Key factors that exacerbate declines in exploited multispecies systems

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Abstract

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Extinction rates are increasing globally, and direct exploitation is an important driver. Many pathways have been proposed to explain how exploitation can lead to extinction. One of these proposed but understudied multispecies pathways is opportunistic exploitation, which occurs when a highly valuable but rare species is encountered and targeted during exploitation of a less valuable, but more common, target species. Using individual-based simulations of exploiters in a two-species spatial model, we show that opportunistic exploitation increases depletion when compared to single-species exploitation, and is as detrimental to the more valuable, rare species as the anthropogenic Allee effect (where price increases with rarity) and the Allee effect (where population growth declines at low abundance). The most important factors affecting the impact of opportunistic exploitation are gross revenue and abundance of the more common, less valuable species, while ease of capture and growth rate of the more common, less valuable species are less important. Thus, valuable but rare species are most at risk when harvested alongside low-value abundant species; this information is relevant for managers focused on protection of rare species in multispecies systems.

Fisheries independent survey data can provide novel insights into global fisheries status and the status of individual taxa but there is no central location where fishery-independent survey-indices of abundance are stored and available for scientific use. Therefore, we compiled a database of estimated abundance or biomass by year for each species from 51 fishery independent surveys. One key feature of this database is a consistent data-sharing agreement allowing for broader use of the database while respecting the rights and wishes of data providers. As an illustration of the usefulness of this database, we examined which factors explain trends in abundance of different fish stocks, finding that declining trends are most closely associated with longer maximum length, highly commercial fished status, and deeper habitats. We anticipate that this database will facilitate new research directions and encourage the contribution of additional surveys.

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Introduction

Humans utilize wildlife species for many reasons – food, clothing, medicine, pets, trophies. Since humans rely on wildlife to fulfill these needs, it is important that we effectively manage their populations. Determining population size for exploited species is essential for many wildlife management, recovery, harvest, and conservation plans. Knowing the population size allows scientists to determine the health of a population and whether the population is stable, increasing, or decreasing over time. Additionally, it allows scientists to understand whether management actions are successful.

Since 1970, the Living Planet Index shows an average 68% decrease in population sizes of mammals, birds, amphibians, reptiles, and fish based on nearly 21,000 populations (Almond et al., 2020). Populations decline for many reasons, most of which are anthropogenic in origin. These include direct human exploitation, habitat loss, climate change, and introduced species (Diamond et al., 1989; Ichii et al., 2019; Keith et al., 2008; Purvis et al., 2000; Thomas et al., 2004).

We first explored the mechanisms behind these population declines. When exploitation is directly targeted on a single species, extinction and serious depletion is expected to be relatively uncommon since as population size decreases, search costs nearly always begin to outweigh revenue (e.g. Grafton et al., 2007). Nevertheless, extinction and serious depletion have been reported for many exploited species resulting in numerous single-species and multispecies hypotheses that seek to explain extinction. However, none of these hypotheses develop a firm mathematical foundation for a general understanding of extinction risk that include both single species and multispecies factors. We used individual-based models to replicate conditions that can lead to extinction from human exploitation, finding that opportunistic exploitation in multispecies systems increases extinction risk of the more valuable, rare species (and, surprisingly, also increases risk to the common, less valuable species), compared to exploitation of a single target species.

Next, we explored real world factors which explain trends in population size. Fisheries independent survey data can provide novel insights into global fisheries trends in (i.e. Branch et al., 2010). Currently, there is no central location where this data is stored and available for scientists to explore for further analysis. We compiled a database of fishery independent survey data with a consistent data sharing agreement allowing for broader use of the database. We used this data to explore which factors explain trends in abundance of different fish stocks, finding that fishery status, maximum length, and habitat are influential factors in predicting the trend in biomass over time

Chapter 1 Modeling opportunistic exploitation: increased extinction risk when targeting more than one species

1.1 Introduction

Although extinction itself may ultimately be inevitable, the rate at which it is occurring has been exacerbated by human activity (Bascompte, 2003). Compelling evidence shows that Earth's biota is amid its sixth mass extinction, and recent extinction rates are both unparalleled in human history and highly unusual in Earth's history (Baillie et al., 2004; Ceballos et al., 2015). Many major processes driving an increase in extinction rates are anthropogenic, including direct human exploitation, habitat loss, climate change, and introduced species (Diamond et al., 1989; Ichii et al., 2019; Keith et al., 2008; Purvis et al., 2000; Thomas et al., 2004). The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services identifies direct exploitation as the second most important driver of change in the global state of nature (Ichii et al., 2019), and biological resource use is listed as a threat for all 189 species listed as "extinct" or "extinct in the wild" on the IUCN Red List (IUCN, 2020).

When exploitation is directly targeted on a single species, extinction is expected to be relatively uncommon (e.g. Grafton et al., 2007). This is because as population size decreases, search costs nearly always begin to outweigh revenue, except in obvious cases where species are extraordinarily valuable or can be easily exploited (e.g., dodos). Nevertheless, extinction and serious depletion have been reported for many exploited species, resulting in a variety of hypotheses that provide explanations for high extinction risks under single-species exploitation, including tragedy of the commons (Feeny et al., 1990; Feeny et al., 1996; Hardin, 1968; Ostrom, 1999; Ostrom et al., 1999), economics of overexploitation (Clark, 1973; Grafton et al., 2007), the Allee effect (Allee, 1931; Stephens et al., 1999), and the anthropogenic Allee effect (Courchamp et al., 2006).

Intrinsic biological factors that decrease mean individual fitness at low population sizes can also increase extinction risk, collectively termed the Allee effect (Allee, 1931; Stephens et al., 1999). Reproduction and survival can be diminished in small populations through numerous mechanisms, which include mate shortage, lack of cooperation, and genetic Allee effects such as inbreeding depression. In such cases, species can suffer reproductive failure at low densities, resulting in rapid extinction once the population falls below a minimum population size. This phenomenon has been blamed for the demise of passenger pigeons (e.g., Stephens and Sutherland, 1999).

An allied hypothesis is the anthropogenic Allee effect, where instead of lower survival at low numbers, income from exploitation increases markedly at low numbers (Courchamp et al., 2006). The classic case is when rare products such as beluga sturgeon caviar become disproportionately valuable because of their rarity, allowing for profitable overexploitation. Examples of species experiencing anthropogenic Allee effects include spectacular butterflies sought by collectors, goat-antelopes (family Caprinae) sought by trophy hunters, geckos (*Goniurosaurus luii*) captured to be exotic pets, large game birds (*Tetrao urogallus*) impacted by ecotourism, and the Chinese bahaba exploited for its perceived medicinal value (Courchamp et al., 2006; Holden and McDonald-Madden, 2017). In short, sometimes people are prepared to pay exorbitant prices to hunt, collect, or own specimens of the rarest species.

All preceding explanations assume single-species exploitation, but when exploitation directly targets more than one species, the number of extinction pathways expands. For example, when many species are exploited together (e.g., through fisheries trawling gear), attempting to maximize overall revenue causes some species to decline to low levels (e.g., Hilborn et al., 2012; Ricker, 1958). Three modes of exploitation can be distinguished depending on the relative value of the various species: accidental exploitation, where there is accidental by-catch while targeting a species with economic value (Hall et al., 2000; Rasmussen et al., 2011); incidental exploitation, in which a less-desirable species with lower economic value is exploited while pursuing a higher-value target species (Megalofonou, 2005); and opportunistic exploitation, where a rare species with high monetary value is stumbled upon during targeted exploitation of a more abundant, less valuable target species (Branch et al. 2013). Opportunistic exploitation allows for valuable, yet scarce, species (hereafter, rare species) to be exploited while profitably targeting another more common species, because there are reduced (or zero) search costs associated with exploitation of the rare species. Thus, in multispecies exploitation scenarios there is a continuum of extinction pathways from accidental exploitation to incidental exploitation to opportunistic exploitation as value of the vulnerable species increases relative to other targeted species. Of these three pathways, opportunistic exploitation is most problematic since this mode involves the greatest economic incentive to continue exploitation of the species most at risk (Branch et al., 2013).

Consider the case where black rhinoceroses (*Diceros bicornis*) were hunted to extinction in the Luangwa Valley, Zambia, even though illegally poaching rhino alone was not profitable due to their rarity (Milner-Gulland and Leader-Williams, 1992). Hypotheses assuming only single-species systems cannot fully explain this extinction event. In this case, illegal poaching was profitable when elephants and rhinos were hunted together, and as rhinos became rare, elephants became the main target (Milner-Gulland and Leader-Williams, 1992). Thus, opportunistic exploitation contributed to the extinction of black rhinoceros in Zambia in the 1990s (Chomba and Matandiko, 2011).

While hypotheses based on both single-species and multispecies exploitation pathways have been proposed to explain extinctions, none develop a firm mathematical foundation for a general understanding of extinction risks that includes single-species and multispecies pathways. Although opportunistic exploitation is likely the most destructive pathway to extinction, it is also least understood. To fill this gap, we developed models to examine the effect of key biological and economic factors that influence extinction risk and assess both single-species and multispecies modes of extinction. We used individual-based models to replicate conditions that can lead to extinction from human exploitation, finding that opportunistic exploitation in multispecies systems increases extinction risk of the more valuable, rare species (and, surprisingly, also increases risk to the common, less valuable species), compared to exploitation of a single target species.

1.2 Methods

We developed models to evaluate factors that we thought were likely to influence extinction risk of exploited species: (1) patchiness, distribution, and movement of species, (2) catchability, which combines detectability of the species and search effort of the exploiter, (3) population dynamics governing how abundance varies over time, (4) exploiter knowledge of species distribution, and (5) net revenue from exploitation.

We simulated the population of three types of entities: exploiters and two types of harvestable species. The agents of these two harvestable species inhabited a grid of g^2 discrete sites, where each site has a specified habitat quality for each species. At the beginning of each time step, the population size of each harvestable species changed according to discrete-time logistic growth equation with Poisson process error. After the population size was calculated, individuals of both harvestable species moved throughout the grid according to habitat quality. Once individuals moved, exploitation occurred. Exploiter agents had the opportunity to enter the grid sequentially from a single entry point on the outside of the grid once per time step, and their cost to harvest increased with distance travelled. Exploiters did not learn over the course of the simulations, so there was no change over time in how well they were able to predict locations of individual animals. Each exploiter could capture either zero or one individual per time step. Exploiters were assumed to be identical in knowledge, costs, and search abilities. Values used for parameters can be found in Table 1.1 Parameters, associated symbols, and values used in all base case models. Values for sensitivity tests are mentioned in text.and a general simulation framework can be found in Figure 1.1. These simulations were completed in R (R Core Team, 2021) and source code is available at github.com/sthurner11. A detailed model description, which follows the ODD (Overview, Design Concept, Details) protocol for describing individual-based models (Grimm et al., 2010; Grimm et al., 2020), is available in the Supplementary material Appendix S1.

1.2.1 Generating habitat grids

Habitat quality values ($H_{s,i}$) were assigned to every cell in the g×g grids (10×10 by default) grid for each species s, denoting habitat quality for that species at each grid cell $i = 1 \ldots . g^2$. Grid cells are referred to hereafter as sites. Habitat quality grids were generated using random fields as implemented in R package RandomFields (Schlather et al., 2015; Schlather et al., 2020), where covariance changes between sites as a Matérn function of distance (Thorson et al., 2015). The resulting values were log(habitat quality) with low values representing areas of poor quality and high values representing areas of good quality.

We generated habitat grids along a gradient from random to patchy by changing parameter m, which governs the smoothness of the Matérn function and ranges from zero (we used 0.0001 to avoid numerical issues) for completely random habitat quality, to 0.8 for highly patchy habitat quality (Figure 1.2). For the simulations, we generated 40,200 pairs of habitat quality grids (where grids were paired for each of two species), with each grid having a randomly selected value of $m \sim U(0.0001, 0.8)$. This ensured enough pairs were generated for the procedure outlined below. Grid pairs were sorted by the randomly emerging correlations between abundance in sites across species, binned into five equal bins with correlations that ranged from -0.5 to 0.5, and then 100 pairs were randomly chosen from each bin. Each of the resulting 500 grid pairs was used as a habitat quality grid for one of $n = 500$ simulations for each scenario.

1.2.2 Distributing habitat grids

The starting population size (we assumed the population starts at carrying capacity, K_s) for each species s was distributed into the relevant grid in proportion to habitat quality. The number of individuals for species s and site i at time period $t = 0$ ($N_{s,i,t=0}$) was obtained by drawing K_s individuals from a multinomial distribution with probabilities p_i derived from the g habitat quality values for each site i:

$$(1.1)\quad p_i = \frac{\exp(H_{s,i})}{\sum_j^g \exp(H_{s,j})}$$

(1.2) $N_{s,i,t=0} = \text{multinomial}(K_s, p_i)$

1.2.3 Population dynamics

At the beginning of each time step, the population of each species changed according to the discrete-time logistic growth equation with Poisson process error. After population growth, individuals were allowed to move, and then exploitation occurred (there was no exploitation in year 0). The sum of individuals across all *i* sites (denoted by •), for species *s* at time *t*, is given by $N_{s,\bullet,t}$. Thus:

(1.3) $N_{s,\bullet,t=0} = K_s$

(1.4) $\theta_{s,t+1} = N_{s,\bullet,t} - C_{s,\bullet,t} + r_s(N_{s,\bullet,t} - C_{s,\bullet,t})\left(1 - \frac{N_{s,\bullet,t} - C_{s,\bullet,t}}{K_s}\right)$

(1.5) $N_{s,\bullet,t+1} \sim \text{Pois}(\theta_{s,t+1})$

Intrinsic growth rates (r_s) and carrying capacities (K_S) were pre-specified for each species and $C_{s,\bullet,t}$ shows the total amount of individuals removed in year *t*. After calculating $N_{s,\bullet,t+1}$ we applied movement, redistributing individuals proportional to habitat quality using the same process applied to distribute individuals at $t = 1$ (Eqs. 1.1 and 1.2).

1.2.4 Cost

The cost for an exploiter to harvest one individual depends on a variable cost (v) multiplied by distance, a fixed cost per trip (f) that combined gear, labor, and opportunity cost (i.e., foregone revenue from alternatives to species exploitation), and a capture cost (a) that is zero if no individual is captured. Capture cost is the cost of gear (e.g., ammunition) and labor needed to capture an individual. Exploiters entered the grid at location (0, 0) and moved to the center of a site (the bottom left site is centered on 0.5, 0.5). We calculated distance as a straight line distance from the origin (0, 0) to the center of each site, creating a matrix of distances to each site, D. The total cost (c) of visiting and capturing an individual in each site was:

$$(1.6)\ c_i = vD_i + f + a$$

1.2.5 Effort, expected gross revenue, and net revenue

The number of exploiters, E, is expected to increase when more gross revenue is available, such that average gross revenue per exploiter is constant as predicted by the ideal free distribution (Fretwell, 1972; Fretwell, 1969). At the start of each simulation, gross revenue available per exploiter ($R_{e,t=0}$) is total gross revenue divided by number of exploiters:

$$(1.7)\ R_{e,t=0} = \frac{R_1K_1 + R_2K_2}{E}.$$

Here R_1 and R_2 are the gross revenues obtained from exploiting one individual of each species. Because we assumed that each exploiter would receive equal gross revenue across simulation scenarios, the number of exploiters in each scenario was determined as a function of $R_{e,t=0}$:

$$(1.8)\ E = \frac{R_1K_1 + R_2K_2}{R_{e,t=0}}.$$

Exploiters entered the grid sequentially, and have no knowledge of which sites they, or other exploiters, have visited. We assumed that each exploiter could only capture one individual in a given time step. To implement this, we first calculated the probability of encountering at least one individual of species s at a given site and time, $P_{s,i,t}$:

$$(1.9)\ P_{s,i,t} = 1-\left(1-q_s\right)^{N_{s,i,t}},$$

where q_s is catchability—the probability of encountering one individual of species s at a site, given presence—and $N_{s,i,t}$ is the number of individuals of species s in each site. We assumed that an encountered individual can be caught. Using this, we then calculated the potential gross revenue matrix $\rho_{i,t}$, which is the expected gross revenue from successfully exploiting species 1, plus the expected gross revenue from successfully exploiting species 2 if you did not exploit species 1, in each site. We assume that if both species are encountered in a given cell, the more valuable species will always be exploited.

$$(1.10)\ \rho_{i,t} = R_1 P_{1,i,t} + R_2 P_{2,i,t}\left(1 - P_{1,i,t}\right).$$

Of key importance, in most scenarios we run and as reflected in Eq 1.10, species 1 will be the rarer and more valuable species, and species 2 the more common and less valuable species, to mimic the kinds of scenarios that lead to opportunistic exploitation.

After calculating potential gross revenue, we calculated potential net revenue for each site as

$$(1.11)\ \pi_{i,t} = \rho_{i,t} - c_i.$$

To relax the assumption of perfect knowledge, we included observation error in the net revenue grid. This converts the potential net revenue grid to a perceived net revenue grid, which is the observed net revenue grid on which the exploiters act and accounts for their imperfect knowledge. We assumed that the coefficient of variation (CV_E) of this observation error was the same for all exploiters and all time steps. Observation error (O_t) was calculated for every site, where

$$(12)\ O_{i,t} = \mathrm{N}\left(0,\, sd = CV_E \frac{\sum_i N_{1,i,0} R_1 + N_{2,i,0} R_2}{g^2}\right).$$

Therefore, the perceived net revenue grid for the exploiter was

$$(1.13)\ \pi_{i,t} = \rho_{i,t} - c_i + O_{i,t}.$$

Using the exploiter's net revenue, we calculated the probability (B) of this individual exploiter going to each site (i) using fleet dynamics equations from Hilborn et al. (2006):

$$(1.14)\ B'_{i,t} = \exp\left[-d(1 - \frac{\pi_{i,t}}{\pi_{\max,t}}) \right]$$

where *d* is the concentration coefficient of exploiters and takes values between 0 and 3. High values of *d* result in more concentrated effort in sites with higher expected net revenue. We then calculated $B_{i,t}$ as:

$$(1.15)\ B_{i,t} = \frac{B'_{i,t}}{\sum_i B'_{i,t}}$$

Exploiters were assigned to each site using a multinomial draw with probability $B_{i,t}$ of being in site *i*. If the site they were assigned to had negative estimated net revenue ($\pi_{i,t} < 0$), exploiters did not venture forth.

Once an exploiter was assigned a site to visit, we conducted separate binomial draws for each species to determine if one of the individuals present in the site was encountered with probability of success $P_{s,i,t}$. If only one species was encountered, they were taken, unless the gross revenue of the individual was less than the capture cost, *a*. If the exploiter encountered individuals of both species, the more valuable species was taken, or if both species had the same gross revenue, there was a 50% chance of taking each. Steps were repeated for each exploiter in every time step (total removals in year *t* are shown in Eq 1.5). Since exploiters were assumed to be identical in all respects, multiple exploiters taking single trips is functionally equivalent to a single exploiter taking multiple trips. At the end of time step *t*, the total number of individuals remaining in the population is the number that were there at the start minus the total number caught ($C_{s,\bullet,t}$).

1.2.6 Metrics

At the end of the final time step (*T*), we calculated depletion as the proportion of the initial population that was remaining for each species $(N_{s,\bullet,t=T} - C_{s,\bullet,t=T}) / K_s$ in each simulation. We computed the median and

95% intervals of these depletion values across all 500 simulations for a given scenario, where each scenario refers to a structural or parametric change to the model, and the 500 simulations within a scenario are associated with each of the 500 habitat quality grids pairs described in section 2.1. These metrics allow us to compare depletion levels between species and among scenarios. In addition, we calculated extinction risk for both species as the proportion of simulations where the species goes extinct.

1.2.7 Scenarios

We developed a single-species base case and compared this to single-species scenarios with Allee effects and with anthropogenic Allee effects. Next, we developed a multispecies base case which modeled opportunistic exploitation to examine the comparative effect of adding a second species. Lastly, we examined the effects of changing species value, population growth, population size, catchability, exploiter knowledge, gross revenue per exploiter, the concentration coefficient of exploiters, and cost levels on the intensity of opportunistic exploitation.

1.2.7.1 Exploitation scenarios

Single-species base case

The single-species base case explored the scenario where only one species is exploited, as would occur if rhinos were the only targeted species and elephants had no value. We chose parameter values which resulted in the population size of the rare exploited species declining, on average, by about60% at the end of the simulation period (300 years) (Table 1). These parameter values were retained for other scenarios, except for adjustments to test hypotheses. In this case, species 2 is twice as numerous (2000 vs. 1000) and has no value (gross revenue 0 vs. 2000), but is otherwise identical to species 1 (the less common but more valuable target species).

Allee effect

In populations affected by the Allee effect, as population size decreases, per capita rate of increase declines (Courchamp et al., 1999a), instead of increasing as would be expected under negative density-dependence (i.e., Eq 1.4). We implemented the Allee effect (depensation) using a modified version of Hilborn et al. (2014), where population growth rate declines by 50% when population size is N_{50}:

$$(1.16)\ N_{s,\bullet,t+1} = N_{s,\bullet,t} - C_{s,\bullet,t=T} + r_s(N_{s,\bullet,t} - C_{s,\bullet,t=T})\left(1 - \tfrac{N_{s,\bullet,t} - C_{s,\bullet,t=T}}{K_s}\right)\left(1 - 0.5^{\frac{N_{s,\bullet,t} - C_{s,\bullet,t=T}}{N_{50}}}\right).$$

We specified $N_{50} = 0.25K_s$, which has the effect of reducing population growth by 29% at 40% of carrying capacity, and by 86% at 5% of carrying capacity, for the base parameter values. The gross revenue of species 2 was set to zero as in the single-species base case.

Anthropogenic Allee effect

Under the anthropogenic Allee effect, the value of products increases considerably at low abundance. We assumed the revenue-abundance relationship in Holden and McDonald-Madden (2017) for gross revenue:

$$(1.17)\ R_{s,t} = m_s + \frac{b_s}{\left(N_{s,\bullet,t}\right)^{Z_s}}.$$

Here, m_s is the minimum value per individual harvested when the species is abundant, and $m_s + b_s$ is the price paid when there is a single individual left ($N_{s,\square,t} = 1$). When Z_s is greater than 0, gross revenue is highest when the species is rare, and as Z_s increases gross revenue increases more steeply with rarity (Holden and McDonald-Madden, 2017). Using this equation, we recalculated the gross revenue for the rare species (“rhinos”) at the beginning of each time step, using the values $m_1 = R_1 = 2000$, and assumed that gross revenue doubled at the lowest abundance, hence $b_1 = 2000$. We chose a moderate value of $Z_1 = 0.5$ for the rate of price increase. The gross revenue of species 2 was set to zero.

Multispecies base case for opportunistic exploitation

Opportunistic exploitation arises when a common species has non-zero value (the “two-species” case). Branch et al. (2013) predict that opportunistic exploitation will occur when a more common but less valuable species is also exploited. In this scenario, the more common species was half as valuable as the rare species (R_1= 2000, R_2 = 1000), and had twice as many individuals at t = 1 (K_2 = 2000), but in all other respects was identical to the rare species, and all other parameters were the same as in the single-species base case (Table 1).

1.2.7.2 Impact of model attributes on opportunistic exploitation

The remaining scenarios all use the same parameters as the multispecies base case for opportunistic exploitation, except for changes to specific parameters mentioned below.

Gross revenue per species

Opportunistic exploitation is predicted to be more severe as gross revenue increases for the rare species (R_1), or the more common species (R_2), or as the ratio of the two ($R_2 : R_1$) increases. In the first scenario, we varied gross revenue for the rare species between 1000 dollars and 10000 dollars, so that $R_2 : R_1$ ranged from 1 to 1/10. In the second scenario, we varied gross revenue for the more common species between 0 dollars and 2000 dollars, so that $R_2 : R_1$ ranged from 0 to 1.

Growth rates

We examined the sensitivity of our results to intrinsic growth rates (r) of each species in two ways. First, we held growth rates of both species equal ($r_1 = r_2$) and looked at the impact of a range of growth rates between 0 and 0.4. Then we examined the impact of unequal growth rates by setting the growth rate of one species to the multispecies base case value of 0.1 and changing the growth rate of the other species between 0 and 0.4. We repeated this for both species.

Population size

Depletion of the rare species will be dependent on abundance of the rare species in the system: greater abundance results in more available gross revenue. In this scenario, we examined a range of values for abundance at time 0 of the rare species from 100 to 2000.

Opportunistic exploitation is predicted to be more problematic when the common species is more abundant because the common species will allow for a longer period of profitable exploitation. In this scenario, we examined a range of values for abundance at time 0 of the common species from 1000 to 50,000.

Ease of capturing species (catchability)

We investigated the sensitivity of our results to catchability (q_1 and q_2) of each species in two ways. First, both species had equal catchability ($q_1 = q_2$) and this ranged from 0 to 0.5. Next, we set catchability of one species to the base value of 0.04 and changed catchability of the other species from 0 to 0.5. We repeated this for both species.

Imperfect exploiter knowledge

We examined the effect of imperfect exploiter knowledge of expected net revenue in each site by allowing the coefficient of variation of process error (CV_E , Eq. 1.12) to range from the multispecies base case value of 0 (perfect knowledge) to 0.15.

Number of exploiters (available gross revenue per exploiter)

Altering the initial gross revenue per exploiter (R_e) changes the maximum number of exploiters in the system, since number of exploiters is inversely related to R_e. We allowed R_e to range from 5000 to 45,000 (the multispecies base case value is 25,000).

Concentration coefficient of fleet dynamics equations

The concentration coefficient (d) in the fleet dynamics equation (Eqs 1.14-1.15) determines the degree to which exploiters concentrate their effort in the best places. In the multispecies base case, $d = 2$ and we examined the influence of values of d from 0 to 3.

Costs

When costs (fixed and variable) increase, we expect fewer individuals to be exploited since it will be less profitable to take them. Additionally, as costs increase, individuals farthest from the entry point should experience less exploitation since they will be most expensive to harvest. For the first cost scenario, fixed cost (*f*) ranged between 0 and 1500 (base case value was 600). For the second cost scenario, variable cost (*v*) ranged from 0 to 250 (base case value was 100).

1.3. Results

1.3.1 Exploitation scenarios

Single-species base case

This scenario serves as a point of comparison to quantify the impact on depletion for each additional scenario. Parameters were selected so that across all 500 simulations in the single-species base case, median abundance of the target species was 38% of initial abundance in year 300 (Figure 1.3, Figure 1.4), and no simulations resulted in extinction.

In all scenarios, spatial distribution of individuals played an important role. Because habitat grids were randomly generated, there was variability in mean distance of individuals from the point where exploiters entered (0, 0), and the nearer the rare species was to the entry point, on average, the more depleted it was at the end of the simulations (Figure 1.5).

Allee effect

With an Allee effect, target species abundance declined further than in the single-species base case, stabilizing at 32% of initial population size, and 95% confidence intervals changed from 9-68% in the single-species base case to 0-64% for the Allee effect (Figure 1.4). In addition, 5% of simulations resulted in extinction.

Anthropogenic Allee effect

For the anthropogenic Allee effect, the target species also stabilized at a lower population size than the single-species base case (32% vs. 38%, Figure 1.4), but unlike the Allee effect scenario, no simulations resulted in extinction.

Multispecies base case for opportunistic exploitation

When a second species was added to the single-species base case, median depletion of the rare species decreased from 38% to 32%, and the percent of simulations in which the rare species went extinct increased from 0% to 1%.

Declines were greater when starting population grids were more correlated between the two species (Figure 1.6). Figure 1.3 demonstrates this outcome. There was relatively little effect of adding a second species if the correlation between the distribution of both species was strongly negative (top row, Figure 1.3), whereas opportunistic exploitation occurs more often and the rare species declines to extinction when there is strong positive correlation (bottom row, Figure 1.3).

1.3.2 Impact of model attributes on opportunistic exploitation

We compared the extent of population depletion at the end of 300-year simulations for 15 different scenarios, each investigating the impact of different parameter changes or model scenarios on opportunistic depletion (Figure 1.7).

Gross revenue per species

As gross revenue of the rare species increased, the rare species was further depleted (Figure 1.7a) relative to the multispecies base case. The impact on the common species was more complicated: it was most depleted when the rare species gross revenue was 1.38 times larger than common species gross revenue and was least depleted when the common species had no value.

As gross revenue of the common species increased, the impact of opportunistic exploitation on the rare species increased somewhat, and was greatest when the gross revenue of the common species was at 73% of the rare species (Figure 1.7b). Above this point, the common species itself was almost as valuable as the rare species, and the rare species was relieved of some exploitation pressure. Across the range of values examined, median final abundance of the rare species was 28–38% of initial abundance.

Growth rates

As population growth rate of the rare species increased, the rare species was less depleted (Figure 1.7c). When growth rate of the common species increased, the common species was much more resilient to exploitation, which allowed continued opportunistic exploitation to occur on the rare species, resulting in it becoming slightly more depleted (Figure 1.7d). When growth rates for both species were allowed to increase at the same time, they both became more resilient to exploitation and had higher terminal abundance (Figure 1.7e). Thus growth rate of the rare species was the most influential factor in determining its extinction risk.

Population size

When the carrying capacity of the rare species was higher, it ended up more depleted as a ratio of initial size, because there was more gross revenue in the system, which encouraged more exploiters to join the system (Figure 1.7f). Increasing the carrying capacity of the common species also greatly increased the median depletion of the rare species, which declined from 35% to 4% of initial abundance (Figure 1.7g).

Ease of capturing species (catchability)

As the probability of capturing one individual increased for the rare species, its abundance declined rapidly to extinction, and this was true whether the catchability for the common species remained the same (Figure 1.7h) or increased (Figure 1.7j). If the probability of successfully capturing the common species alone increased, however, this did not have a large impact on the depletion of the rare species (Figure 1.7i) and demonstrated a small but interesting effect: at intermediate catchability of the common species, the rare species was more depleted, but at high catchability the common species declined and it was no longer profitable to continue exploitation, resulting in the rare species recovering slightly.

Imperfect exploiter knowledge

With slightly imperfect knowledge ($CV_E = 0.0092$), exploiters explored more of the sites, resulting in the rare species becoming more depleted, down to 9% of initial abundance; but as sigma increased further, the rare species actually recovered to levels well above the multispecies base case in which knowledge was perfect (Figure 1.7k).

Number of exploiters (available gross revenue per exploiter)

The available gross revenue per exploiter, and in turn the number of exploiters in the system, had very little impact on the final depletion of the common species (Figure 1.7l). However, when there were fewer exploiters, it took longer to reach the equilibrium level of depletion.

Concentration coefficient of fleet dynamics equations

At high concentration coefficients, exploitation effort was more concentrated in sites with higher net revenue, and this resulted in primary and common species both being more depleted (Figure 1.7m). Above a certain level of concentration (about 1.5), however, there was little change in final depletion levels.

Costs

With increases in either variable costs (Figure 1.7n) or fixed costs (Figure 1.7o), there was less depletion of both the primary and common species.

1.4. Discussion

We analyzed four possible extinction pathways: single-species exploitation, the Allee effect, the anthropogenic Allee effect, and opportunistic exploitation. Our analysis demonstrated key factors that influence the exploitation of a species, including how exploitation of one species influences depletion of another. When compared to our single-species base case model, the Allee effect, the anthropogenic Allee effect, and opportunistic exploitation all increased depletion of the rare species, capturing the effects predicted by the original hypotheses. While opportunistic exploitation caused the quickest decline in abundance, the Allee effect, the anthropogenic Allee effect, and opportunistic exploitation resulted in comparable equilibrium depletion levels. As predicted by Branch et al. (2013), under certain circumstances opportunistic exploitation can result in increased depletion or extinction of the rare and more valuable species that would not occur in a single-species scenario. We identify high gross revenue, ease of capture, and a high population size of the more common and less valuable species as the main factors that increase the effect of opportunistic exploitation.

Our results suggest that the economic attributes of the system are the most important drivers of opportunistic exploitation. In our simulations, available gross revenue from the common species drove opportunistic exploitation: it must be profitable to continue exploiting the common species even when the higher value species is scarce. We found that the rare species was more depleted when the common species had sufficient value to continue exploitation, supporting the hypothesis behind opportunistic exploitation. Unexpectedly, as gross revenue of the common species increased towards a level that is equal to that of the rare species, we found the rare species was less depleted. This occurs because when the common species is only marginally less valuable than the rare species, exploiters will target it more heavily, resulting in declines and reducing opportunities for encountering the rarer species while exploiting the common species. Similarly, our results suggest that cost of exploitation influences depletion of both species. The common species is more impacted by changes in costs, and a diminished ability to profitably harvest the common species decreases the intensity of opportunistic exploitation.

Not only do the underlying economics of the system matter, but the exploiters perception of the profitability of the system matters as well. In our simulations, when exploiters have perfect knowledge about expected net revenue of each site, they never visit sites with a negative expected net revenue. These sites may have individuals of the rare species in them, but they are ‘economically extinct’. When exploiters have slightly imperfect knowledge, however, there was some probability that they would visit sites they would not have visited given perfect knowledge, and thus further deplete the rare species. As uncertainty continued to increase, though, both species became less depleted. In such circumstances, neither species is ‘targeted’ but instead both are randomly captured—similar to throwing darts blindfolded. These results suggest that it is important to understand how decisions are made by exploiters when investigating potential for extinction. Our models of exploiter behavior are relatively simplistic, opening up an avenue for future work to develop better models of human learning and knowledge acquisition.

The ease of capture of each species was one of the few factors with a close correlation to extinction risk in our analysis. Our results show that catchability of the rare species has a high, direct, correlation with extinction risk. While the probability of successfully capturing the common species did not have a large impact, high correlations between the distributions of the species makes capturing the rare species much easier.

Based on this research, the population size of the common species is also influential: the larger the common species carrying capacity was, the further depleted the rare species became. When there were more individuals of the common species, increased gross revenue in the system allowed for more encounters of the rare species. This can be compared to hyperpredation, where a supplemental food source for predators allows them to increase in abundance and drive down particular prey species (Courchamp et al., 1999b), such as introduced rabbits subsidizing a cat population, which can then deplete native birds (Courchamp et al., 1999b, 2000).

Our results indicate that populations with higher growth rates can sustain higher levels of exploitation. When the common species had a higher growth rate than the rare species, its population was maintained at a larger size. This allowed exploiters to continue profitably searching areas for longer periods of time, encountering more of the rare species. These findings are consistent with the high threat of overexploitation in high trophic level, large-bodied, slow growing, and low fecundity species (e.g., Cardillo and Bromham, 2001; Larson and Olden, 2010; Owens and Bennett, 2000; Purvis et al., 2000; Reynolds, 2003). Such species could face additional pressure when harvested alongside a faster growing species, analogous to pressures faced by multispecies fisheries, where less-productive stocks are commonly overfished (e.g., Hilborn et al., 2012).

There are additional factors beyond those we examined that are likely to influence extinction risk. One is range size of each species. We assumed that each species had an equivalent range size and that individuals could move anywhere in our grid. We therefore could not draw conclusions about the impact of range size on the effect of opportunistic exploitation. It is well recognized in the literature that geographic range size is a strong predictor of extinction vulnerability, where species with small range sizes are more at risk (e.g., Cardillo et al., 2008; Cooper et al., 2008; Jones et al., 2003; Purvis et al., 2000). In some cases, it is more advantageous to allocate conservation resources on the basis of small geographic range size than on body size or fecundity (Jones et al., 2003). It is thus reasonable to hypothesize that opportunistic exploitation would have larger effects on species with smaller range sizes. Further, the effect would be largest when the rare species has a small range that completely overlaps with good habitat for the common species, as we have shown that high spatial correlation leads to further depletion.

Here we only simulated situations with one or two species that are exploited. In reality, many ecosystems include more than two exploited species—examples in Branch et al. (2013) include logging of many species of trees resulting in declines in large-leaf mahogany, and fishing for multiple sea cucumber species causing major declines in the most valuable species. We expect the impact of opportunistic exploitation to be magnified when more than two species are harvested, since this is analogous to increasing the common species population size and gross revenue, or further reducing search costs.

While the simplicity of our model allows for generalizations, it does not include specific ecological attributes of each species or behavioral attributes of the exploiter that could have significant impacts on depletion of each species. Future work could take advantage of advances in machine learning to allow exploiters to automatically improve their search techniques over time with increased knowledge of species distribution, investigate impacts of opportunistic exploitation within metapopulations, and build models based on specific attributes of species that are likely to be impacted by opportunistic exploitation. Another dimension that could be explored in great detail is criminality (i.e. poaching) and the impact of punitive costs or perceived enforcement on exploiter behavior. Our models also assume that each extinction pathway acts in isolation. In reality, extinction risk will be increased due to interactions between extinction pathways: opportunistic exploitation could lead to the rare species passing below an Allee effect threshold, or a great increase in price due to the anthropogenic Allee effect, potentially leading to greater depletion than either pathway would cause independently.

Conservation implications

Our results emphasize how sensitive extinction is to factors intrinsic to each species and the exploitation system. Perhaps most importantly, our results support that the multispecies attributes of a scenario are as important, if not more important, than the attributes of individual species in predicting depletion. Many factors influence the intensity of opportunistic exploitation, but we conclude that the factors most critical to predicting depletion rate are profitability of capturing the common species and abundance of the common species.

Conservation budgets are insufficient to conserve all of the world's biodiversity, and there is increasing pressure for triage investment (Balmford et al., 2003; Joseph et al., 2009; Wilson et al., 2011). Giving resources to the most endangered or charismatic species will not usually maximize the number of species saved (Balmford et al., 2003). However, investments in multispecies systems may be effective at maintaining biodiversity when targeted at rare species that are vulnerable due to profitable exploitation of more common species. Additionally, our work highlights the critical importance of tracking emerging markets—species that were once safe because exploitation was unprofitable could face new risks if harvest is initiated on common species in the same area. This occurred when the bottom trawl fishery off India's Coromandel Coast commercialized formerly discarded bycatch species, allowing the continued harvest of rare species beyond the former point of unprofitability (Lobo et al., 2010). As climate changes, distributions of many species will shift in latitude, elevation, and size (Carroll et al., 2003; Chen et al., 2011; Kelly and Goulden, 2008; Parmesan and Yohe, 2003), resulting in sympatry of species that were formerly separated. We show that spatially correlated distributions among species greatly increases depletion risk to rare species. Thus, as we study the impact of these range shifts, it will be important to understand how spatial distributions of harvest will change, how local communities will change, and where new instances of opportunistic exploitation will emerge.

We show that single-species exploitation models can miss important drivers of depletion. Because of this, we believe more accurate management models can be achieved by accounting for multispecies dynamics in the evaluation of policies. Until we incorporate multispecies drivers of exploitation into models in which these dynamics are relevant, extinction risk will be underestimated. As managers and researchers continue to understand which species are most at risk of extinction and how to best spend conservation resources, it will be important to protect rare species that are most likely to be the targets of opportunistic exploitation.

Table 1.1 Parameters, associated symbols, and values used in all base case models. Values for sensitivity tests are mentioned in text.

Parameter	Symbol	Values
Habitat grid size	g	10
Number of simulations	N_{sims}	500
Number of time steps	T	300
Growth rates	r_1, r_2	0.1
Observation error CV	CV_E	0
Variable cost	v	100
Fixed cost	f	600
Cost to exploit	a	5
Concentration coefficient	d	2
Gross revenue per exploiter	R_e	25000

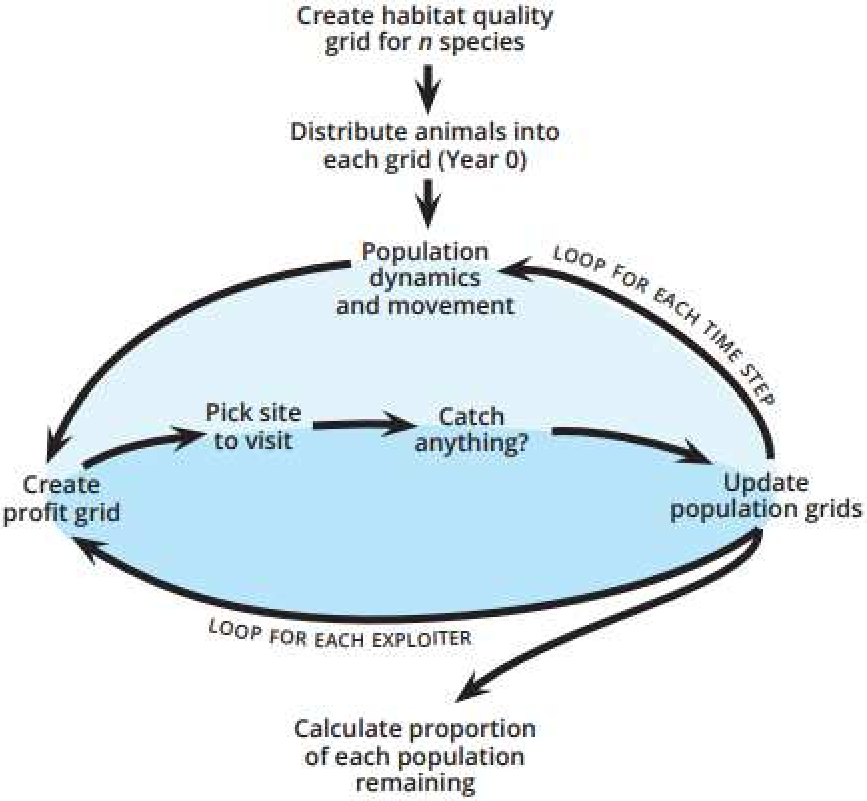


Figure 1.1 General simulation framework

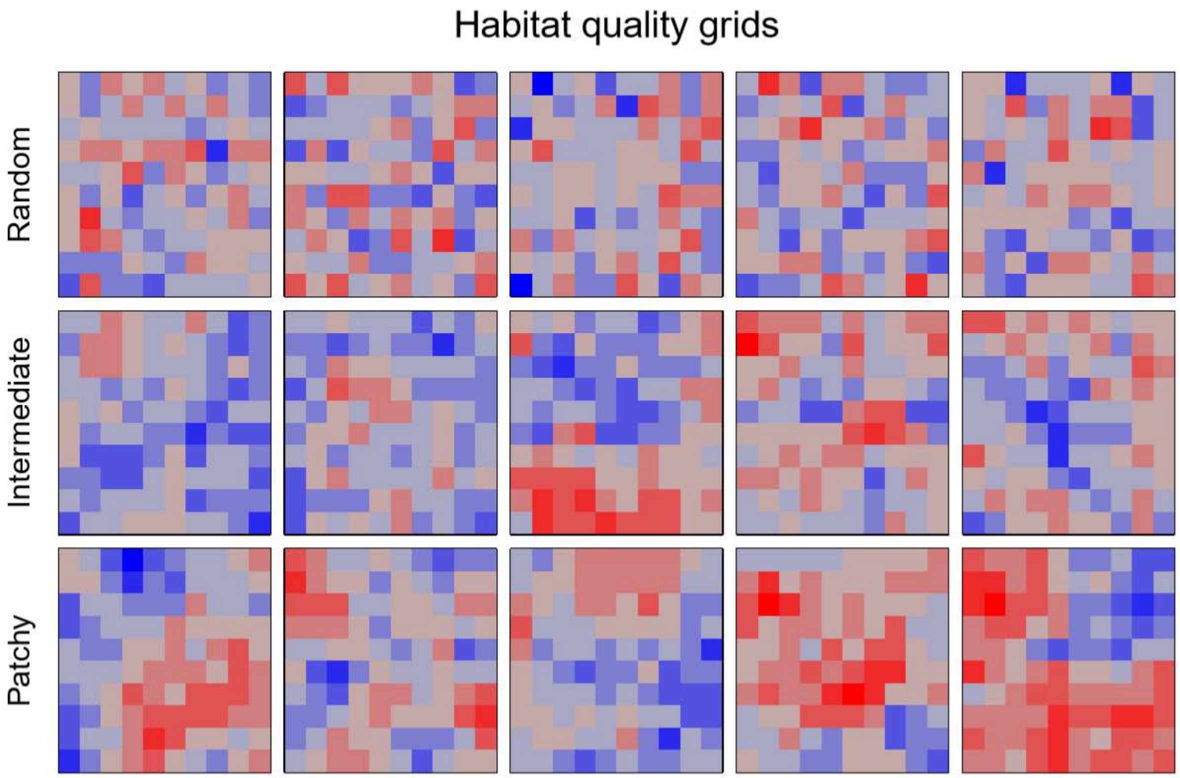


Figure 1.2 Examples of random (*m* = 0.0001), intermediate *(m* = 0.4) and patchy (*m* = 0.8) habitat quality grids.

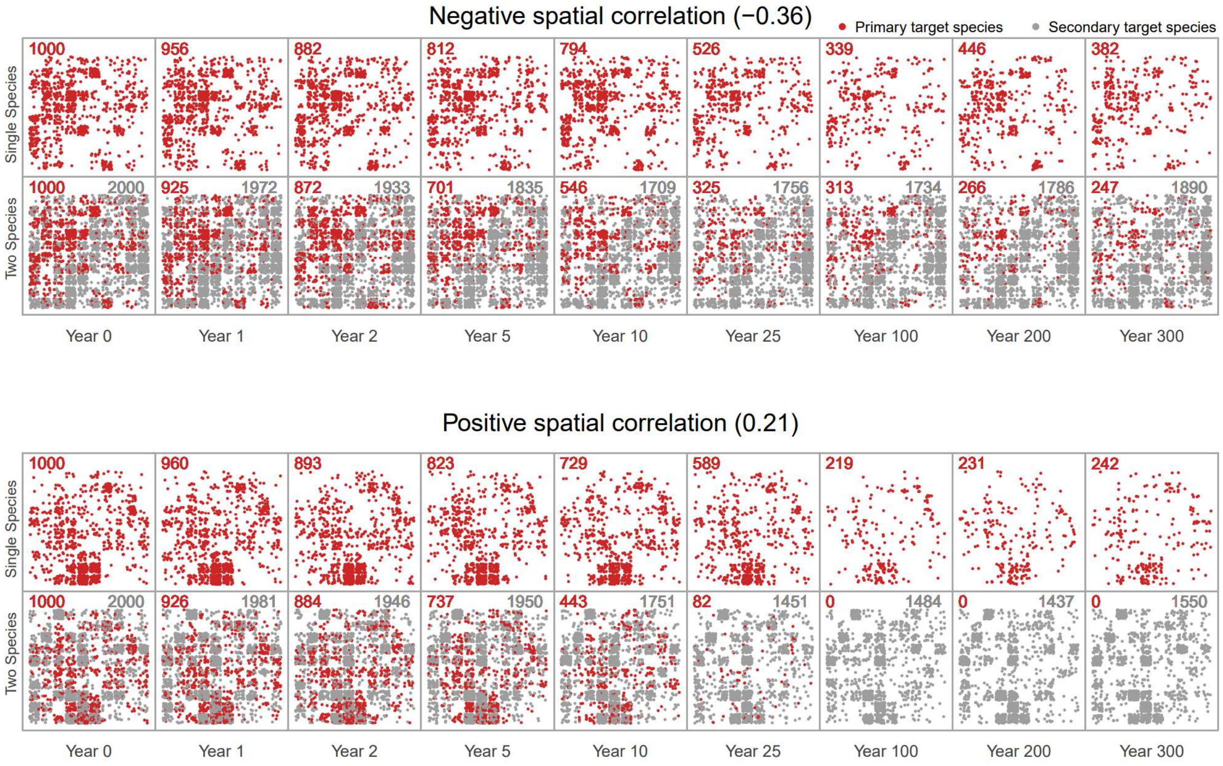


Figure 1.3 Examples of exploitation effects for single-species and two-species scenarios when the distribution of the two species is negatively correlated (first two rows) and positively correlated (last two rows). Abundance (numbers in each panel) and distribution of high-value rare species (red) and low-value common species (grey) are shown in different years. Exploiters enter the grid at the bottom left corner. In the first and third rows only the rare species is harvested, while in the second and fourth rows, a lower-value, common species is added with gross revenue per individual equal to 50% of the high value species.

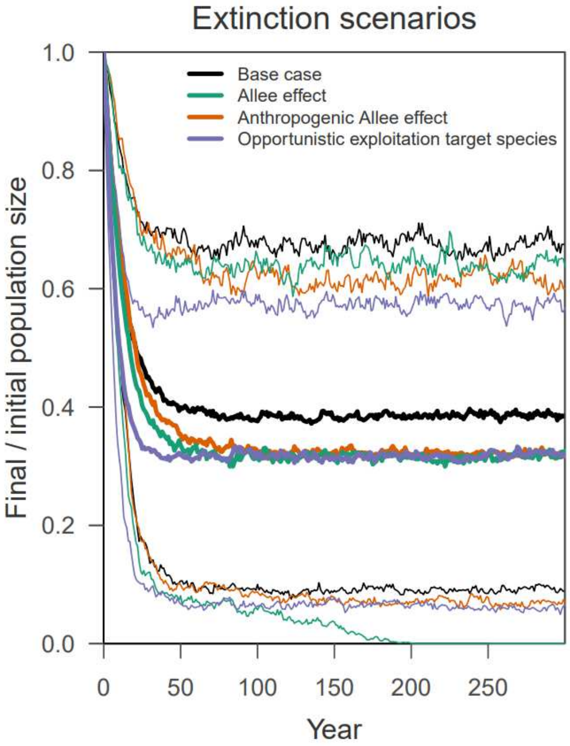


Figure 1.4 Median (bold lines) and 5th and 95th quantiles (thin lines) of final abundance divided by initial abundance for the rare species under four different exploitation scenarios: single species, Allee effect, anthropogenic Allee effect, and opportunistic exploitation. The results are summarized from 500 simulations.

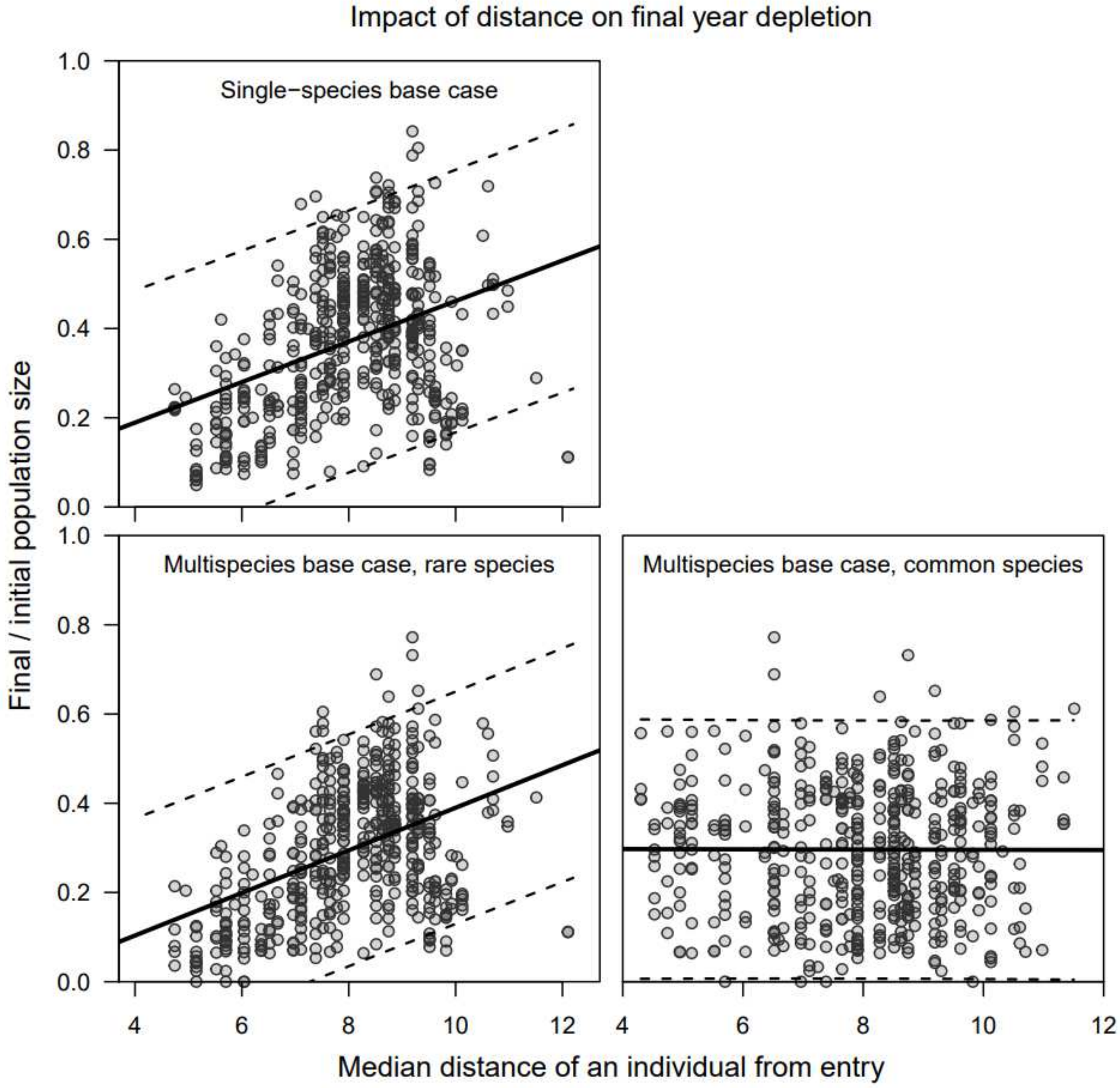


Figure 1.5 Relationship between the median distance of individuals of a given species in year 0 from the entry point of the grid and depletion of that species in year 300. Each point represents one simulation from each scenario. Top row shows results for the single species scenario, and bottom row shows the results for each species in the multispecies base case. The solid line shows a linear regression fit to the data, and the dashed lines show the 90% predicted interval.

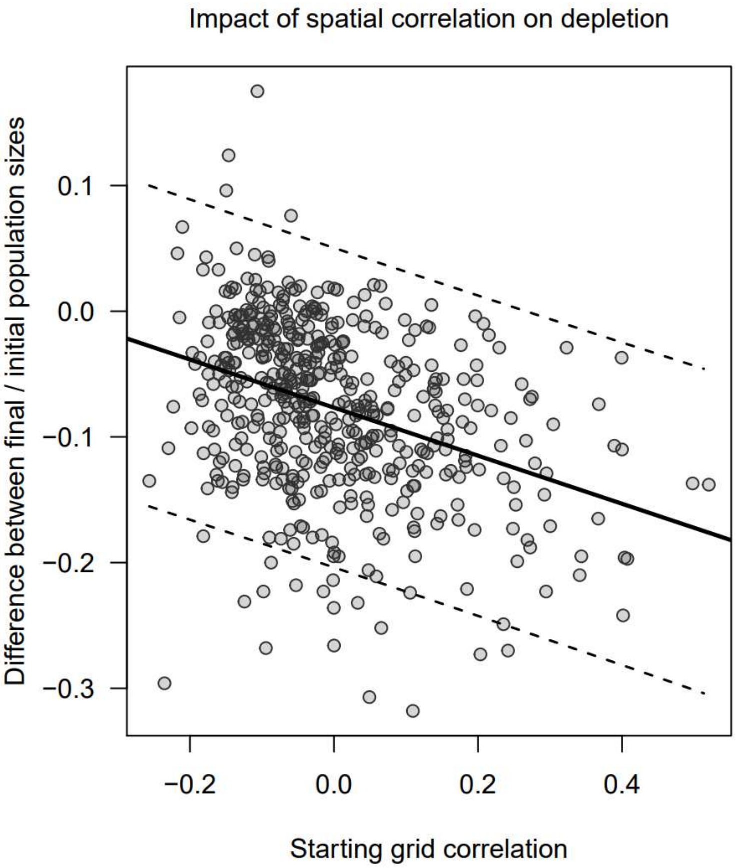


Figure 1.6 The opportunistic exploitation effect as a function of spatial correlation in individuals of rare and common species in year 0. For each simulation, the effect on the rare species is measured as final year depletion in the two-species model, minus final year depletion in the single-species base model. For all negative values the rare species was more depleted in the two-species model. The solid line shows a linear regression fit to the data, and the dashed lines show the 90% predicted interval.

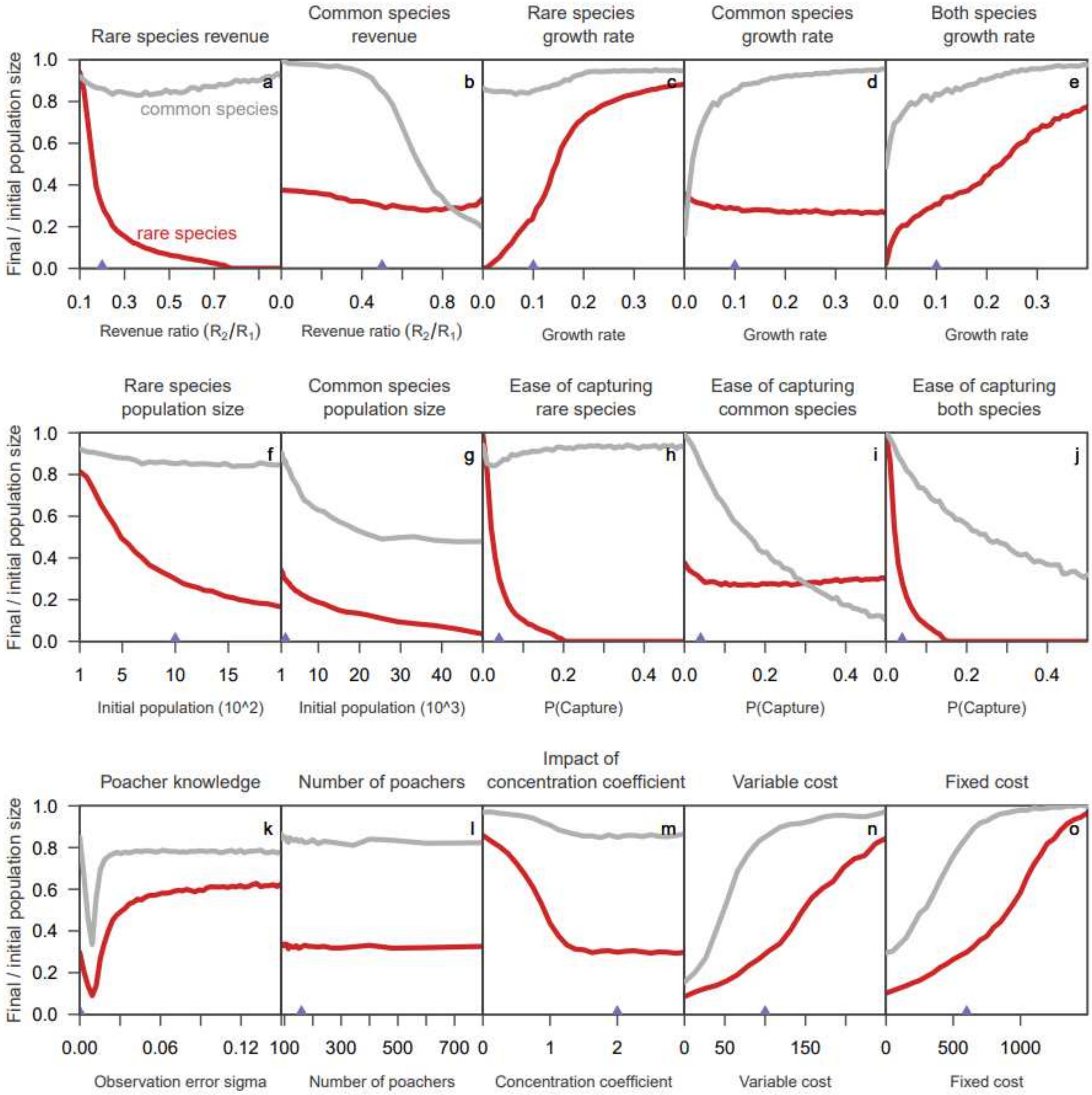


Figure 1.7 Panels indicate the median final-year depletion of the rare species (red) and the common species (grey) across 500 simulations for each sensitivity in section 2.7.2. Purple triangles on the x-axis show the value of each parameter in the base-case opportunistic exploitation scenario.

Chapter 2 Predictors of changes in biomass based on a new marine survey database

2.1 Introduction

Capture fisheries are culturally, socially, and economically important, and global landings have increased substantially over time. In the second half of the 20th century, marine catches increased as fishers explored new fishing grounds and technology improved, and then leveled off or declined after the mid-1990s (Food and Agriculture Organization, 2020; Pauly and Zeller, 2016; Swartz et al., 2010). Currently, global capture fisheries employ 39.0 million people, provide 96.4 million tons of fish, and contribute US$164 billion to global trade (FAO, 2020). Many studies seek to identify the status of global fisheries (i.e. Costello et al., 2012; Hilborn et al., 2020; Worm et al., 2009) based on fisheries stock assessments. While there are conflicting opinion about their overall status (Froese et al., 2012), especially when based on catch-only data, it is well recognized that sustainable management of many wild-caught fisheries has led to better outcomes in many regions of the world in recent years (Costello et al., 2016; Hilborn et al., 2020; Melnychuk et al., 2021; Worm et al., 2009).

Fisheries management systems encompass a suite of policies and regulations to meet conservation, economic, and cultural objectives (e.g. Beddington et al., 2007; McClanahan et al., 2015; McGoodwin, 2001; Rudd, 2004). A variety of solutions have been employed to achieve these objectives including marine protected areas and the enforcement of catch limits set by fisheries stock assessments (Anderson et al., 2019). Management strategies are not ‘one size fits all,’ and vary widely between and among countries and fish stocks. For fish stocks which are scientifically assessed, on average, abundance is increasing and is at proposed target levels (Hilborn et al., 2020; Hilborn and Ovando, 2014). Furthermore, intensively managed regions with assessed stocks have lower harvest rates and higher abundance than regions with less-developed fisheries management (Hilborn et al., 2020). However, it is believed that fish stocks in regions without fisheries stock assessments are in poor condition (Hilborn et al., 2020), and that countries with ineffective and inefficient management systems have the greatest potential to improve the status of their fisheries stocks (Melnychuk et al., 2017).

The most reliable assessments of marine fish status come from fisheries stock assessments, which are based on both fishery independent data (such as surveys) and fishery dependent data (such as catches). Fishery dependent data are captured in the process of fishing, making these data less expensive and easier to obtain. However, fishery dependent indices can be misrepresentative since changes in catch rates can be a result of other factors such as changes in where fishing occurs, when fishing occurs, or the composition of the fishing fleet (Cooke and Beddington, 1984; Hilborn and Walters, 1992; Maunder and Punt, 2004). Even after standardization there is no guarantee catch-per-unit-effort data will provide a reliable index (Dennis et al., 2015; Harley et al., 2001; Maunder and Punt, 2004). In contrast, fishery independent data are obtained from surveys not associated with fishing and are usually collected by management agencies (Dennis et al., 2015). Fishery independent data are collected through scientific sampling or within an experimental design that generally takes into account confounding factors that complicate fishery dependent data (Rago, 2005). Studies show that using both fishery independent and fishery dependent data reduces the variance of the estimable parameters, substantially improving the precision of model predictions (e.g. Bentley and Stokes, 2009; Dennis et al., 2015).

Collections of stock assessments and catch data exist and are used widely to draw conclusions about fisheries status. The Sea Around Us database is a collection of catch data for fisheries across the globe (Pauly et al., 2020) that has been used to estimate global catches of marine recreational fisheries (Freire et al., 2020), compare input versus output controls for fisheries management (Bellido et al., 2020), and look at fishery biomass trends across large regions and zones (Palomares et al., 2020). In contrast, the RAM Legacy Database is a collection of stock assessments for commercially exploited marine populations across the globe and contains the best available fisheries status for assessed species (Ricard et al., 2012). This database has been used to analyze the footprint of global fisheries (Amoroso et al., 2018), look at changes in fisheries productivity and food security (Szuwalski, 2016), and understand the potential to increase fish yield (Hilborn and Costello, 2018), amongst many other things.

While fisheries stock assessments are important, it is not feasible to conduct stock assessments on all ~15,500 species of marine fish (Mora et al., 2008). In the United States, less than half of regionally-landed species have been assessed (Neubauer et al., 2018). Species which have high landed tonnage, high ex-vessel price, are larger-bodied, or are vulnerable to fisheries are more likely to be assessed (Neubauer et al., 2018). This means we have little information about fish species which are not commercially valuable, are small in size, or are species of less-concern for extinction. While we cannot do assessments for all species, we can use fishery independent survey data to draw conclusions about these unassessed species when possible. The available survey data can be used for gathering information to make more informed decisions on low-priority species for assessment in data rich regions, or target species in data poor regions. In this way, we could greatly increase the number of stocks that have some trend information compared to the number in the RAM legacy database. Survey data thus provide a middle-ground in the debate between catch only methods and stock assessments (Hilborn and Branch, 2013; Pauly, 2013).

Previously, data from fishery independent surveys were used to look at global fisheries status (Worm et al., 2009) and the trophic fingerprint of marine fisheries (Branch et al., 2010), in addition to other papers (e.g. Bell et al., 2014). These studies involved compiling 29 research surveys, each spanning at least 15 years and including 10 survey events. However, these surveys included only trawl surveys, and are not available in an open database for scientists to explore for further analysis.

To fill this need, we compiled a revised, expanded, and updated survey database consisting of estimated abundance or biomass by year for each species, which includes additional surveys beyond trawl surveys (e.g., acoustic and longline surveys). To promote data sharing, we developed a data-sharing agreement allowing for broader use of the database while respecting the rights and wishes of data providers. In a survey of principal investigators by Mills et al. (2015), 91% of respondents supported data-sharing when there were clear rules for how the data would be shared. A clear data-sharing agreement alieves apprehension amongst researchers about sharing data, allows for data providers to choose their involvement level with future projects for which the data could be used, and increases the availability of data for future research.

We used the new database to test our prediction that fish species with declining trends in biomass will tend to be heavily fished, have high trophic level, large maximum length, and be caught in nearshore habitats. In addition, we predict that there will be strong regional differences in trends. Previous studies have found a high threat of overexploitation in high trophic level, large bodied, slow growing, and low fecundity species (Cardillo and Bromham, 2001; Larson and Olden, 2010; Owens and Bennett, 2000; Purvis et al., 2000; Reynolds, 2003). Similarly, the 'fishing down the food web' hypothesis predicts that long-lived, high trophic level, bottom dwelling fish are declining, and there is a rise in low trophic level pelagic fish and invertebrates (Christensen et al., 2014; Pauly et al., 1998). Identifying the most important factors will allow predictions of which taxa with unknown abundance trends require more monitoring and protection.

2.2 Methods

2.2.1 Fishery-independent survey database

Time series of indices of abundance or biomass from fishery independent surveys form the core of the database, in addition to measures of uncertainty when these are provided. Indices of abundance are typically measured as the number or weight of a species caught per standard unit of fishing effort, and these can be model-based or design-based indices (Chen et al., 2004). Metadata for each survey consist of the location, duration, and gear of the survey, the management body that conducted the survey, and any additional notes from survey providers.

For any data that is not published or publicly available online, data providers completed a data sharing agreement (see Supplementary 1). A formal data-sharing agreement addresses some of the concerns which ecologists have about open- access data including concerns about plagiary, who uses the data, recognition, and datasets being used for incorrect purposes (Costello, 2009). Our agreement respects the wishes of data-providers increases the amount of data which can be included in our database and allows providers to be involved in the future-use of their data should they wish to be involved. This agreement enables data providers to indicate the appropriate level of data sharing for their dataset: a) Openly available with no further permissions required, b) openly available but data providers must be contacted at least 30 days before papers using the data are submitted, c) available but permission to use the data must be requested, d) data only supplied upon request, or e) not available for outside use.

We collected taxonomic and biological information about each species included in the database from FishBase and SeaLifeBase (Froese and Pauly, 2010; Froese and Pauly, 2021; Palomares and Pauly, 2020). When available, taxonomic categories, maximum length, trophic level, water type, habitat, and fisheries categorization were recorded. To facilitate the use of this database with other databases, each species was assigned a FishBase code and Aquatic Sciences and Fisheries Information System code where applicable (Garibaldi and Busilacchi, 2002).

The database is hosted within the open source Open Science Framework (Foster and Deardorff, 2017). The Open Science Framework enables us to make all openly available surveys easily accessible for other users (levels a and b above), while keeping private survey data that require permission to be granted from survey providers. As new data are obtained, the database can be easily updated (Thurner and Branch, 2021).

2.2.2 Data analysis

To assess the impact of different factors on trends in abundance, we used generalized least squares models to analyze a subset of the data from the database. The underlying data were the indices of abundance from the surveys, except that we only included data for taxa that accounted for 99% of the total biomass or abundance survey (of the taxa identified to the species level) caught in each survey. In this way, we removed taxa that were not well represented by the data. The measures of uncertainty for these indices of abundance that were provided for a subset of surveys were not used.

Since units varied by survey, we converted the survey data ($B_{i,t}$) for each stock and year into a log-transformed standardized index (B^{scaled}). For a given stock *i* in year *t* the index was scaled as follows:

$$(2.1) \qquad B^{scaled}{}_{i,t} = \frac{\ln\left(B_{i,t}\right) - \overline{\ln\left(B_i\right)}}{\sigma_{\ln\left(B_i\right)}}$$

This scaled index was used to explore which factors best predict the trend in indices over time.

Index data for most taxa were auto-correlated in time. Since it is common for the residuals of time series variables to have a time series structure, and this violates the usual assumption of independent errors, we extended the model to include a residual temporal autocorrelation structure by stock into all of our models. We fit order 1 autoregressive (AR-1) generalized least-squares (GLS) regressions to examine trends in log-transformed standardized abundance/biomass indices, and explore which predictors influence the trend in species over time. While the dataset has a nested structure, the model was not improved by added random effects for species or survey (as determined by the global model with random effects having a higher AIC than the global model without random effects) and was not considered further for analysis.

We used Akaike's Information Criterion (AIC) to rank our models and conduct multi-model inference (Akaike, 1973a, b, 1998; Bozdogan, 1987). AIC evaluates model fits and penalizes model complexity in order to avoid model overfitting, and this was the basis for enforcing parsimony given our large dataset. All models included an effect of (centered) year. Explanatory variables included trophic level (trophiclevel), maximum length (maxL in m), habitat (bathydemersal, bathydemersal & benthopelagic, benthopelagic, bathypelagic, demersal, pelagic-neritic, and pelagic-oceanic), fishery status (unfished or unknown, subsistence fishery, minor commercial, commercial, and highly commercial), and the six World Bank Regions (World Bank, 2007). Data were only included for species where these explanatory variables were all known. Since we were interested in the effect of explanatory variables on trend, we only investigated models that contained interactions between year and these covariates. Our global model was:

$$\begin{aligned}\text{(2.2)}\quad Index_i = {} & \beta_0 + \beta_1[year_i] + \beta_2[maxL_i] + \beta_3[year_i][maxL_i] + \\ & \beta_4[trophiclevel_i] + \beta_5[year_i][trophiclevel_i] + \\ & \beta_{6,region}[region_i] + \beta_{7,region}[year_i][region_i] + \\ & \beta_{8,habitat}[habiat_i] + \beta_{9,habitat}[year_i][habitat_i] + \\ & \beta_{10,fishery}[fishery_i] + \beta_{11,fishery}[year_i][fishery_i] + \varepsilon_i\end{aligned}$$

$$\begin{aligned}\text{(2.3)}\quad & \varepsilon_{i,t} = \rho\varepsilon_{i,t-1} + w_t \\ & w_t \sim N(0,\sigma^2)\end{aligned}$$

We used these models to assess the relative importance of different variables for predicting trends in survey indices over time. We combined the five possible year and predictor interactions to form 32 GLS AR(1) regression models, including a null model (Year only, no interactions). Equation 2.3 is indicative of an AR(1) structure in the errors. All models were fitted through maximum likelihood using the ‘nlme’ package in R (Pinheiro et al., 2017; R Core Team, 2021). Models were ranked using AIC, and the residuals of the global model were checked for normality.

For the top models, Nagelkerke’s pseudo R-squared values were calculated using the ‘rcompanion’ package (Nagelkerke, 1991; Salvatore, 2021). These cannot be compared to R-squared for ordinary least squares models and cannot be used to interpret the proportion of the variability in the dependent variable that is explained by the model (Salvatore, 2021). Pseudo R-squared values are relative, and show how well the model explains the data compared to a null model which only includes year as a covariate.

Estimated marginal mean plots were generated for all interactions in the top model using the emmeans package in R (Lenth et al., 2021). Estimated marginal means tell you the mean response for each interaction, adjusted for any other variables in the model. Model averaged estimated marginal mean plots were generated for the interactions which occurred in more than one of the top models with ΔAIC less than two and with no more parameters than the best model. Models were AIC weighted and confidence intervals were calculated using the delta-method (Burnham and Anderson, 2002). Model averaging acknowledges that there might be multiple models which could be used to describe our data and incorporate model uncertainty.

2.3 Results

2.3.1 Fishery-independent survey database

The marine survey database includes data from 51 surveys (version 1.0, 2021, Table S1), encompassing trawl, longline, seine, setline, RV, and acoustic survey types. More surveys come from North America than any other country or region (Table 1). Most (49 of 51) surveys include trends for taxa identified to the species level (Figure 1), except for the Gulf of Thailand survey and Relative cephalopod abundance in the UK waters survey which only included taxa identified to the order and family level. The basic unit in the database is a time trend of index values for the combination of taxon and survey, which we refer to as a "stock" hereafter. Together, the database includes time series data for 1836 stocks of 358 species, 112 families, and 38 orders. The most common orders are Perciformes (44%, *n* = 156), Pleuronectiformes (9.8%, *n* = 35), Gadiformes (9.8%, *n* = 35), Rajiformes (7.0%, *n* = 25), and Decapoda (6.1%, *n* = 22). Most of the surveys focused on fish species, resulting in under-representation of marine invertebrates in the database, which likely occurs in marine surveys in general (Collier et al., 2016; Tardy, 2010).

2.3.2. Data analysis

Out of the stocks identified to species level, 695 were included in the top 99% of summed survey index values for each survey. These stocks cover 210 species from 80 families and 25 orders. Full data for all explanatory variables were available for 658 of these top stocks, which were used in the data analysis.

The most parsimonious model, which best explained changes in indices over time, included interactions between year and maximum length, fishery category, and habitat covariates. All coefficient estimates are shown in Table 2. Seven coefficients had 95% confidence intervals that did not include 0. The main effect of year for the reference groups (not currently fished or unavailable and bathydemersal) was 0.028 (95% CI: 0.0209–0.0343), i.e. on average displaying an increasing trend for these groups. Other significant coefficients are the interactions between year and the following variables or categories: maximum length, minor commercial fishery status, highly commercial fishery status, bathydemersal and bethopelagic habitat, bathypelagic habitat, and demersal habitat. All significant interaction coefficients were estimated to be negative.

Three other models all had AIC values within two units of the best model and with the same number of parameters or less, resulting in four plausible models (Table 3) (Arnold, 2010). All four included *Fishery* and *Habitat* as predictors for trends in index values by year. For all top models, the confidence intervals did not include zero for the *Year* coefficient, for fishery interactions (minor commercial and highly commercial), and for habitat interactions (bathydemersal and benthopelagic, bathypelagic, and demersal) (Table 4). No top models included both maximum length and trophic level interactions, and models with maximum length as a predictor performed better than the corresponding models with trophic level.

Maximum length categories had larger differences in slope amongst them than trophic level categories, and thus on average the interaction between year and maximum length was greater than the interaction between year and trophic level. Larger bodied species had steeper declines over time than smaller bodied species (Figure 2). The habitat of each species was also influential, where deep-water species have the steepest declines over time, and pelagic species are increasing (Figure 2, Figure 3). Lastly, fishing had a major effect on declines, in the expected order from greater to smallest declines of highly commercial, commercial, minor commercial, subsistence, and not fished or unavailable (Figure 2, Figure 3). In models which included trophic level, higher trophic level species have greater declines over time than lower trophic level species.

2.4 Discussion

Our marine survey database provides time series abundance/biomass indices from available fishery independent surveys, and species-level characteristics for the taxa surveyed. While the database has a broad time span (1963 to 2019) many fisheries began long before this, with the start of modern industrial fisheries in some areas beginning around 1880 (Swartz et al., 2010), and global-level collection of catch data by FAO beginning in 1950. Historical data provide context for present observations and allow for studies of long-term changes in population size and species composition. Our focus on the most recent years can be misleading, as we are looking at data from an already degraded ecosystem and thus our point of reference for which we are measuring decline is inaccurate due to shifting baselines (Pauly, 1995). This lack of information about historical population sizes is a widespread problem across fisheries assessments.

The majority of surveys included in our database are from North America. This is reflective of accessible stock assessments being from more economically developed countries which devote more resources to management (Melnychuk et al., 2020; Ricard et al., 2012). Our results are therefore influenced by North American stock status, and may change as the database expands to include more stocks from other regions around the world that may have less intensive management, higher levels of unregulated fishing, and more remote and pristine locations. The database has been designed to be easily extensible to add indices from more surveys in the future.

While stock assessments provide the highest quality and most detailed information about different populations of fish over time, these calculations are costly, time-intensive, and require large amounts of data. Because of this, they are only conducted for a small number of species (Hilborn et al., 2020; Neubauer et al., 2018; Ricard et al., 2012). Fishery-independent survey data fills the gap between these intensively managed highly valuable and very abundant species (most of which are assessed), and the myriad stocks with low abundance and no commercial value that are not assessed or impacted by fishing (e.g., hadalpelagic fish, tiny tide-pool fish species). In between these two extremes are many fish species with low or little commercial value that are consistently captured by gear used for surveys where trends in survey abundance indices could be used as a rapid metric of status over time. The number of stocks with some trend information could be greatly increased compared to the number in the RAM legacy database. This information is important for drawing conclusions about global fisheries status, monitoring the health of community compositions, identifying species which could be utilized further, understanding trends in population size for species which may not be commercially valuable but perform important ecosystem services, determining changes in biodiversity, or extrapolating information about species in areas where we have less information. Additionally, these trends, rather than stock assessment derived estimates, have potential for use for adaptive management in data-limited locations (e.g. McDonald et al., 2017).

By conducting our analyses on surveys, which include data for many more stocks, we can draw conclusions that extend across both assessed and unassessed species. In our analyses here, maximum length, fishery status, and habitat were the most important predictors of trend in taxa over time.

Our results are consistent with other studies which have found that large fish have experienced larger declines (Baum et al., 2003; Christensen et al., 2014; Ward and Myers, 2005), and we additionally found that maximum length is a better predictor of declines in abundance than trophic level. Some studies have shown that high trophic level species have experienced greater declines (Christensen et al., 2003), while other studies have found more ambiguous effects of trophic level on catch, survey, and stock assessment trends (Branch et al. 2010), and have found that maximum length, price, depth, and abundance are better predictors of fishery development than trophic level (Sethi et al., 2010). It should be noted that while our best model preferred maximum length over trophic level as a predictor of declines, our models that included trophic level did show that higher trophic level stocks experienced greater declines than lower trophic level stocks.

All of our top models include habitat as an important predictor of trend in abundance. This is consistent with other studies which find that deep-water fish have less resilience than shallow-water fish, where pelagic fish have a higher percentage of species with a high resilience rating than demersal, bathypelagic, and bathydemersal species (Norse et al., 2012). However, due to their shorter lifespan, small pelagic fishes are twice as prone to collapse as larger species (Pinsky et al., 2011) and exhibit boom-bust cycles naturally (McClatchie et al., 2017). Many deep sea fish species are comparable to old growth trees (Barnett et al., 2017), where their large biomass and low productivity makes them more difficult to exploit sustainably (Morato et al., 2006; Norse et al., 2012; Winemiller and Rose, 1992). Additionally, deep sea fish are typically caught with low-selectivity methods (i.e. trawl), placing non-target deep sea fishes at greater risk (Roda et al., 2019).

We limited our exploratory analysis five main covariates: maximum length, trophic level, habitat, region, and fishery status. There are many possible covariates which could be influential predictors of abundance trends such as Human Development Index, body mass relationships (i.e. Jennings and Blanchard, 2004), stock size (Hilborn and Ovando, 2014), regional fisheries management strategy. Additionally, more complex model structures could be explored. There is also room to incorporate fishery-independent assessment methods that can capture signals in biomass for stocks (Mesnil et al., 2009).

While fishery independent indices of abundance have many assets, they also have limitations. Analysis of these trends in abundance only provide relative values and cannot provide estimates of absolute abundance (Mesnil et al., 2009) except when included in a full stock assessment. General studies such as ours provide a useful starting place, but to draw more specific conclusions it is important to make sure that the survey is representative of the species samples across the duration of the time series and all data sources are considered.

Since it is both costly to obtain fishery independent surveys and to conduct fisheries stock assessments, it is advantageous to make the most of the information we have. By making these annual abundance indices openly available and consolidating them in one location, we increase their availability for future studies. Future versions of this marine survey database will include updated data for already included surveys and additional surveys. Our ultimate goal for this database is to provide indices of abundance for researchers to use for their own applied and fundamental research to advance fisheries science and conservation research.

Tables

Table 2.1 Surveys which are included in the current version of the database.

Survey code	Survey name	Start year	End year	World Bank Region	Gear Type	Organization	Main contact
AFSC-BT-A	Aleutian Islands	1980	2016	North America	Trawl	NOAA AFSC	Stan Kotwicki
AFSC-BT-EBS-SHELF	Eastern Bering Sea Shelf	1987	2017	North America	Trawl	NOAA AFSC	Stan Kotwicki
AFSC-BT-GOA	Gulf of Alaska Trawl	1984	2017	North America	Trawl	NOAA AFSC	Stan Kotwicki
AFS-GLS-A	NOAA AFSC Groundfish Longline Survey Aleutians	1990	2017	North America	Longline	NOAA AFSC	Cara Rodgveller
AFS-GLS-BS	NOAA AFSC Groundfish Longline Survey Bering Sea	1990	2017	North America	Longline	NOAA AFSC	Cara Rodgveller
AFS-GLS-CGOA	NOAA AFSC Groundfish Longline Survey Central Gulf of Alaska	1990	2017	North America	Longline	NOAA AFSC	Cara Rodgveller
AFS-GLS-EYS	NOAA AFSC Groundfish Longline Survey East Yakutat/Southeast	1990	2017	North America	Longline	NOAA AFSC	Cara Rodgveller
AFS-GLS-WGOA	NOAA AFSC Groundfish Longline Survey Western Gulf of Alaska	1990	2017	North America	Longline	NOAA AFSC	Cara Rodgveller
AFS-GLS-WY	NOAA AFSC Groundfish	1990	2017	North America	Longline	NOAA AFSC	Cara Rodgveller

	Longline Survey West Yakutat						
APS-IMP	Australian Prawn Survey	2002	2019	East Asia and Pacific	Trawl	CSIRO	Eva Plaganyi-Lloyd, Kenyon et al. (2018)
BGAS	Blue Grenadier Acoustic Survey	1993	2010	East Asia and Pacific	Acoustic	CSIRO	Kloser et al. (2016)
FIS-GABTS	Great Australian Bight	2005	2015	East Asia and Pacific	Trawl	Fishwell	Matt Koopman, Ian Knuckley
FWC-FIMP-AB	Florida Estuarine FIMS Apalachicola Bay	1998	2017	North America	Seines and Trawls	FWC	Tim MacDonald, Deb Leffler
FWC-FIMP-CH	Florida Estuarine FIMS Charlotte Harbor	1996	2017	North America	Seines and Trawls	FWC	Tim MacDonald, Deb Leffler
FWC-FIMP-CK	Florida Estuarine FIMS Cedar Key	1997	2017	North America	Seines and Trawls	FWC	Tim MacDonald, Deb Leffler
FWC-FIMP-IRL	Florida Estuarine FIMS Indian River Lagoon	1996	2017	North America	Seines and Trawls	FWC	Tim MacDonald, Deb Leffler
FWC-FIMP-NEF	Florida Estuarine FIMS Northeast Florida	2001	2017	North America	Seines and Trawls	FWC	Tim MacDonald, Deb Leffler
FWC-FIMP-SB	Florida Estuarine FIMS Sarasota Bay	2009	2017	North America	Seines and Trawls	FWC	Tim MacDonald, Deb Leffler
FWC-FIMP-SL	Florida Estuarine FIMS St Lucie (Southern Indian River Lagoon)	1997	2017	North America	Seines	FWC	Tim MacDonald, Deb Leffler
FWC-FIMP-TB	Florida Estuarine FIMS Tampa Bay	1996	2017	North America	Seines and Trawls	FWC	Tim MacDonald, Deb Leffler

GSL-RV	Gulf of St Lawrence RV Survey	1971	2017	North America	RV	DFO	Daniel Ricard
GT	Gulf of Thailand Published data	1961	1995	East Asia and Pacific	Trawl	Worldfish center, DOF Thailand	Pauly (1988); Stobutzki et al. (2006)
HBLL INS N	Hard Bottom Lonline Inside North Survey	2003	2014	North America	Longline	DFO, Pacific Biological Station	Sean Anderson
HBLL INS S	Hard Bottom Longline Inside South Survey	2005	2018	North America	Longline	DFO, Pacific Biological Station	Sean Anderson
HBLL OUT N	Hard Bottom Longline Ouside North Survey	2006	2017	North America	Longline	DFO, Pacific Biological Station	Sean Anderson
HBLL OUT S	Hard Bottom Longline Outside South Survey	2007	2016	North America	Longline	DFO, Pacific Biological Station	Sean Anderson
IPHCSS	Pacific Halibut Commission Fishery-Independent Setline Survey	1977	2018	North America	Setline	IPHC	IPHC SECRETARIAT (2020)
NEFSC-GB-F	NEFSC Bottom Trawl Survey Georges Bank Fall	1963	2019	North America	Trawl	NEFSC	Michael Fogarty and Sean Lucy
NEFSC-GB-S	NEFSC Bottom Trawl Survey Georges Bank Spring	1968	2019	North America	Trawl	NEFSC	Michael Fogarty and Sean Lucy
NEFSC-GOM-F	NEFSC Bottom Trawl Survey Gulf of Maine Fall	1963	2019	North America	Trawl	NEFSC	Michael Fogarty and Sean Lucy
NEFSC-GOM-S	NEFSC Bottom Trawl Survey Gulf of Maine Spring	1968	2019	North America	Trawl	NEFSC	Michael Fogarty and Sean Lucy

NEFSC-MAB-F	NEFSC Bottom Trawl Survey Mid Atlantic Bight Fall	1963	2019	North America	Trawl	NEFSC	Michael Fogarty and Sean Lucy
NEFSC-MAB-S	NEFSC Bottom Trawl Survey Mid Atlantic Bight Spring	1968	2019	North America	Trawl	NEFSC	Michael Fogarty and Sean Lucy
NEFSC-SS-F	NEFSC Bottom Trawl Survey Scotian Shelf Fall	1963	2019	North America	Trawl	NEFSC	Michael Fogarty and Sean Lucy
NEFSC-SS-S	NEFSC Bottom Trawl Survey Scotian Shelf Spring	1968	2019	North America	Trawl	NEFSC	Michael Fogarty and Sean Lucy
OR-AC-SH	Orange Roughy Acoustic St Helens	1990	2013	East Asia and Pacific	Acoustic (tow)	CSIRO	Kloser et al. (2015)
PELMED	Gulf of Lion Small Pelagics	1993	2017	Europe and Central Asia	Acoustic	IFREMER	Claire Saraux, Jean-Herve Bourdeix
PWSSC	PWSSC Adult Herring Acoustic Biomass	1993	2015	North America	Acoustic	PWSCC	Pete Rand, Dick Thorne
RCA	Relative cephalopod abundance in the UK waters	1998	2018	Europe and Central Asia	Trawl	CEFAS	Vladimir Laptikhovsky
SCBLG	Southern California Bight Longline Shark Survey	1994	2013	North America	Longline	NMFS and CDFG	Runcie et al. (2016)
SESSF-FIS	SESSF-FIS	2008	2016	East Asia and Pacific	Trawl	Fishwell	Matt Koopman, Ian Knuckley
SGA	South Georgia Antarctica	1970	1992	Antarctic	Trawl		Kock and Shimadzu (1994)

SGL-SC	S Gulf St Lawrence Snow Crab Trawl Survey	1988	2018	North America	Trawl	DFO, Gulf Fisheries Centre, Crustaceans Section	Tobie Surrette, Stephanie Boudreau
SYN HS	Hectate Strait Synoptic Bottom Trawl Survey	2005	2019	North America	Trawl	DFO, Pacific Biological Station	Sean Anderson
SYN QCS	Queen Charlotte Sound Synoptic Bottom Trawl Survey	2003	2017	North America	Trawl	DFO, Pacific Biological Station	Sean Anderson
SYN WCHG	West Cost Haida Gwaii Synoptic Bottom Trawl Survey	2006	2018	North America	Trawl	DFO, Pacific Biological Station	Sean Anderson
SYN WCVI	West Coast Vancouver Island Synoptic Bottom Trawl Survey	2004	2018	North America	Trawl	DFO, Pacific Biological Station	Sean Anderson
TAN1614	New Zealand Subantarctic trawl	1991	2018	East Asia and Pacific	Trawl	NIWA (on behalf of Fisheries New Zealand)	Richard O'Driscoll
TSCR	New Zealand Chatham Rise trawl	1982	2018	East Asia and Pacific	Trawl	NIWA (on behalf of Fisheries New Zealand)	Richard O'Driscoll
USWC-AC-H	US West Coast Late hake acoustic survey	1995	2017	North America	Acoustic	NOAA NOAA AFSC	Sandy Parker-Stetter
USWCGBT	NWFSC West Coast Groundfish Bottom Trawl Surveys	2003	2019	North America	Trawl	NOAA NWFSC	Chantel Wetzel

Table 2.2 The estimate and 95% confidence intervals for coefficients in the model of best fit. Significant coefficients are bolded ($p<0.05$, confidence interval does not overlap zero). The AR(1) coefficient phi estimate is also included.

	Estimate	95% Confidence Interval
Phi	0.422	(0.435, 0.447)
(Intercept)	-0.00864	(-0.0818,0.0645)
Year	**0.0276**	**(0.0209,0.0343)**
MaxL	0.00392	(-0.0309,0.0388)
FisherySubsistence fisheries	-0.0147	(-0.351,0.322)
FisheryMinor commercial	0.0118	(-0.0679,0.0915)
FisheryCommercial	0.00670	(-0.0532,0.0666)
FisheryHighly commercial	0.0186	(-0.0436,0.0808)
HabitatBathydemersal and benthopelagic	0.0351	(-0.266,0.336)
HabitatBathypelagic	-0.0523	(-0.262,0.157)
HabitatBenthopelagic	-0.0200	(-0.101,0.0608)
HabitatDemersal	-0.00875	(-0.0703,0.0528)
HabitatPelagic-neritic	-0.0158	(-0.141,0.109)
HabitatPelagic-oceanic	-0.0233	(-0.194,0.148)
HabitatReef-associated	-0.0210	(-0.167,0.125)
Year:MaxL	**-0.00285**	**(-0.0056,-0.00011)**
Year:FisherySubsistence fisheries	-0.0146	(-0.0403,0.0112)
Year:FisheryMinor commercial	**-0.0114**	**(-0.0182,-0.00459)**
Year:FisheryCommercial	-0.00218	(-0.00667,0.00232)
Year:FisheryHighly commercial	**-0.0203**	**(-0.0249,-0.0157)**
Year:HabitatBathydemersal and benthopelagic	**-0.0832**	**(-0.117,-0.0496)**
Year:HabitatBathypelagic	**-0.0476**	**(-0.0679,-0.0273)**
Year:HabitatBenthopelagic	-0.00736	(-0.0148,0.0001)
Year:HabitatDemersal	**-0.0206**	**(-0.0268,-0.0144)**
Year:HabitatPelagic-neritic	0.00147	(-0.00906,0.0120)
Year:HabitatPelagic-oceanic	-0.00464	(-0.0189,0.00959)
Year:HabitatReef-associated	-0.0112	(-0.0273,0.00487)

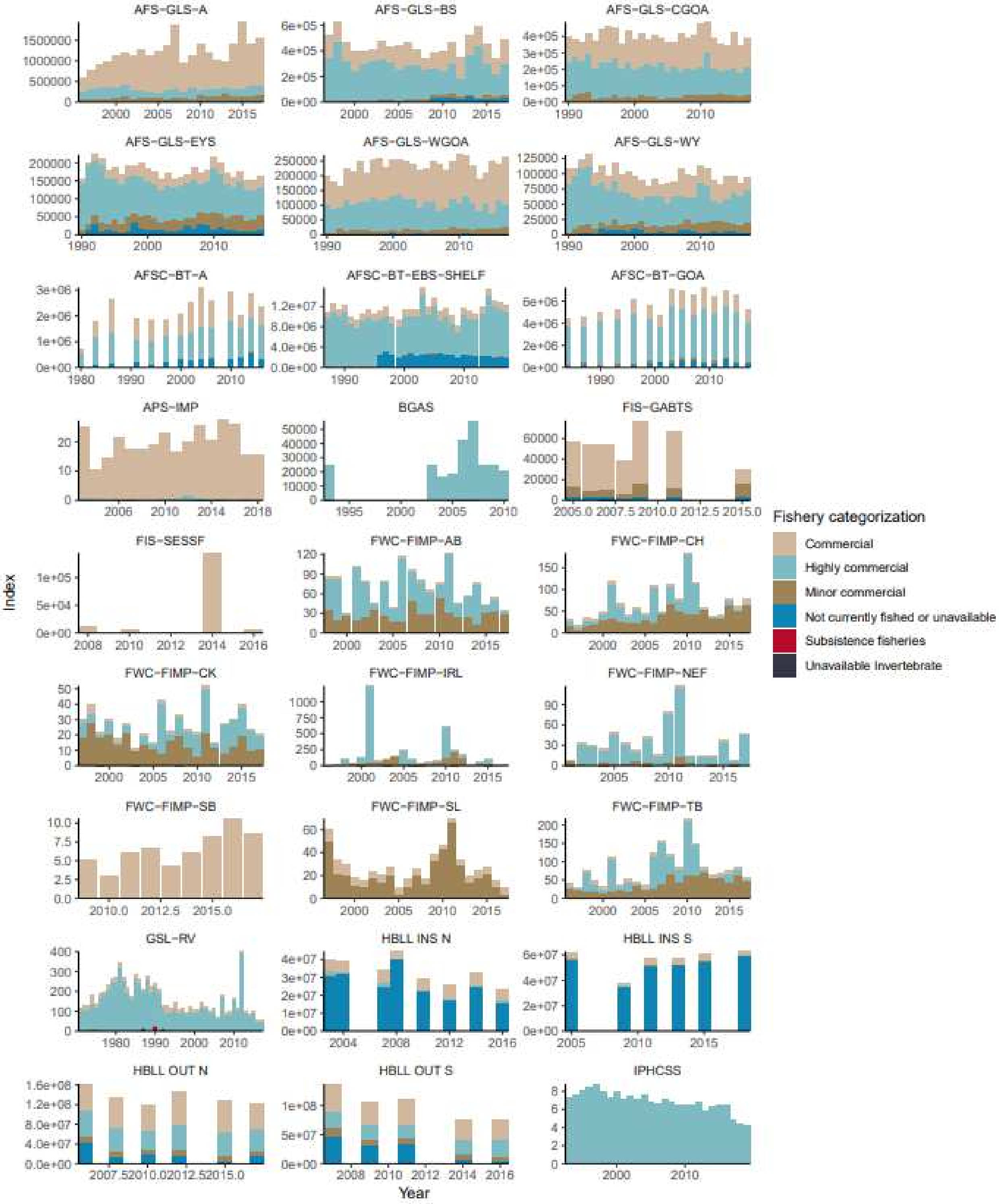
Table 2.3 Model selection to assess explanatory variables influencing trend over time. Models with ΔAICc < 2 and the same number of parameters or fewer than the best model are included and are considered to be competing.

Rank	**Covariates**	**ΔAIC**	**Nagelkerke's R^2**
1	MaxL + Fishery + Habitat	0	0.0141
2	Fishery + Habitat	0.230	0.0138
3	Fishery + Habitat + Region	0.461	0.0145
4	TrophicLevel + Fishery + Habitat	1.39	0.0140

Table 2.4 Significant (p <.05) coefficients for the best models (delta AIC < 2)

	Significant (p<.05) coefficients in the top models										
Model rank	**Year**	**Year:MaxL**	**Year:Trophic**	**Year:Fishery Minor Commercial**	**Year: Fishery Highly Commercial**	**Year:Habitat Bathydemersal and benthopelagic**	**Year: Habitat Bathypelagic**	**Year:Habitat Demersal**	**Year: Region East Asia and Pacific**	**Year: Region Europe and Central Asia**	**Year: Region North America**
1	+	+		+	+	+	+	+			
2	+			+	+	+	+	+			
3	+			+	+	+	+	+	+	+	+
4	+		+	+	+	+	+	+			

Figures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1000000
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4e+05
2e+05
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2000 2005 2010 2015
AFS-GLS-CGOA
4e+05
3e+05
2e+05
1e+05
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1990 2000 2010
AFS-GLS-EYS
200000
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AFS-GLS-WGOA
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AFS-GLS-WY
125000
100000
75000
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25000
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AFSC-BT-A
3e+06
2e+06
1e+06
0e+00
1980 1990 2000 2010
AFSC-BT-EBS-SHELF
1.2e+07
8.0e+06
4.0e+06
0.0e+00
1990 2000 2010
AFSC-BT-GOA
6e+06
4e+06
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20
10
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2006 2010 2014 2018
BGAS
50000
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10000
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1995 2000 2005 2010
FIS-GABTS
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2005.0 2007.5 2010.0 2012.5 2015.0
FIS-SESSF
1e+05
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2008 2010 2012 2014 2016
FWC-FIMP-AB
120
90
60
30
0
2000 2005 2010 2015
FWC-FIMP-CH
150
100
50
0
2000 2005 2010 2015
FWC-FIMP-CK
50
40
30
20
10
0
2000 2005 2010 2015
FWC-FIMP-IRL
1000
750
500
250
0
2000 2005 2010 2015
FWC-FIMP-NEF
90
60
30
0
2005 2010 2015
FWC-FIMP-SB
10.0
7.5
5.0
2.5
0.0
2010.0 2012.5 2015.0
FWC-FIMP-SL
60
40
20
0
2000 2005 2010 2015
FWC-FIMP-TB
200
150
100
50
0
2000 2005 2010 2015
GSL-RV
400
300
200
100
0
1980 1990 2000 2010
HBLL INS N
4e+07
3e+07
2e+07
1e+07
0e+00
2004 2008 2012 2016
HBLL INS S
6e+07
4e+07
2e+07
0e+00
2005 2010 2015
HBLL OUT N
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1.2e+08
8.0e+07
4.0e+07
0.0e+00
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HBLL OUT S
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0e+00
2008 2010 2012 2014 2016
IPHCSS
8
6
4
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Commercial
Highly commercial
Minor commercial
Not currently fished or unavailable
Subsistence fisheries
Unavailable Invertebrate

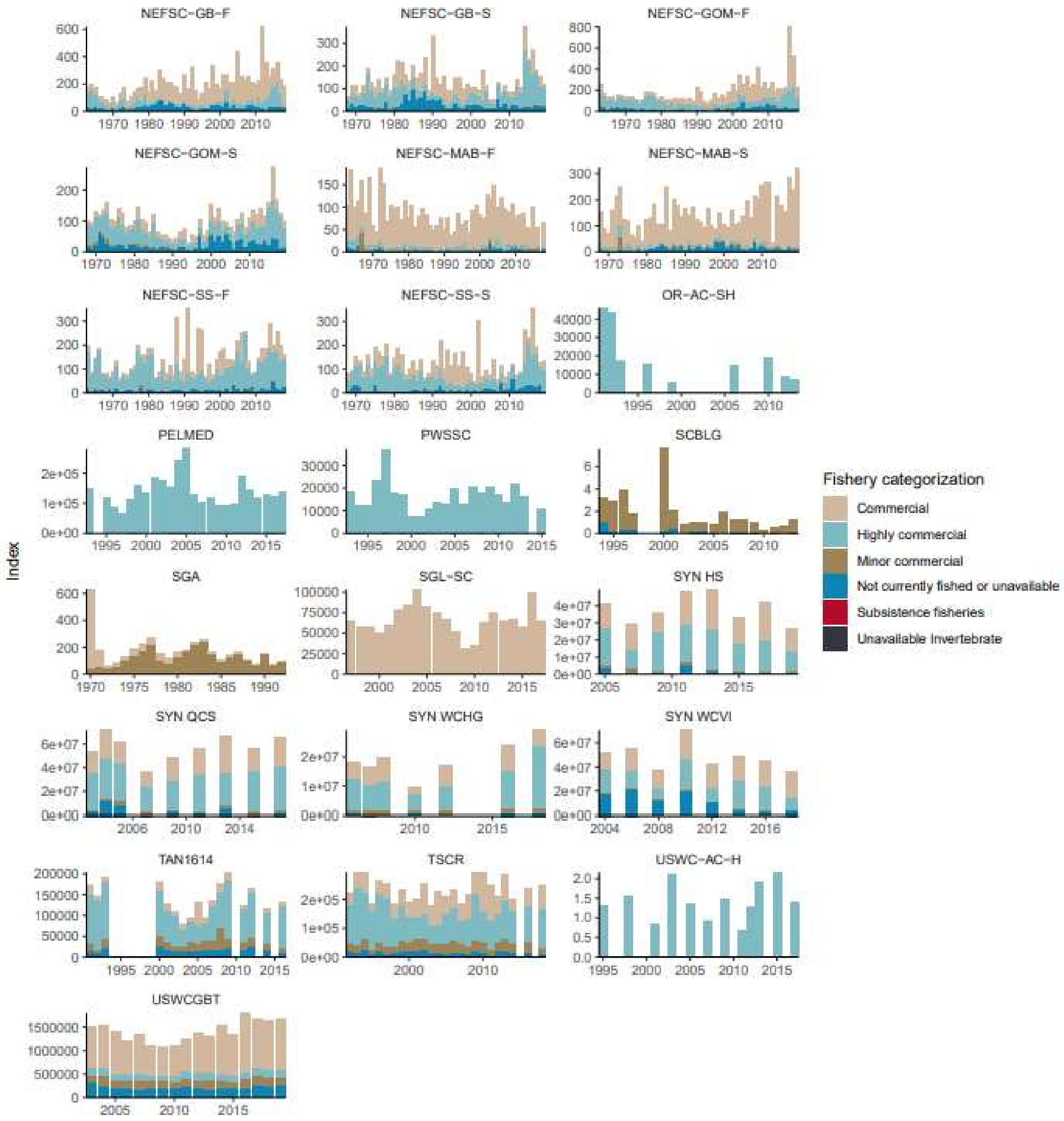

Figure 2.1 Total indices by survey. Bars are colored by human use fishery category.

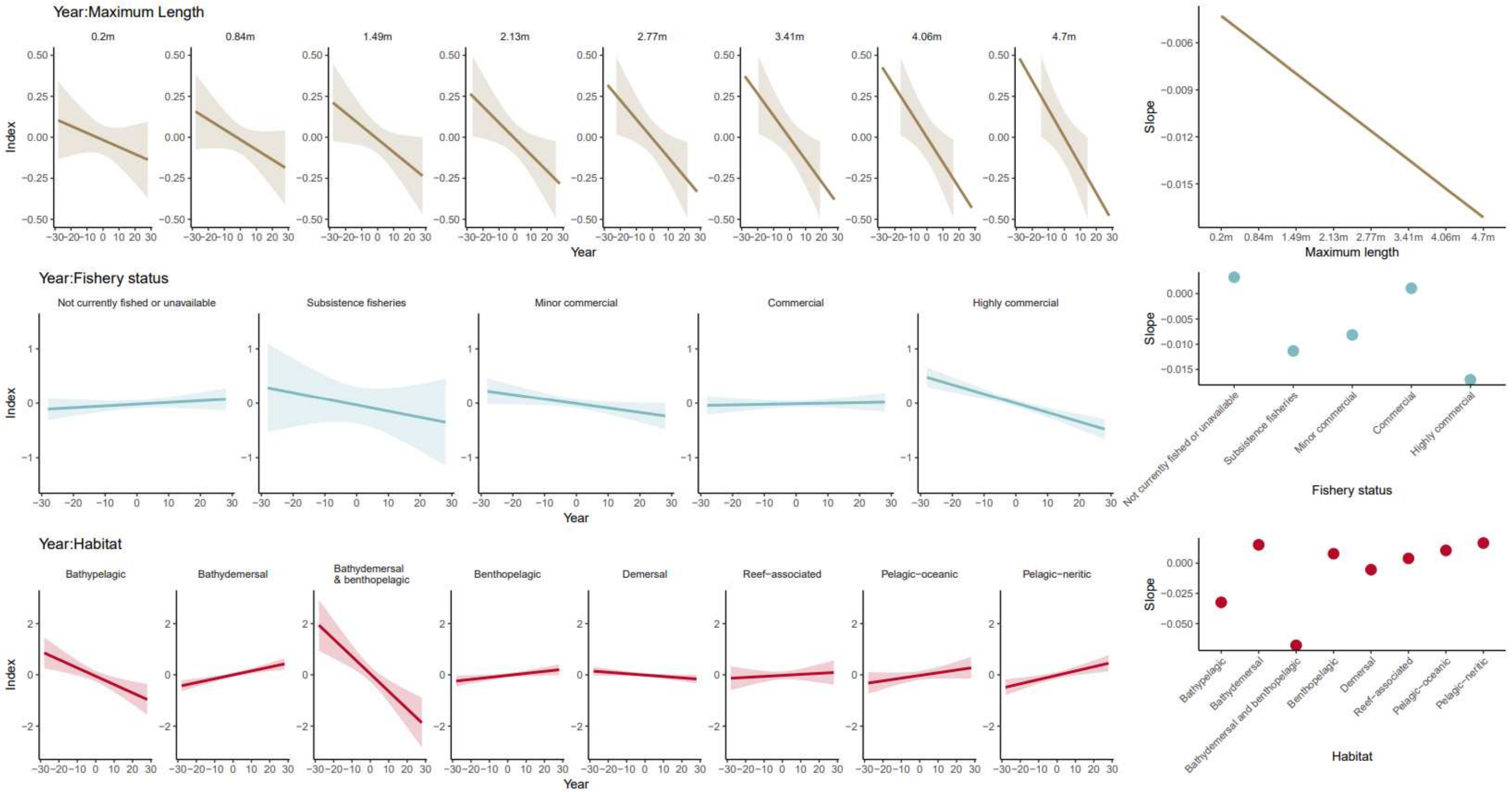

Figure 2.2 Marginal means plots for the best model using emmeans package in R.

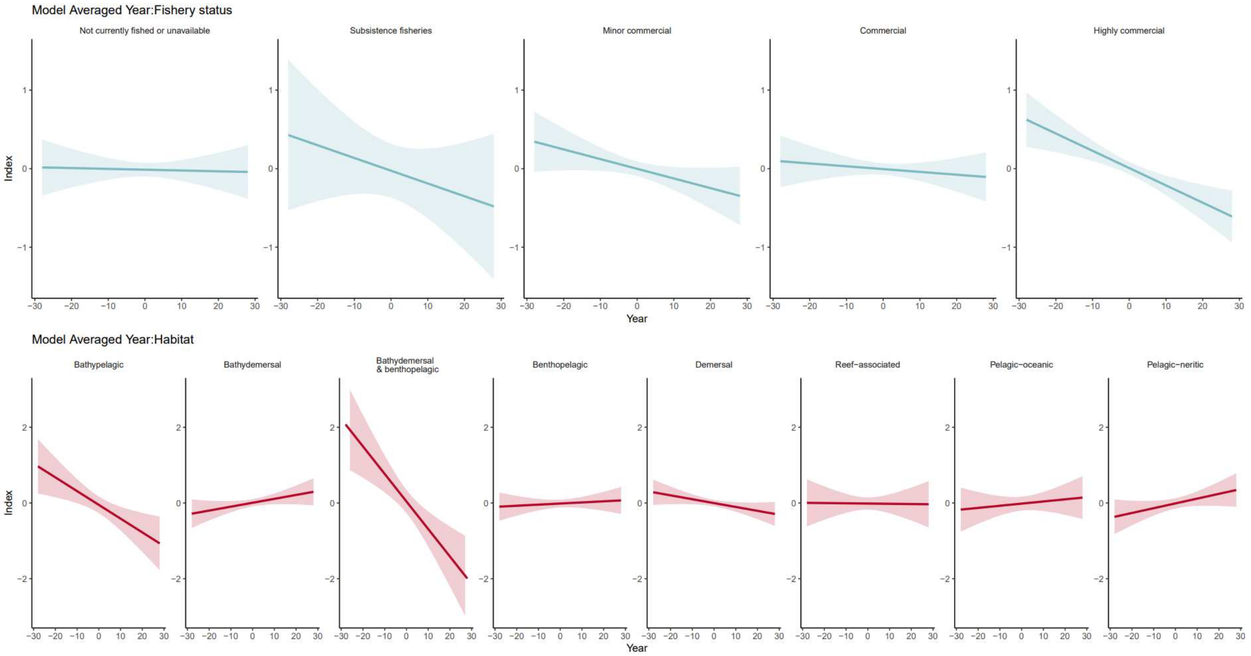

Figure 2.3 Model averaged marginal means plots for the top four models for interactions which are included in more than one model. Standard errors calculated using the delta method.

Conclusion

This thesis provides the first simulation study of extinction hypotheses and the first publicly available database of trends in abundance from fishery-independent marine surveys. Given the caveats identified earlier, through simulation studies I have found that the multispecies attributes of a scenario are as important, if not more important, than the attributes of individual species in predicting depletion. Many factors influence the intensity of opportunistic exploitation, but we conclude that the factors most critical to predicting depletion rate are profitability of capturing the common species and abundance of the common species. Using real world data, more specifically, I also identified maximum length, fishery category, and habitat covariates as the best predictors of trends in marine species stock size over time.

Combined, this thesis demonstrates that more accurate management models can be achieved by accounting for multispecies dynamics as well as using fishery-independent data to make inferences about a stock's status where fisheries stock assessments are unavailable. As wildlife and fish habitat management budgets remain insufficient for conserving all the world's biodiversity and triage investment continues to be needed, maximizing the usage of fishery independent survey data and investing in studying multispecies systems is a cost-effective way of maintaining biodiversity. Much work remains to best understand extinction hypotheses and maximize our understanding from fishery-independent survey data. We anticipate that our marine survey database will expand and be used by managers and scientists to draw additional conclusions that extend across both assessed and unassessed species.

Appendix

Marine survey database

Principal investigator: Trevor A. Branch, School of Aquatic and Fishery Sciences, University of Washington

Motivation and background

There is a substantial need for a database of marine abundances over time for management, conservation, and science. Previously, 29 research trawl surveys were compiled, each spanning at least 15 years and including 10 surveys, and was the basis of papers in Science and Nature looking at global fisheries status (Worm et al. 2009) and the trophic fingerprint of marine fisheries (Branch et al. 2010), in addition to other papers (e.g. Bell et al. 2014).

We propose a revised, expanded, and updated survey database that will extend the current surveys (from 2007 to 2017 or later), and that will be expanded to include other types of surveys (e.g. acoustic, pot, longline). The data collected will consist of estimated biomass by year for each species consistently captured in the survey. One key feature of the Marine Survey Database is a consistent data sharing agreement allowing for broader use of the database while respecting the rights and wishes of the data providers.

Funders

Database compilation is being led by Stephanie Thurner and Prof. Trevor Branch, who is funded by a Richard C. and Lois M. Worthington Endowed Professor in Fisheries Management; with additional funding from the Environmental Defense Fund.

Key initial outputs

1. A scientific paper describing the database and general trends in marine species, with coauthorship offered to all survey data contributors who assist in analysis and writing.

2. A website allowing download of all publicly available survey data, and links to ask for permission to access survey data with permission constraints.

3. Additional papers exploring questions of conservation, fisheries, and scientific interest.

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Collaborators and database users

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Kirsty Nash, University of Tasmania, Australia

Data sharing agreement

What kind of data sharing is appropriate for your research survey dataset? (Delete inapplicable options)

(a) Data are openly available for inclusion in survey database, no further permissions are required.

(b) Data are openly available for inclusion in survey database, but please contact data providers 30 days before submitting papers for analysis, to check that data have been correctly used.

(c) Data can be included in survey database, permission to use data must be requested separately for each use.

(d) Data may not be included in survey database, data may be supplied upon request.

(e) Data are not available for outside use.

Preferred name for survey dataset: __________________

Time span and frequency of survey (e.g. 1980-2017, annual): __________________

Type of survey (e.g. trawl, longline, acoustic): _______________

Reference that describes survey: __________________

Data provider(s) and institute: _________________

Email of data provider(s): ______________

Further comments or questions:

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