

#### Prey-linked models

To evaluate the influence of prey abundance on predator productivity, we extended the base model to include a multiplicative influence term:

$$SP_{i,t} = \frac{r_i}{p} B_{i,t} \left( 1 - \left( \frac{B_{i,t}}{K_i} \right)^p \right) * \exp(\text{prey}_{i,t} * \theta_i) + \varepsilon_i, \quad (3)$$

where  $\text{prey}_{i,t}$  is the scaled abundance of prey and  $\theta_i$  is the influence of scaled prey abundance on productivity. We scaled prey abundance as z-scores to allow the comparison of influences among populations. The multiplicative influence term monotonically modifies population growth rates ( $r_i/p$ ) based on prey availability, where  $\theta_i > 0$  means that increasing prey abundance magnifies productivity (i.e., population growth rate) and  $\theta_i < 0$  means that increasing prey abundance reduces productivity. A population's growth rate is determined by rates of natural mortality, somatic growth, and recruitment (Hilborn & Walters, 1992), and the influence term represents the net impact of prey availability on these 3 processes. The value of the influence can be interpreted as the expected percent change in a population's productivity if prey availability were to change 1 SD from the population's average historical experience (e.g., an influence of 0.5 means that a 1 SD increase in the prey availability would

increase productivity by 50% and a 1 SD decrease in prey availability would decrease productivity by 50%).

We evaluated 2 measures of prey abundance: the abundance of the primary prey species (i.e., species representing the highest percentage of a predator's diet, 13–100% (Appendices S6, S7, S9, S10, & S11) and the sum abundance of all important prey species with available data (i.e., sum of species individually comprising  $\geq 10\%$  of a predator's diet). A composite abundance could be calculated only for the 18 predator populations overlapping with critical prey populations described in the same units (i.e., all metric tons) and was calculated only for years with data for all important species. We used data for only the primary prey species for the remaining 27 populations. We present the impacts of concurrent prey abundance on predator productivity in the main text and the sensitivity of these results to lagged prey abundance in Supporting Information.

We evaluated both models that estimate prey influences as fixed effects and models that estimate prey influences as random effects. On the one hand, estimating prey influence as fixed effects imposes no constraints on the magnitude and distribution of the influences and could more accurately identify influences that deviate from the patterns exhibited by other populations. On the other hand, estimating prey influence as random effects constrains poorly informed influences. Thus, we also evaluated models with prey influences estimated as random effects:

$$\theta_i \sim N\left(\mu_{\text{prey}}, \sigma_{\text{prey}}^2\right), \quad (4)$$

where  $\mu_{\text{prey}}$  and  $\sigma_{\text{prey}}$  are the mean and SD of the global distribution of prey influences ( $\theta_i$ ), respectively. The assumption of a normal distribution of random effects is consistent with the distribution of fixed effects estimates across model configurations (Appendices S15 & S16).

To evaluate the hypothesis that prey abundance influences predator productivity, we compared the prey-linked production models with the base model with Akaike information criterion (AIC) (Akaike, 1974). We adopted the view that only the 2 hyperparameters ( $\mu_{\text{prey}}$ ,  $\sigma_{\text{prey}}$ ) count toward the number of parameters (i.e.,  $\theta_i$ , the individual influence parameters, do not count) in our AIC calculations.

#### Temperature-linked models

We compared the level of effect of prey abundance on predator productivity relative to that of SST, a widely available ecosystem indicator that can encapsulate a wide variety of individual-, population-, and ecosystem-scale changes that can affect predator productivity. For example, ocean warming can increase or decrease population growth rates (Free et al., 2019) through direct impacts on individual metabolism (e.g., elevated stress,

faster growth rates, and increased mortality) or through indirect impacts on the broader ecosystem (e.g., shifting phenology, altered prey availability, reduced cross-shelf transport, and increased storminess). The temperature-linked models were structurally identical to the fixed- and random-effects prey-linked models but used mean annual SST as a covariate instead of prey abundance. We calculated the mean annual SST experienced by each population based on the population centroid and the COBE SST data set (COBE 2) (Ishii et al., 2005), which provides monthly SST on a globally complete  $1^\circ \times 1^\circ$  grid from 1850 to present based on an interpolation of in situ and satellite-derived SST observations (Appendix S13). Although bottom- or mid-water temperature experience may be more suitable for benthic or mesopelagic species, we used SST for all species given the lack of accurate, globally complete, historical subsurface temperature data. We scaled SST experiences as z-scores to allow comparison of SST influences and prey influences among populations. We used AIC to compare support for the prey-linked and temperature-linked production models.

#### Power Analyses

We measured the ability of the prey-linked fixed-effects model to detect an influence of prey abundance on predator productivity by applying the model to simulated predator populations representing the 45 populations in our data set (Appendix S17). We simulated each predator population in scenarios combining each of 4 prey-influence strengths (0.25–1.00 by 0.25) and 4 levels of process variability (0.1–0.4 by 0.1). These levels were selected because they span the range of prey influence and process variability values estimated by the prey-linked fixed effects models. Each simulation began at the reported initial abundance and progressed with catch determined by the reported exploitation rate and population growth rate determined by the carrying capacity and time-varying intrinsic growth rate estimated based on the composite prey-linked fixed effects model (the best prey model) (Table 1). Population growth rates were influenced by the reported composite prey abundances and the evaluated combination of prey influence and process variability parameters following Eq. 3. In the operating model, we used reported prey abundances and exploitation rates rather than simulated prey abundances and exploitation rates to evaluate the ability of the statistical model to detect prey influences given our specific data. We performed 100 iterations of each scenario, fitted the fixed effects model to each scenario iteration (45 populations per scenario iteration), recorded the percentage of populations estimated to be significantly positively influenced by prey abundance, and calculated the mean percentage across the 100 iterations performed for

**Table 1.** Akaike information criterion (AIC) comparison of 10 candidate surplus production models.<sup>a</sup>

Model	k	NLL	AIC	$\Delta AIC^b$
Question 1: Is productivity symmetric?				
no covariate (MSY@45% K) (base model)	135	-1938.3	-3606.6	0.0
no covariate (MSY@40% K)	135	-1937.6	-3605.2	1.4
no covariate (MSY@37% K)	135	-1935.3	-3600.5	6.0
no covariate (MSY@50% K)	135	-1934.8	-3599.5	7.1
Question 2: Does prey abundance influence productivity? <sup>c</sup>				
primary prey (fixed effects) (best prey model)	180	-2000.3	-3640.6	0.0
composite prey (fixed effects)	180	-1997.7	-3635.4	5.2
primary prey (random effects)	137	-1940.6	-3607.2	33.4
no covariate (MSY@45% K) (base model)	135	-1938.3	-3606.6	34.0
composite prey (random effects)	137	-1940.2	-3606.5	34.2
Question 3: Does primary prey influence productivity as much as SST?				
SST (fixed effects) (best SST model)	180	-2006.5	-3652.9	0.0
primary prey (fixed effects) (best prey model)	180	-2000.3	-3640.6	12.3
composite prey (fixed effects)	180	-1997.7	-3635.4	17.5
SST (random effects)	137	-1947.3	-3620.7	32.2
primary prey (random effects)	137	-1940.6	-3607.2	45.7
no covariate (MSY@45% K) (base model)	135	-1938.3	-3606.6	46.3
composite prey (random effects)	137	-1940.2	-3606.5	46.4

<sup>a</sup> Abbreviations: K, carrying capacity; k, number of parameters; MSY, maximum sustainable yield; NLL, negative log-likelihood; SST, sea surface temperature.

<sup>b</sup> All covariate-linked models are fitted with the shape parameter of the base model ( $p = 0.55$ ), which maximizes productivity at 45% of carrying capacity.

<sup>c</sup> Common rules of thumb suggest that models with  $\Delta AIC \leq 2$  have substantial support ( $\geq 37\%$  as likely as best model), models with  $4 \leq \Delta AIC \leq 7$  (3-14% as likely as best model) have considerably less support, and models with  $\Delta AIC \geq 10$  have essentially no support ( $\leq 1\%$  as likely as best model) (Burnham & Anderson, 2004). The parenthetical likelihoods were calculated using the formula  $\exp(-\Delta AIC/2)$  from (Akaike, 1981).

each scenario. We assessed significance at the 5% level in the empirical analyses and power analyses.

## Results

Significant influences of prey abundance on predator productivity were detected only when estimating prey influences as fixed effects (Figure 2). Neither of the prey-linked random effects models identified significant influences of prey abundance on predator productivity and both failed to garner more support than the base model in terms of AIC (Table 1). By comparison, both the random and fixed effects temperature-linked models identified significant influences of ocean warming on predator productivity (Figure 2) and both garnered more support than the base model based on AIC (Table 1). The fixed effect temperature-linked model was the best overall descriptor of predator population dynamics (Figure 2 & Table 1).

Both fixed effects prey-linked models identified the same 13 predator populations (28.8% of evaluated populations) as being significantly influenced by prey abun-

dance. They identified significant positive influences for only 6 populations (4 fish and 2 seabirds) and significant negative influences for 7 populations (3 fish, 2 seabirds, and 2 mammals) (Figure 2). The influence of prey abundance on predator productivity when estimated as a fixed effect was weakly dependent on the importance of forage fish to predator diets (Figure 3). Populations of species with a greater proportion of forage fish in their diet were slightly more likely to experience increasing productivity with increasing prey abundance. However, even populations with high dependence on forage fish (e.g., >75% of diet) exhibited as many or more significant negative influences of prey abundance as positive influences (Figure 3). We found similarly low rates of positive prey influence when we used lagged prey abundances (Appendix S20).

The prey-linked fixed effects model had high power to detect significant influences of prey abundance on predator productivity (Figure 4). Even with weak prey influences ( $\theta = 0.25$ ) and high process variability ( $\sigma_P = 0.4$ ), the model successfully detected 77% of positive prey influences. With stronger prey influences and lower process variabilities, the model successfully detected 85-99% of positive prey influences (Figure 4).

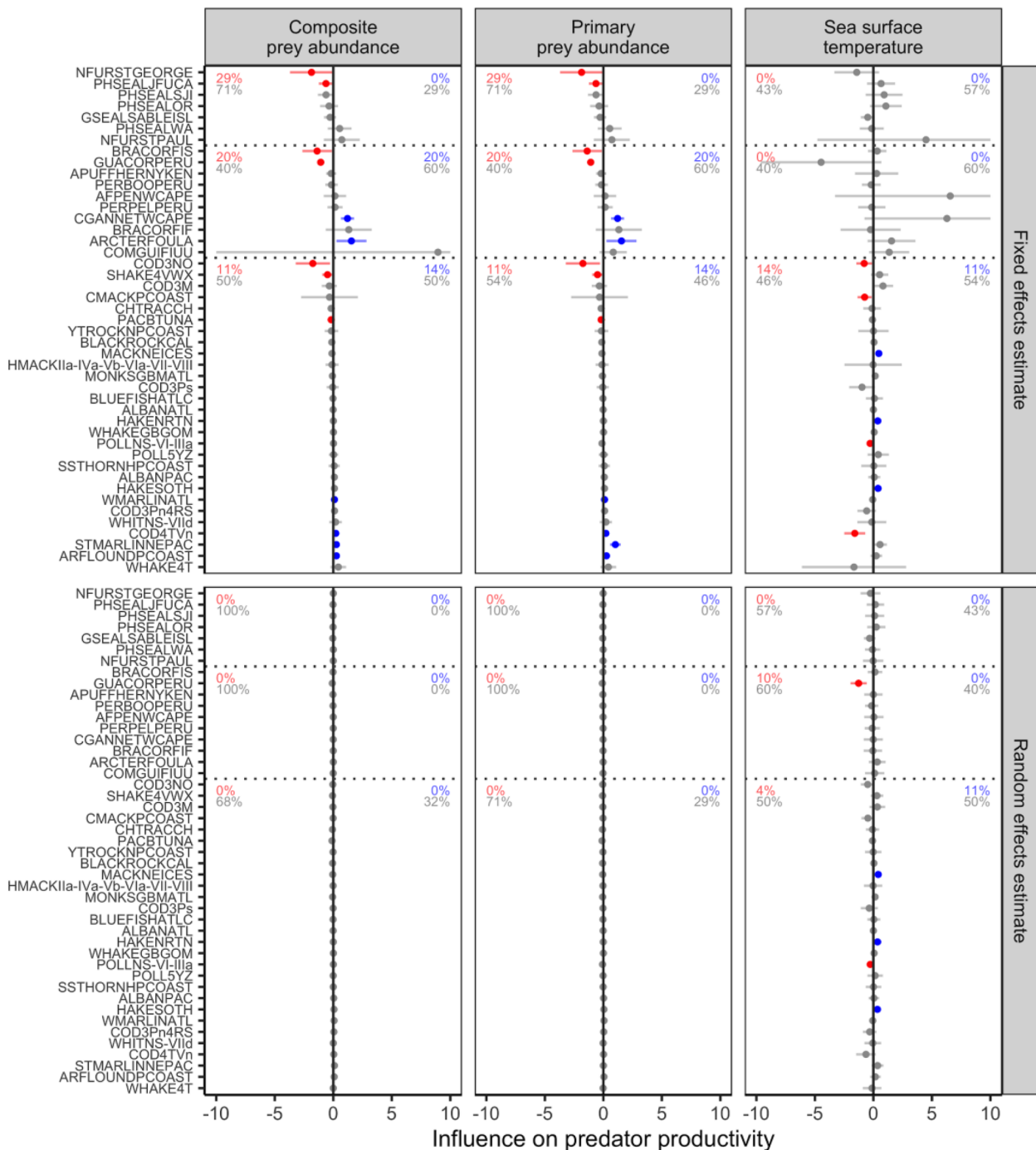
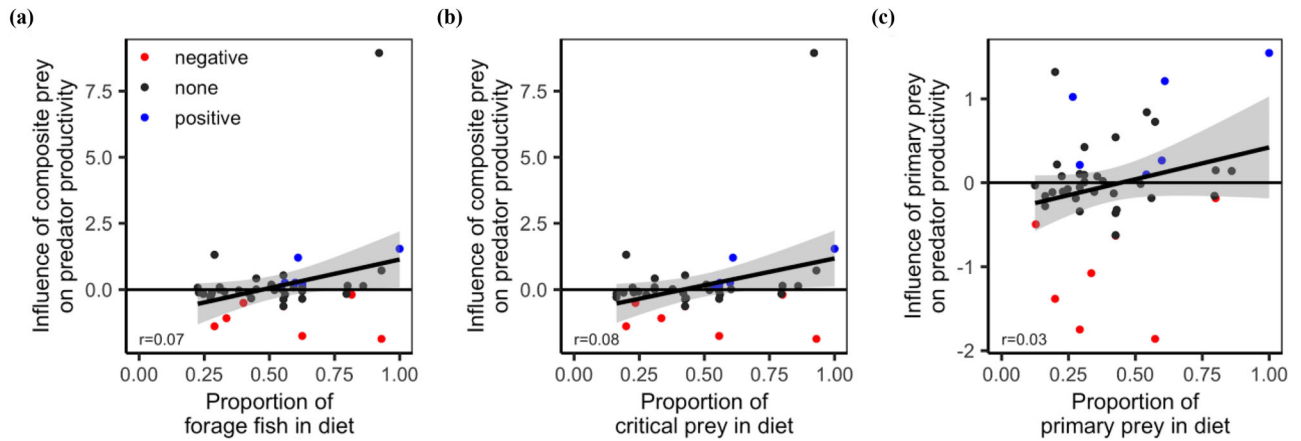
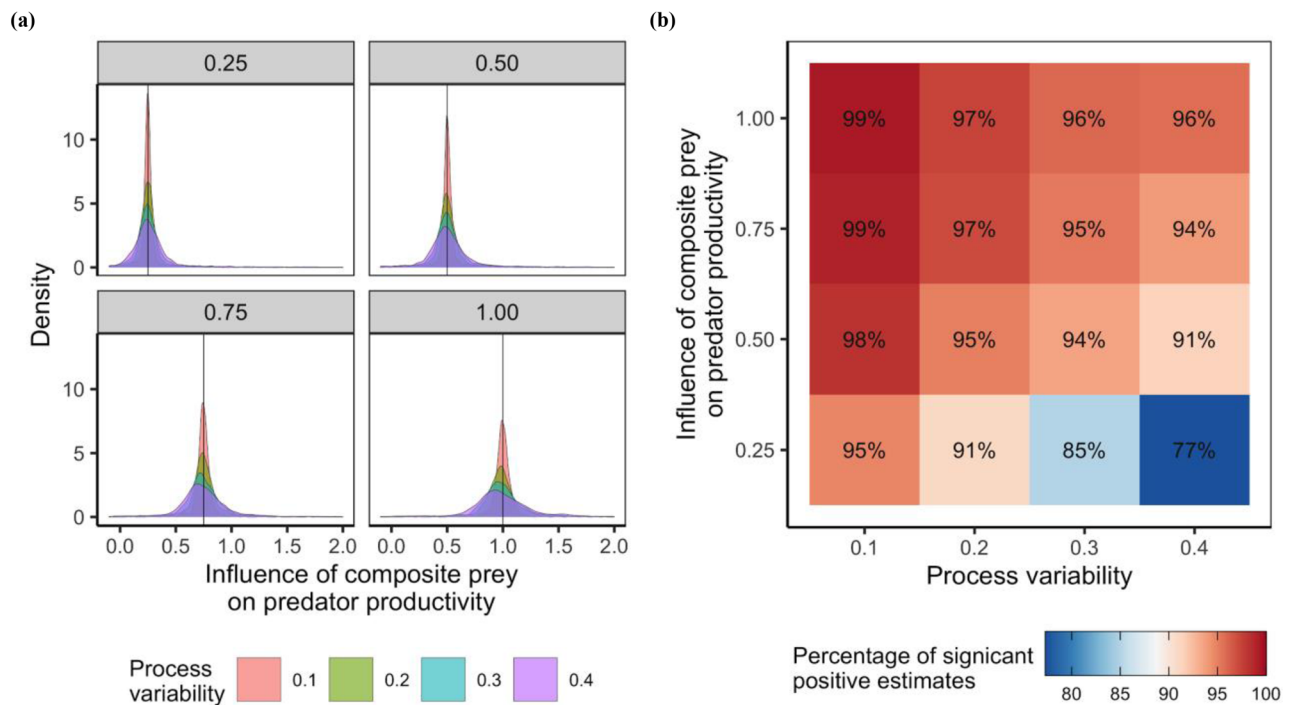


Figure 2. Influence of composite prey abundance, primary prey abundance, and sea surface temperature on predator productivity when estimated as either random or fixed effects (points, estimates; error bars, 95% CIs; blue, significant positive effects; red, significant negative effects; blue percentages, percentage of significantly positive point estimates; red percentages, percentage of significantly negative point estimates; horizontal lines, divisions between estimates for fish, seabird, and marine mammal predators, respectively). The value of the influence can be interpreted as the expected percent change in a population’s productivity if prey availability or temperature were to change 1 SD from the population’s average historical experience (e.g., influence of 0.5 means that a 1 SD increase in prey availability increases productivity by 50% and a 1 SD decrease in prey availability decreases productivity by 50%). See Appendices S6 and S7 for more information on each predator population.



**Figure 3.** Impact of the contribution of forage fish to predator diets on the influence of prey abundance on predator productivity as measured in the fixed effects framework (point color, direction of statistical significance of the prey influence estimate; line, linear regression fit; shading, 95% of linear regression fit).



**Figure 4.** (a) Density distribution of prey-influence estimates relative to the specified prey-influence strength (dark vertical line) in simulations with varying levels of process variability and (b) percentage of statistically significant, positive prey-influence estimates at specified levels of prey influence and process variability.

## Discussion

Our model had high power to detect the influence of prey abundance on predator productivity, and we found that predator population growth rates were rarely influenced by abundance of their forage fish prey. We detected significant influences of prey abundance on predator productivity only when estimating these influences as fixed effects, which are more likely to overestimate the magnitude and significance of influences than

when estimated as random effects, especially for small and noisy data sets (Bell et al., 2019). Even with the fixed effects models, only 13% of predator populations exhibited a positive response to increasing prey abundance. By comparison, the influence of SST—a broader indicator of ecosystem change (Free et al., 2019)—was strong enough to detect in both the random and fixed effects modeling frameworks; the fixed effects temperature-linked model garnered the most statistical support among all the evaluated models.



The resilience of predator populations to changing prey conditions is supported by a large number of field studies documenting behavioral plasticity in diet composition, foraging sites, and breeding-site selection across taxa and geographies (Brakes & Dall, 2016; Gilmour et al., 2018). For example, Great Skuas (*Stercorarius skua*) in the North Sea have switched prey in response to fisheries-driven declines in sandeel (*Ammodytes* spp.) abundance, allowing them to maintain functioning population status (Church et al., 2019). Because prey availability affects reproductive performance and colony health (Kowalczyk et al., 2014), Little Penguins (*Eudyptula minor*) in southeast Australia adaptively change forage locations based on catch rates in prior visits and social cues (Carroll et al., 2018). Humpback whales (*Megaptera novaeangliae*) in the Gulf of Maine exhibit high behavioral plasticity based on the movement and structure of prey fields (Kirchner et al., 2018). Furthermore, seabirds and marine mammals with location-based breeding have evolved to select breeding sites adjacent to areas with high, stable, and diverse prey availability, which can buffer against changing prey conditions, especially if the changes are asynchronous (Hilborn et al., 2017a). Finally, diet specialization (i.e., diet dominated by a single prey species) was rare except in seabirds, and generalist diet strategies can be more robust to fluctuations in prey (Schoen et al., 2018). Furthermore, instances of apparent specialization in highly mobile predators based on stomach contents are often an artifact of prey patchiness in space and time and may not accurately reflect the dietary flexibility of an individual or population (Young et al., 2018).

The counterintuitive finding that predator population productivity can be negatively affected by increasing prey abundance could arise through several mechanisms. For fish predators, this could occur through the cultivation-dependence hypothesis or intense overfishing. The cultivation-dependence hypothesis (Walters & Kitchell, 2001) suggests that adult prey species often consume or compete with juvenile predator species and that the depletion of adult predators from fishing can result in the release of prey from predation. This results in an increase in prey abundance while predator productivity declines. Although empirical studies testing this hypothesis are limited, strong evidence for cultivation-dependence effects has been found for North Atlantic cod (*Gadus morhua*) and herring (*Clupea harengus*) populations (Minto & Worm, 2012) and is supported for Atlantic cod and herring in the North Atlantic NAFO 3NO statistical area in our analyses. Alternatively, the continuation of excessive fishing for predators could reduce predator productivity while reforms in forage fisheries rebuild prey abundance (Hilborn & Litzinger, 2009), leading to a spurious negative relationship between predator productivity and prey abundance. For central place foragers, reduced prey abundance in local

foraging grounds but increased abundance at wider population scales can reduce predator productivity and misleadingly suggest that productivity is negatively affected by increasing prey abundance. This is likely the case for the St. George Northern fur seal (*Callorhinus ursinus*) population, which were estimated to have been most negatively affected by the abundance of their primary prey (walleye pollock). Although Bering Sea walleye pollock (*Gadus chalcogrammus*) abundance has remained relatively stable (Appendix S18), declines in local pollock abundance have contributed to increased energy expenditure, decreased investment in lactation, and reduced breeding success (Kuhn et al., 2014; McHuron et al., 2020). Finally, the recovery of fish, seabird, or mammal predators can result in reduced prey abundance (i.e., through top-down control) leading to a spurious relationship between increasing predator productivity and decreasing prey abundance (van Gemert et al., 2018).

Although seabird and marine mammal populations have rarely benefitted from increases in population-wide prey abundance, they could see greater benefits from increases in local abundance, which can be achieved by restricting fishing near breeding locations. For example, the Cape Gannet (*Morus capensis*) population on the Western Cape of South Africa, 1 of 2 seabird populations identified as having been positively influenced by prey abundance, has declined since the 1950s, which is argued to be due in part to declines in local prey abundance (Sherley et al., 2019). As in the Northern fur seal and walleye pollock example discussed above, declines in the local abundance of sardine and anchovy resulted in increased adult foraging effort, which reduced adult body condition, increased chick predation risk via reduced nest attendance, and slowed chick growth (Cohen et al., 2014). A number of other studies confirm that predator reproductive success is linked to local prey abundance (Cury et al., 2011), suggesting that spatial-temporal restrictions in fishing around breeding sites (e.g., closing fishing within 20 km of a breeding site during breeding season) could be more effective than extra-precautionary population-wide regulations (Pichegru et al., 2010, 2012), which likely fail because local abundance is not necessarily correlated with total abundance (Kuhn et al., 2014).

The impact of prey on predator productivity is inherently difficult to detect (Sydeman et al., 2017; Sherley et al., 2018), and our study is subject to several analytical constraints. First, we were unable to evaluate the influence of a predator's entire prey field on its productivity because many prey species and populations have not been assessed. Second, the strength of the prey influence could be biased because we did not consider the size selectivity of predation (i.e., changes in abundance within particular size classes could show a stronger signal than changes in total or spawning stock abundance). Third, the predator populations we evaluated come from

regions with strong fisheries management (Hilborn et al., 2020), and populations of forage fish in these areas have been relatively well managed over the past 35 years (Appendix S8). Increasing prey abundance must benefit predators below some threshold of low prey availability (Cury et al., 2011), but fisheries management consistent with modern precautionary principles may have maintained forage fish abundance above this threshold in the 5 study regions. Finally, the use of output of stock assessment as data has been criticized because of difficulties in accounting for model assumptions, uncertainty, and bias in post hoc analyses (Brooks & Deroba, 2015). We reduced these concerns by following best practices for stock assessment meta-analysis (Thorson et al., 2013) and note that the use of stock assessment output was vital for creating the composite prey abundance, which required prey abundances to be in identical units (i.e., metric tons).

Our results indicate that the abundance of forage fish rarely affects predator productivity, which suggests that the extra-precautionary management of forage fish would rarely achieve the intended benefits for marine predator populations. Furthermore, forgoing sustainable harvest of forage fish places greater pressure on other protein sources—a trade-off with important conservation implications that will vary depending on the protein source that replaces forage fish (Hilborn et al., 2018). Thus, conservation actions that effectively enhance the resilience of marine predator populations while minimizing impacts on fisheries that provide food, support livelihoods, and offset terrestrial impacts are central to advancing holistic sustainability. These measures could include efforts to reduce bycatch and incidental mortality, a serious threat to both seabirds and marine mammals, through modifications to fishing gear or dynamic ocean management (Hazen et al., 2018); protect breeding sites by restoring habitat, removing invasive species, and reducing human disturbance (Croxall et al., 2012); or restrict fishing close to breeding sites. The relative performance of and trade-offs among these strategies can be weighed through tailored management strategy evaluation models, which use simulation to compare the performance of alternative management strategies (Plagányi & Butterworth, 2012; Feeney et al., 2019; Koehn, 2019; Deroba et al., 2019). Seabirds and marine mammals are among the most highly threatened marine animals (Dias et al., 2019), and preserving these important members of marine ecosystems (Heithaus et al., 2008; Ritchie & Johnson, 2009) will depend on implementing measures that are confirmed to be effective.

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## Supporting Information

Additional information is available online in the Supporting Information section at the end of the online article. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. All data and code are available from [https://github.com/cfree14/forage\\_fish](https://github.com/cfree14/forage_fish).

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